Modelling the Population and Catchability of the Southern Rock Lobster (*Jasus edwardsii*) in South Australia and Victoria Using Commercial Fisheries Catch Rate Data

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Contents

Abstract

The aim of this thesis is to contribute to the field of fisheries science and population modelling, having as subject matter the stocks of southern rock lobster (*Jasus edwardsii*) exploited by the commercial fisheries of the Southern Zone in South Australia (SZRLF) and the Western Zone in Victoria (WZRLF), Australia. The utility of a statistic known as "catch rate" is explored in regard to inferences drawn about the population and catchability of these southern rock lobster stocks. This thesis is in the form of "by publication" and contains three papers, two of which are published ("Paper One" and "Paper Three") while one is submitted and under review ("Paper Two").

Studies on some crab and lobster fisheries have shown that natural anomalies in water temperature can substantially impact catch rates. Paper One involved a multivariate regression study of abiotic environmental influences considered to act through catchability on daily catch rates of the SZRLF stock, finding that moon phase, bottom temperature, and wave action were retained in the final model but explained relatively little variance or trend in catch rate. However, the study determined several qualitative outcomes regarding the nature of the influences on catch rates that were not previously reported in the literature for southern rock lobster. Mean catch rate was estimated to be 10% greater just prior to full moon than at new moon, wave height lagged at three days had a positive influence, while bottom temperature and (contemporary) wave height had a negative influence. Similar findings were determined for WZRLF except for moon phase. Paper One compared these outcomes to those from studies on other lobster species, and proposed several hypotheses as explanations.

In Paper Two a GLM analysis was performed on WZRLF catch rates that included vessel identifier as a covariate, which represents a fishery influence on catchability, and found that it was substantially more influential on the trend in catch rate than was observed for the environmental influences reported in Paper One. Results suggest that the composition of the WZRLF vessel fleet changed over the years due to vessels exiting from the fishery being on average less efficient at fishing than the rest of the fleet, and hence driving an increase in net catchability and an overly optimistic assessment of the stock. Alternative forms of diagnostic indices were developed to study changes in vessel-driven catchability. The underlying mechanisms of vessel fleet dynamics were investigated and discussed in relation to other fisheries.

In Paper Three, novel multi-year depletion models were developed based on extending the Leslie-Davis model. These were applied to data of the SZRLF, producing estimates not only of catchability and yearly trend in relative abundance, but also absolute exploitable abundance and yearly recruitment numbers. Although making strong assumptions about catchability and recruitment for a period in each year, during the rest of the fishing year it avoids the need for such assumptions nor requires fishing effort data. Results compared reasonably with those of a more sophisticated but data hungry integrated stock assessment model.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Signed:

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Introduction

Background

The aim of this thesis is to contribute to the field of fisheries science and population modelling, having as subject matter the stocks of southern rock lobster (*Jasus edwardsii*) exploited by the commercial fisheries of the Southern Zone in South Australia (SZRLF) and the Western Zone in Victoria (WZRLF), Australia. Southern rock lobster is an important economic species for Australia, valued at around $112.8 million for the SZRLF in 2015/16 (Econsearch, 2017). The central theme is the use of a statistic known as "catch rate" (also known as catch-per-unit-effort or "CPUE"), together with total catch, to infer information about population size, trend, and "catchability" of the southern rock lobster stocks of the SZRLF and the WZRLF. Other fisheries for *Jasus edwardsii* include those in the South Australian Northern Zone, the Victorian Eastern Zone, Tasmania, and New Zealand.

Lobsters in the SZRLF and the WZRLF are caught in devices known as "pots" that are cages with an opening allowing lobsters to reach bait inside. The pots are dropped to the sea floor, with each pot capable of trapping and holding several lobsters, which are retrieved by fishers typically after one day. The most resolved form of catch rate used in the analyses for this thesis is that defined for an individual fisher over a 24 hour period - the ratio of the total catch to the total number of pots set and hauled (potlifts). Similarly, catch rates can be defined for time steps of day, month, or year, by summing the catch and potlifts (fishing effort) over fishers and dividing total catch by total effort.

Note that in this thesis the terms "CPUE" and "catch rate" are used interchangeably. By "abundance" is meant either the absolute number of lobsters in a population or the biomass (weight of all lobsters), depending on whether the catch data used to model the population was in terms of the number (Paper Three) or weight of the animals caught (Papers One and Two). The term "relative abundance" is assumed to mean a measure of true abundance, but one that is dimensionless (no information on absolute population size), representing a completely precise and unbiased index of abundance. Hence, CPUE, based as it is on data, can at best be considered as a good proxy index for relative abundance. Instead of "abundance", the term of identical meaning namely "absolute abundance" is used depending on the context to highlight a contrast with "relative abundance".

Catch rates are commonly used in fisheries science and stock assessments as indices of relative change in population size (i.e. abundance) by assuming direct proportionality between catch rate and population size, meaning for example that when catch rate doubles in one year that population size also doubles. This inference about change in population size relies on the absence of other influences on catch rates that may change over time. This is rarely the case, however, and effective monitoring of marine stocks for sustainability management of a fishery requires study of other potential influences on catch rates. Such potential influences may change what is known as "catchability" (Hilborn and Walters, 1992; Arreguin-Sanchez, 1996) because they alter how easily, or efficiently, animals are caught. Catch rates are often regressed against available data sources that are assumed to reflect different components of catchability, and when time is represented as an additional independent variable such regressions are known as catch rate standardizations. However, catch rate standardization informs only on relative changes in abundance, whereas if data on the total amount of catch or effort is considered in combination with catch rate, models that attempt to estimate the absolute level of abundance, such as biomass dynamics, delay-difference, and depletion models (Hilborn and Walters, 1992) can be applied. Catch rate standardization, as well as several absolute abundance models of relevance to this thesis, are described in the literature review further below.

The SZRLF and the WZRLF, apart from being spatially contiguous and fished using similar fishing gear, are also broadly similar in terms of both commercial fishery management and lobster stock attributes (Linnane et al., 2010; Plaganyi et al., 2018), although the total commercial catch from the SZRLF is several times larger than from the WZRLF (in 2014, 1244 t versus 325 t). These fisheries have closely related lobster recruitment processes (Linnane et al., 2010, 2014; Hinojosa et al., 2017). Recreational and indigenous fisheries constitute a relatively minor (< 5%) fraction of total catch for both the SZRLF and the WZRLF (Plaganyi et al., 2018). The commercial sectors of the SZRLF and the WZRLF are similar in terms of gear limitations, temporal closures (SZRLF June-September; WZRLF females June to mid-November and males mid-September to mid-November), minimum legal size limits (SZRLF 98.5 mm CL; WZRLF females 105 mm and males 110 mm), protection of spawning females, and the use of yearly Total Allowable Commercial Catch (TACC) with individual transferable quota (ITQ) (PIRSA, 2013; Linnane et al., 2017; VFA, 2017; VSG, 2017). Catch is recorded both in terms of mass (kg) and number of “landed” lobsters (live, non-spawning, legal sized) in both fisheries.

Summary of paper objectives

This work is a "thesis by publication". The three main papers were the result of co-authorship, with myself as primary author having produced the bulk (~ 90%) of the conception and development of the material. The first and third papers were published in scientific journals as detailed below, and involved studies on respectively the abiotic catchability and absolute abundance of the lobster stock in South Australia's SZRLF. The second paper focusses on the estimation of relative abundance of the lobster stock in Victoria's WZRLF, and is currently submitted and under review.

Paper One: Feenstra, J., McGarvey, R., Linnane, A., Punt, A.E., Bean, N., 2014. Environmental influences on daily commercial catch rates of South Australia's southern rock lobster (*Jasus edwardsii*). Fish. Oceanogr. 23, 362-374.
Abiotic environmental influences have been shown in studies on a variety of lobster species to have had a substantial impact on trends in commercial catch rates. The study presented in this paper had the aim of determining the extent to which environmental factors, for which we possess data, may be impacting on daily catch rates of southern rock lobster (*Jasus edwardsii*) in the SZRLF by inducing non-stationarity in catchability. A multivariate weighted linear regression was applied, involving environmental data sources as covariates and total potlifts to scale the variance given the highly variable levels of daily fishing effort. The covariates used in the analyses were bottom water temperature, wave height and period, moon phase, wind stress, and sea surface height. In addition to reporting on the proportion of variance explained by the environmental factors, and the impact on trend in catch rates, the study determined several qualitative outcomes regarding the nature of the influences on catch rates that were not previously reported in the literature for southern rock lobster.

Paper Two: Feenstra, J., McGarvey, R., Linnane, A., Haddon, M., Matthew, J., Punt, AE. Impacts on CPUE from vessel fleet composition changes in an Australian lobster (*Jasus edwardsii*) fishery. Submitted to New Zealand Journal of Marine and Freshwater Research. (Under review.)
Generalized linear modelling was used to estimate standardized catch rates for the southern rock lobster (*Jasus edwardsii*) stock of the WZRLF, and to determine the direction and extent of induced trend in catchability due to the dynamics of vessel entry and exit into the fishery over time. In particular, less efficient vessels exiting over time can induce an upward bias in the yearly trend of nominal (raw) catch rates, resulting in an overly optimistic indication of the trend in relative abundance that may lead to overexploitation of the stock. The underlying mechanisms of vessel fleet dynamics were investigated, and results discussed including in relation to the influence on the TACC and ITQ management. Several diagnostic indices were created to assist in quantifying discrepancies between trends in nominal and standardized catch rates.

Paper Three: Feenstra, J., Punt, AE., McGarvey, R. 2017. Inferring absolute recruitment and legal size population numbers of southern rock lobster (*Jasus edwardsii*) in South Australia's Southern Zone fishery using extended forms of depletion modelling. Fisheries Research 191: 164-178.
An extension of the Leslie-Davis depletion model was developed, referred to here as EDM (extended depletion model), and applied to the SZRLF, providing a new and simple approach to stock assessment for this resource. It produces estimates for all years of absolute exploitable abundance as well as the number of recruiting animals to the fishery. EDM achieves this by

simultaneously estimating recruitment for all years, which involves combining features of population dynamics from classic within-year depletion models and between-years delay-difference models. EDM requires total fishery catch in number over a fishing year, but monthly catch rate data for only part of the year (for the SZRLF during three months in peak fishing season) when no recruitment and constant catchability are assumed. It neither requires assumptions about catchability, nor the availability of fishing effort data, for the rest of the fishing year. A hybrid model (EDM-CSA) was developed that combines EDM and catch-survey analysis (CSA), expanding EDM by fitting to a yearly recruitment index based on discarded undersize lobsters, which unlike CSA does not require a catchability ratio of legal-size to undersize animals to be assumed *a priori*. Abundance and recruitment estimates from EDM and EDM-CSA were compared with estimates from a more complex, but data hungry, length-based integrated stock assessment model (LenMod). Further outcomes using the EDM framework included the development of a statistical test that checks the validity of the assumption of constant catchability across years, and a generalization of EDM to allow modelling of non-linearity in the CPUE-abundance relationship such as hyperstability. These modelling tools were used to analyse the problematic discrepancy between trend in nominal commercial catch rate and the fishery-independent survey measurements of relative abundance over 2008-2014.

Literature review

Modelling of relative abundance

Catchability and trend in catch rate

Catchability can be defined in terms of the proportion of a population of fish that is caught by a unit of fishing effort (Paloheimo and Dickie, 1964; Ricker, 1975). Hence, for "E" units of fishing effort at time "t" (day, month, or year), q*E(t)=C(t)/N(t), where "q" is catchability, "C" is catch, "N" is population size (abundance). Rearranging the aforementioned equation, we have CPUE(t) = C(t)/E(t) = q*N(t), noting that this assumes that CPUE data are directly and linearly proportional to abundance, with catchability as the constant of proportionality.

The above assumes that catchability is stationary. However, Ricker (1975) noted that catchability often varies over time, and that when the source of that variability is not accounted for in fisheries models, it is likely to be the single most important issue to impact stock assessments. Non-stationarity in catchability can be modelled as the product of separable factors informed by time series of measured data on various sources of influence. This basic multiplicative model for CPUE states that catchability components are assumed to impact CPUE independently of each other, and from abundance, the latter being scaled by each of the catchability components.

The multiplicative model of CPUE is often assumed when conducting a process known as "catch rate standardization", typically involving CPUE data regressed on various covariates that are assumed to relate to catchability, and with an independent variable for time assumed to represent relative abundance (Quinn and Deriso, 1999; Maunder and Punt, 2004). CPUE standardization has the aim of estimating and presenting the above mentioned time variable. Similarly, the extent to which trends and variability in CPUE data are explained by the various sources of catchability is also of interest as part of CPUE standardization. In contrast to standardized CPUE, a CPUE data index that is based directly on the catch and effort data (e.g. sum of catch divided by sum of effort) is sometimes referred to as “raw” or “nominal CPUE.

Since CPUE, ideally, is desired to be an unbiased index for relative abundance over time, usually by year, CPUE standardization models often estimate a yearly trend as a series of estimated coefficients (one per year), referred to as the “year effect”, using a separate variable from the other quantities that are intended to represent components of catchability. Each of the coefficients of the year effect have a value relative to a common “reference” or “base” year that is assumed to have a coefficient value of 0 on the log-scale to avoid parameter confounding, this being so for log-linear regression models with an independent intercept parameter (Maunder and Punt, 2004). Similarly, covariate data for catchability may be modelled as discrete variables (e.g. spatial fishing block, fishing vessel identifier), with each covariate variable having parameters estimated relative to a reference category of value 0 (e.g. a particular block or vessel). Covariate data on catchability may also be continuous, such as temperature recorded in degrees Celsius, with the estimated parameter being the slope of the CPUE response to changes in the covariate. Hence, the concept of catchability in CPUE standardization is different than in fisheries population dynamics models (see further below) in that only relative measures of catchability and abundance are represented, the absolute values of these two quantities being unavoidably confounded with their product represented by the independent intercept parameter.

As a simple demonstration of the potential benefit of including covariate data suppose there exists a fishery that consists of only two vessels (1 and 2) and where catchability for vessel 1 is twice that of vessel 2. If in one year vessel 2 fishes with only half as much effort as vessel 1 when in the previous year they fished with equal effort, and supposing that there has been no change in abundance between those two years, then the yearly CPUE statistic has nevertheless increased by 11%. Maunder and Punt (2004) provide an illustration of a similar example for a two-fisher fishery. Inclusion of fishing record data at the resolution of vessel-by-trip means that in the process of CPUE standardization, which is typically carried out by regression, assuming a given form of error in the dependent variable (CPUE), the changing levels of participation by the vessels is accounted for and separated from the trend in the year factor (Bentley et al., 2012).

Two error distributions for CPUE data that are commonly used, when the multiplicative model of CPUE is assumed, are the lognormal and the gamma distributions. Lognormal errors are modelled using multivariate linear regression on the log-transformed CPUE data values. Gamma errors can be modelled using Generalized Linear Models (GLMs), often with a log-link function connecting the expected (mean) CPUE with a linear combination of covariate terms (McCullagh and Nelder, 1989; Maunder and Punt, 2004; Venables and Dichmont, 2004). In both error models, the standard deviation of the errors is assumed to be proportional to mean CPUE, unlike normally distributed error (i.e. constant variance with mean), which is often unreasonable for CPUE data.

Interactions between time and other factors in the model are possible, and represent a different slope for the response of CPUE to change in temperature in different years, or a different response intercept parameter for each spatial fishing block in different years (i.e. separate time trend per spatial block). However, interactions with year are often avoided when standardizing CPUE given difficulties with interpreting the index of yearly relative abundance that is primarily sought (Maunder and Punt, 2004; Wilberg et al., 2010). Interactions between variables other than year in a CPUE standardization, such as between those representing different sources of catchability, do not present such problems.

Non-linear dependence of CPUE on catchability is implicitly captured in the case of covariate data that may be reported in categorical units, but that are naturally ordered (e.g. depth in units of 10 m), since each individual category, also known as a "level" of the covariate, may vary independently from other levels though relative to a common reference level as noted above. Similarly, the use of separate year levels is an example of how non-linear trend in time of abundance can be captured. It is possible to either convert a continuous explanatory variable into a categorical variable divided into appropriate levels (Maunder and Punt, 2004; Su et al., 2008), or less arbitrarily, use a class of model known as GAM, or generalized additive model (Venables and Dichmont, 2004; Wood, 2006) to model general non-linear dependence of CPUE on sources of catchability. GAMs make explicit the determination of the shape of the non-linear response of CPUE.

Environmental factors

Catch rates of crustaceans in commercial fisheries can be strongly affected by extreme ambient environmental conditions that may directly impact abundance. However, what constitutes extreme conditions is specific to a species and fishery, and can occur over a narrow range for a given environmental variable. For example, Zisserson and Cook (2017) determined that for snow crab on the western Scotian Shelf in the southernmost snow crab fishery in the Atlantic Ocean, the population had undergone substantial mortality over December 2012 to February 2013 along with sharp drops in CPUE, as a result of unusually elevated bottom water temperatures ranging between 7 °C and 10 °C. Given that snow crab are cold-water-adapted over -1 to +6 °C, the authors linked this to experimental studies which showed that exposure of snow crab to those elevated temperatures for more than 21 days led to negative metabolic states. Similarly, Pearce and Balcom (2005) reported increased mortality of American lobster for the Long Island Sound fishery, concluding that this was due to above average water temperatures in 1999 placing additional stress on animals that were already diseased from parasite infections. In contrast, Mills et al. (2013) reported on anomalous warming events in 2012 that increased the abundance of legal size American lobster in the fisheries of the northeast Atlantic Ocean as a result of increased growth rates. Hence, given that crustacean mortality events may result from unusual changes in ambient natural conditions, it is not too extreme an inference to suggest that at somewhat less unusual levels of environmental change animals may not die but merely alter their behaviour and in so doing alter their catchability.

Correlation between environmental variables and CPUE can depend on the temporal scale of the analysis, with the finer scales more likely to be impacted directly by catchability factors in contrast to growth and recruitment (Koeller, 1999). Paper one in this thesis is a study of the impacts on daily CPUE of the SZRLF by environmental variables for which data were available at the time of the study, namely bottom water temperature, wave height and period, moon phase, wind stress, and sea surface height. Despite spanning the period 1998-2008, the seasons 2003-2005 were not modelled due to lack of covariate data (mainly temperature), and similarly so for some months during the rest of 1998-2008 as detailed in Paper One, leaving 1,258 days in the analysis. The main methods of the SZRLF study were also applied to a similar but smaller data set for the WZRLF, and results reported in Paper One. The literature on crustacean fisheries indicates that catchability can be impacted by the environmental factors available in the SZRLF study of Paper One, as will be alluded to below. However, given that regression models do not indicate causes for estimated effect outcomes, and available environmental covariates typically are proxies for more direct factors influencing animal behaviour that may interact with other (including unmeasured) factors, inferences about reasons for the estimated effects are necessarily likely to be speculative to some extent.

Even for water temperature, which is perhaps a more direct measure available on a lobster's ambient environment, the CPUE response may be qualitatively different for different studies on the same species. For example, Watson and Jury (2013) studying American lobster found that most studies reported a positive relationship between temperature and CPUE (the earliest being McLeese and Wilder, 1958) and which often was explained in terms of heightened lobster activity and metabolism with increased temperatures. They also noted some studies report a negative temperature-CPUE relationship (Courchene and Stokesbury, 2011) or no conclusive relationship (Jury, 1999), and they suggested that these three different types of outcomes might be due to different temperature ranges being studied by different researchers. They indicated that the temperature-CPUE relationship is more likely to be positive, nil, or negative, in response to respectively colder, intermediate, or higher temperatures.

Another potential temperature-metabolism mechanism, and one that is proposed in Paper One, is that of aerobic scope for activity (SFA) which was shown for southern rock lobster in the laboratory to peak around the acclimatized temperature (13 °C) and to reduce on either side of that temperature (Crear and Forteath, 2000). Given that at higher values of SFA a lobster can utilize its metabolism for more work (Crear and Forteath, 2000), it is hypothesized in Paper One that a lobster's capacity to actively forage for food may hence be optimal around the acclimatized temperature in a fishery. Note that the SFA hypothesis is not incompatible with the conclusions by Watson and Jury (2013) given that the acclimatized temperature may differ between studies. However, de Lestang et al. (2009) for western rock lobster, reported that catchability rose with increasing temperature, but only when animals were in their sedentary phase and not when they were migrating. They suggested that when animals are sedentary a small increase in temperature may lead to increased appetite and consequently foraging activity, which then increases the pot encounter rate, while animals that are migrating have pre-existing high levels of pot encounters irrespective of temperature. Ziegler et al. (2004) modelled seasonal variation in catchability of southern rock lobster in a scientific reserve in south-east Tasmania, Australia, as a sinusoidal function of water temperature and incorporating proportions of lobsters moulting or mating. Results from that analysis indicated a positive dependency of catchability on temperature, except for females during their moulting period.

Stoner (2004) reviewed the environmental literature on fish regarding feeding behaviour in relation to baited fishing gear, and noted that turbidity and light levels can impact directly on sensory abilities of animals, which in turn can affect activity levels, and feeding capability and motivation. He further notes that, for example, chemical cues stimulate fish to move towards bait, which can be impacted by turbidity, but then when the fish approaches closer to the bait, vision may become more important. Fishes living in turbid waters or in deep shelf environments may have low light thresholds, but catchability will decrease when light levels fall below such thresholds (Stoner, 2004). For the SZRLF, concerning southern rock lobster, fishers anecdotally report improved catch rates on days either just prior to full moon or just after large swells, and these hypotheses were investigated in Paper One.

Aside from some degree of increased turbulence during high swells, in the aftermath of such swells sediments are stirred into the water column along the South Australian continental shelf (Middleton and Bye, 2007). Srisurichan et al. (2005) found increased catch rates of western rock lobster on days after high swells and attributed this to increased food availability and protection from predators. Cobb (1995) suggested that crustaceans have more difficulty following bait odour trails during periods of turbulence and greater fluid velocities, but Major and Jeffs (2017) determined that the effect of this strongly varies between species of crustaceans and depends on hydrodynamics. Ihde et al. (2006) found no difference in sublegal catch rates of southern rock lobster between new moon and full moon in south-eastern Tasmania, but higher catch rates during the new moon have been reported for other spiny lobsters (Morgan, 1974; Yamakawa et al., 1994; Srisurichan et al., 2005). Movements of the Japanese spiny lobster displays a strong diurnal pattern, being predominantly active during the hours of the night, but it was found that lobster activity was suppressed under controlled conditions at night if the brightness level was increased above a threshold value (Nagata and Koike, 1997). These authors implied that these conditions could potentially be met at night around full moon at 15 meters depth around Shima Peninsula, and noted that the latter's lobster fisheries reported little catch on days of the full moon. However, for southern rock lobster studies have determined little change in lobster activity in relation to modified light conditions (MacDiarmid et al., 1991; Williams and Dean, 1989). Given that effects of both light level and turbidity on catchability conceivably may vary with depth of the lobsters, Paper One included sensitivity analyses by running models separately for inshore (<= 40 m) and offshore (> 40 m), and the impact of cloud cover was also investigated.

Drinkwater (2006) reported that for the eastern Canadian fishery of American lobster, which experiences ocean upwelling and downwelling, wind affects catchability primarily due to its influence on bottom water temperatures, consistent with the classical Ekman response. That conclusion is relevant to the SZRLF as it is also subject to upwelling and downwelling (Schahinger, 1987; Middleton et al., 2007). Hence, it may be predicted that bottom water temperature will have a stronger influence than wind on CPUE. This was investigated in Paper One for which wind was included in the starting model prior to backward model selection. Exploratory data analysis found that there was a noisy but linear relationship between the covariates for alongshore wind stress and bottom water temperature, which however involved only modest correlation (-0.32; $P < 0.001$). The latter outcome suggests little associated collinearity concerning the wind and temperature covariates. Further regarding collinearity, the exploratory data analysis found that the maximum correlation between the covariates was between Sea Surface Height and temperature, with both Pearson and Spearman coefficients of +0.53.

There exists a potential problem for the SZRLF concerning interpretation of the estimated temperature effect as being due to catchability rather than abundance. As explained in Paper One, the SZRLF environment features seasonality of bottom water temperature within a year that partly coincides with seasonality of lobster abundance and vulnerability, these being driven by changes in growth and population depletion (due to fishing). This suggests the possibility of confounding in the CPUE standardization between the estimated categorical 'month' effect (proxy for seasonal abundance) and the temperature effect, something that is not an issue for moon phase and wave effects. Hence, the 'month' effect may reflect some of the influence on CPUE of temperature, or the temperature effect may partly reflect population dynamics. Similarly, the 'month' effect potentially may be inadequate to account for finer temporal scale population dynamics. Paper One considered these aspects of confounding and explored it using sensitivity analyses. Ideally, such problems would be minimized in a context of classic controlled experiments in which levels of some factors are varied in relation to other factors. However, the very nature of exploited wild populations means such controlled conditions rarely are possible. Alternatively, use of a series of research surveys in a no-fishing area, involving sampled locations with measures of absolute abundance, provides another potential means to model dependency of catchability on water temperature (Ziegler et al, 2004).

Note that daily totals of potlifts varied substantially for the SZRLF data used in Paper One, with a 10^{th} percentile value of 500 potlifts, 25^{th} percentile of 2,400 potlifts, median of 7,000 potlifts, and 75^{th} percentile of 10,000 potlifts, unlike at coarser levels of temporal resolution such as month or year which varied much less. This high level of day-to-day variability in effort leads to high variability in the precision of CPUE, with the variance of the errors in CPUE scaling inversely with levels of effort. This follows sample size considerations (Cochran, 1977), and means that CPUE data is likely to vary much more for a day involving little fishing than on a day with normal levels of fishing, regardless of whether these two days differ much in their covariates. As explained in Paper One, this was accommodated in the multivariate weighted linear regression analysis using a variance weight that is a power function of potlifts.

Fishery factors

Given the relatively minor estimated impact of environmental influences on CPUE for both the SZRLF and the WZRLF (see Paper One, and Conclusion), a reasonable question is to wonder whether factors such as changing vessel composition of the fishing fleet over time impacts CPUE more. Previously, a CPUE standardization on commercial fisheries data for the WZRLF by Walker et al. (2013) had, along with other variables, included a covariate that combined information on vessel registration and fisher license into an alpha-numeric identifier. That study, substantial and detailed as it was, did not focus on the extent to which vessel information influenced the trend in relative abundance nor on the associated vessel entry-exit dynamics of the fleet.

Paper Two studies the effects on CPUE trend over a long time frame (1978-2014) of a large and diverse data set of vessel composition information on the WZRLF fleet. At the time of writing Paper Two such data were not available for the SZRLF due to lack of an unambiguous and up-to-date database key to track consistent vessel information over time. The simple illustration provided above of a two-vessel fishery fleet is an example of a phenomenon hypothesized to have occurred for substantial periods in the WZRLF, namely of an increasing trend in net fleet catchability due to disproportional numbers of individual vessels of low catchability (low fishing power or efficiency) exiting the fishery. This has been shown for many other fisheries and species as being of importance when determining a more accurate trend of relative abundance, including for crustacean fisheries - O'Neill and Leigh (2007) and Braccini et al. (2012) for Australian eastern king prawn, and Eigaard and Munch-Petersen (2011) for Danish northern shrimp. The mechanisms driving net increases in catchability of a fleet over many years can involve variously the rate of turnover of vessels of differing individual catchabilities, technological improvements to individual vessels (Ye and Dennis, 2009; Bishop, 2006; Branch et al., 2006), and the existence of TACC/ITQ management (Branch et al., 2006; Pascoe et al. 2013). These factors are further discussed in relation to CPUE standardization results for the WZRLF in the Conclusion, while the possible existence and consequences of technological changes to vessels having occurred in the WZRLF is discussed here further below.

Bentley et al. (2012) found an effect on CPUE of New Zealand trevally due to changes in fleet composition, and they developed a diagnostic index to assist exploration and identification of covariates that influence the trend in catchability. They showed that such covariates may not necessarily explain a large proportion of the variance in CPUE, but that those covariates do show changes in their effort distribution over time. Bentley et al. (2012) calculated a yearly "influence" index (denoted "I") for a covariate in order to provide a measure of the impact on the trend of nominal CPUE, from yearly changes in the distribution of effort among coefficients of the covariate effect estimated in the CPUE standardization. For example, for the vessel effect (*Vessel*), index "I" is calculated in a year as the exponential of the weighted (by record count) mean of estimated *Vessel* coefficients normalized to 1 across the years. For a given year, the larger the value of "I" the greater the net contribution by *Vessel* to the value of nominal CPUE compared to its net contribution in a year with a lower "I" value. Bentley et al. (2012) used a figure showing combined coefficient–distribution–influence information ("CDI") for each covariate. However, the net contribution of *Vessel* to the trend in total catchability is not easily apparent from plots, and another type of index for graphing is suggested in Paper Two and described next.

The absolute value of "I" for two covariates in a given year do not compare directly due to their separate normalization factors. However, ratios between years for a given covariate do compare appropriately with the same ratio for another covariate (normalization constants cancel). Similarly, for a given year, the product of the "I" for each covariate all multiply together to provide a valid "I" for total catchability (due to the same number of records having been used in the normalization constants of each covariate). Since total catchability depends on all the covariates in a model, it is useful to plot on the same graph "I" for the covariate, "I" for total catchability, and "I" for total catchability excluding the covariate to discern contribution to trend in total catchability by a particular covariate of interest. If desired, this approach can be extended to compare two covariates simultaneously in relation to total catchability, by adding the "I" of an additional covariate to the plot and adjusting the "I" series for the "excluding" case.

A further index is introduced in Paper Two that quantifies the direction and extent of yearly changes in net total catchability. This index is constructed (see "V" in equation 2 of Paper Two) entirely using nominal and standardized CPUE, with the latter mean-scaled to nominal CPUE, which thus allows proportionate differences between two years in nominal and standardized CPUE to reflect changes in the absolute size of catchability. When "V" is shown on the same graph as the nominal and standardized CPUE series, it may be used as a tool to help characterize discrepancies between nominal and standardized CPUE more easily, which can be of interest in stock assessments (Maunder and Punt, 2004; Maunder and Punt, 2013). "V" will be impacted by high noise levels in the nominal CPUE series, although for a commercial fishery with many thousands of data points for each year such levels of noise may be less common (and may be discerned from the errors on standardized CPUE).

Regarding technology uptake by individual vessels, it is probable that this occurred for the WZRLF, at least up to the mid-1990s, in terms of upgrades to on-board equipment such as GPS. Catchability for spiny rock lobsters in the Western Australian rock lobster fishery has been estimated to have increased over the years prior to 1995 by between 1-3% per year due to adoption by individual vessels of echo sounders and GPS (Fernandez et al., 1997). Similarly, another study on the same species by de Lestang et al. (2009) found a 0.5-2.2% increase in fishing power over the period 1986-2005. The Australian northern prawn fishery is another example of an Australian crustacean fishery in which vessels have undergone substantial changes in fishing power due to the adoption of on-board equipment (GPS, plotters) (Robins et al. 1998).

The consequences for standardization of CPUE of individual vessels adopting better technology include a positive bias in the estimated change of relative abundance over time (Ye and Dennis, 2009). It is separate from the effects of changes in net vessel fleet composition because these relate only to differences in catchability among vessels (Bishop, 2006). Although the impact of bias in individual vessels may lessen to an extent when turnover of vessels is high, such as in the WZRLF (over 1978-2014, most reside < 10 years, few > 20 years), because vessels exist in the fishery for less time, and so accumulation of inaccuracy per vessel is lower. Models that incorporate pertinent covariate data on vessel specific attributes are best equipped to capture changes in attributes of individual vessels (Bishop, 2006; Ye and Dennis, 2009). Such data were unfortunately not available for the WZRLF.

Caveats on the estimation of catchability and abundance

The trend in relative abundance inferred by CPUE standardization, and the absolute abundance levels estimated by population dynamics models (see below), only relate to the animals that can be directly accessed by the fishing gear, with such abundance also known as exploitable, vulnerable, or available abundance. For example, a fraction of animals across a certain size range may be inaccessible by fishing gear, or alternatively the biology of an animal at certain times may mean reduced movements with hypothesized lower probability of encountering gear (Miller, 1990) such as during moulting by females later in the fishing season for southern rock lobster (Ziegler et al., 2004). Hence, the estimated catchability is strictly a constant of proportionality between CPUE and exploitable abundance, rather than between CPUE and total abundance (Maunder et al., 2006). This suggests, for example, that yearly nominal CPUE can change between years merely due to a change in fishing effort from the middle or later in the year to earlier in the year, if the proportion of animals that is vulnerable is different earlier compared to later in the year (Bentley et al., 2012). In this case, inferences about changes in relative abundance may be misleading, but standardized CPUE should correctly indicate the trend in abundance with year, assuming that a factor for month is included in the standardization, and no unmeasured influences exist that varies within a year independently from exploitable abundance.

Implicit assumptions of the CPUE standardization models, and for many population models, exist in regard to the spatial dimension of analyses (Paloheimo and Dickie, 1964; Hilborn and Walters, 1992; Quinn and Deriso, 1999; Walters, 2003; Maunder et al., 2006), including most fundamentally that the total spatial extent of the population under study does not change over time and that it is closed to immigration and emigration. Similarly, inferences regarding estimated relative abundance at the zone scale often assume that the spatial distribution does not change over time in levels for one or more of the following: fishing effort, animal abundance, or catchability. For example, in CPUE standardization a factor may exist in the model for fishing block, but if that is assumed to represent spatially-varying catchability then it must be assumed that animal abundance is spatially uniform given that in CPUE standardization varying amounts fishing effort is the norm rather than the exception. Inclusion of a spatial block covariate in a CPUE standardization may only partially account for spatial heterogeneity in catchability given that in some fisheries the reporting blocks represent a large spatial extent and fisher movement within which is not captured by the data (e.g. SZRLF, up to season 2016).

Space-time assumptions are often unmet given both the nature of the fishing process and natural population dynamics, but may be worth identifying, explaining, and attempting to model. For example, if a fishing zone initially had relatively uniform lobster abundance, after which fishers concentrated effort in a specific subsection of that fishing zone while ignoring other areas in the fishing zone that also contain animals, then over time CPUE for the whole zone may decrease more rapidly than abundance. This is due to the zonal CPUE statistic being based on a part of the whole fishing zone that suffers a disproportionate degree of depletion, and this phenomenon is an example of hyperdepletion (Hilborn and Walters, 1992; Arreguin-Sanchez, 1996; Harley et al., 2001). If after some time fishers shift most effort into other areas of the fishing zone that meanwhile increased their lobster abundance due to reduced levels of fishing, then this may give rise to hyperstability of CPUE (Hilborn and Walters, 1992; Arreguin-Sanchez, 1996; Harley et al., 2001) since CPUE will increase more rapidly than abundance for the whole zone.

Density dependence in catchability can arise from natural competition between animals around fishing gear (Stone, 2004) and can lead to hyperdepletion or hyperstability of CPUE. For example, if smaller lobsters are deterred from entering pots due to the presence of larger lobsters near those pots (Frusher and Hoenig, 2001; Ihde et al., 2006), then this may lead to hyperstability if it is assumed that CPUE decreases less rapidly than abundance due to catchability increasing with decreasing abundance. That is, at lower levels of abundance it is assumed that there is less competition around pots thus allowing some lobsters to be caught that would not have been when abundance was higher.

One way in which hyperdepletion and hyperstability has been accounted for in population dynamics models is to model CPUE(t) as q*(N(t)^beta), where “t” is time, “N” is abundance, “q” is a stationary catchability parameter, and “beta” is a new parameter to quantify non-linearity between CPUE and abundance. Note that CPUE(t) = q*(N(t)^(beta-1))*N(t) and hence this models non-linear density dependence of catchability, with hyperdepletion indicated when beta is estimated > 1, and hyperstability when < 1 (Hilborn and Walters, 1992; Wilberg et al., 2010). The parameter beta can be difficult to estimate without independent information on relative abundance. However it is important to account for density dependence if it exists, or at least determine the direction and extent of bias from not accounting for it, as it will mean the risk of stock collapse is underestimated (hyperstability) or alternatively the TACC may be set too conservatively (low) (hyperdepletion) in fisheries linking the TACC to CPUE (e.g. the SZRLF). Studies have indicated the presence of the hyperstability form of density dependent catchability for southern rock lobster the fisheries off Tasmania (Ziegler et al., 2003) and New Zealand (Haist et al., 2009), and in South Australia's northern zone (Linnane et al., 2010). Paper Three includes an analysis aimed at determining the extent of density dependence in catchability for South Australia's southern zone.

Modelling of absolute abundance

Models for CPUE standardization, aside from CPUE data, incorporate no explicit catch data on the total numbers or weight of all the animals removed from a population being fished. Hence, such models do not involve equations to represent the natural and fishing history of an exploited population, and they cannot estimate total exploitable abundance. Models exist that are “catch-conditioned”, meaning that they model depletion of a population by removal of total catch that is assumed to be without error and hence is not fitted. Note that in the case of total catch this needs to include more than all animals landed by the commercial fishery, but additionally requires (if these exist) catch from the recreational fishery, as well as animals caught but discarded as dead. The “EDM” and “LenMod” models described further below, which were applied to the SZRLF data, are catch-conditioned and incorporate both commercial dead discards and recreational catch.

Biomass dynamics models

Biomass dynamics models, also known as surplus production models, use total catch and CPUE provided in weight of animals (Schaefer 1954, 1957; Polacheck et al. 1993; Breen and Kendrick, 1998; Smith and Addison, 2003). A discrete equation form for such models is, B(t+1) = B(t) + g(B(t)) - C(t), where "B" is exploitable biomass at time "t", "C" is total catch in weight, and "g" models the production of new biomass as a function of existing biomass alone.

Note that this model formulation does not allow recruitment to be estimated explicitly, and instead models population reproduction along with growth and natural mortality, using the surplus production function "g" (Smith and Addison, 2003). Population stability is achieved when a natural increase in biomass is balanced by human exploitation as catch in weight. Outcomes vary greatly depending on the form of the production function (Maunder, 2003) and many biomass dynamics models ignore any biomass-independent yearly variation in recruitment. Estimation outcomes can be very sensitive to having enough contrast in the abundance index for which CPUE is often employed. Ideally data periods fitted should include both high and low CPUE levels to enable the production function to be estimated (Hilborn and Walters, 1992).

Delay-difference models

Delay-difference models use total catch and CPUE provided as either in weight or numbers of animals (Deriso, 1980; Schnute 1985, 1987; Smith and Addison, 2003). In terms of discrete time and population (rather than biomass), this involves a spatially-closed population birth-death equation where the population is the stock of exploitable animals, births are recruits to that population, and deaths are represented by two components namely animals that died due fishing and those that died naturally (old-age, predators). Symbolically, N(t+1) = N(t) + R(t) - C(t) – M(t), where "N" is exploitable abundance at time "t", “R” is the number of recruits (“recruitment”), "C" is total catch in number, and “M” is the number of animals that die naturally (often applied as a known natural survival factor to “N”). If biomass is to be estimated then the data needs to be in terms of weight, and the birth component would involve an additional term that is proportional to biomass representing growth of fishable animals to heavier body weights, involving further forms of parameterization (Quinn and Deriso, 1999).

Recruitment can be estimated directly as an estimated parameter representing a pulse addition to the population at time “t”, or else using an assumed “stock-recruitment” function

(Deriso, 1980). Note that, considering only the former approach and the case of "knife-edged" fisheries (involving a minimum legal size limit) modelled using yearly time-steps, the estimated recruitment is in reality composed of an aggregation of undersized animals in various age groups of the previous year that grew above the legal size limit by the start of the current year. In general, these models require auxiliary information on natural mortality, recruitment and/or growth for realistic results (Quinn and Deriso, 1999; Smith and Addison, 2003).

CSA (Catch-survey analysis)

CSA is an example of a delay-difference model that, additional to CPUE and total catch in numbers of animals, requires an index of recruitment to be fit. CSA originated from the work of Collie and Sissenwine (1983), and since then modified versions of that model have been applied to many crustacean species (Smith and Addison, 2003; Paper Three).

The population dynamics equation is N(t+1) = (N(t) + R(t))*exp(-M) - C(t), where "N", “R”, “C” are as described for delay-difference models above, and “t” is in years. However, here “M” is the yearly rate of natural mortality, and the appearance of “M” in the population dynamics equation may be varied slightly according to the fraction into the year catch is assumed to be taken. The basic implementation of CSA involves modelling mean CPUE as “q*N(t)” where “q” is a stationary catchability parameter, and similarly the mean recruitment index is recruitment as “qr*R(t)” where “qr” is another stationary catchability parameter. The CPUE data and the recruitment index are fit simultaneously, assuming log-normally distributed independent observation errors.

CSA is an example of what is known as an open system depletion model (Smith and Addison, 2003) in that, unlike the more elementary within-year Leslie-Davis closed depletion models (described further below), recruitment into the population is modelled. CSA fits to yearly data simultaneously across multiple years, estimating recruitments in each of those years and from which start-year abundances can be inferred. CSA requires relatively little data given that it provides estimates of both recruitment and population size, and in particular it does not need age or length composition data, which are more expensive to obtain and is less commonly available. Cadrin (2000) compared CSA to biomass dynamics models, fitting both models to simulated data, and found that CSA performed better than the latter under reasonable levels of uncertainty in the data.

Note that CSA additionally requires an externally informed constraint on “q” and “qr”, typically by fixing the ratio of these two parameters at a pre-specified value. The parameter estimates from CSA are very sensitive to the value of the ratio of the catchability parameters (Cadrin, 2000; Mesnil 2003, 2005).

Leslie-Davis depletion models

All model types described above have the following in common: their population dynamics are yearly, a single (two for CSA) catchability parameter is estimated which is shared by all years, and the model is fitted to data for all years simultaneously. An alternative class of model that estimates start-period abundance, but not recruitment, are Leslie-Davis depletion models (Leslie and Davis, 1939; Ricker, 1975), which are applied for periods within a year and generally are not fit to multiple years of data simultaneously.

These models require CPUE and total catch at several times within a period during the year for which it is assumed there is no recruitment or natural mortality, nor changes in catchability.

As no natural mortality or recruitment is assumed (and no movement in or out of the study area), these models are broadly known as closed system depletion models (Smith and Addison, 2003). The assumption of uniformity of catchability is in common with biomass dynamics and delay-difference models. However, Leslie-Davis models are particularly sensitive to this assumption (Miller and Mohn, 1993; Smith and Addison, 2003).

The Leslie-Davis depletion model utilizes the closed system condition by fitting to CPUE data over several time steps for which exploitable abundance is modelled as a strictly decreasing quantity due to animals being caught (rats in traps, for Leslie and Davis, 1939). Hence, when abundance is plotted against cumulative catch the line is linear and decreasing, and fitting to CPUE data occurs via a linear regression with cumulative catch as the covariate. The magnitude of the slope provides the catchability parameter, with the ratio of the intercept to the slope providing the value for initial abundance. Note that if additionally it is assumed that there is no growth among animals in the exploitable population, then using total catch and CPUE in weight of animals caught can be used to estimate initial exploitable biomass (instead of abundance).

Depletion models, along with biomass dynamics models, are commonly used in data-limited fisheries (Smith and Addison, 2003; Edwards et al., 2012). The requirement of depletion models is that there is a period within a year for which no recruitment occurs to the exploitable population may be reasonable for crustaceans as they grow only during discrete periods in a year. For southern rock lobster fisheries, growth for individual lobsters occurs over only a few weeks (Musgrove, 2000) and collectively occurs over a few specific months (MacDiarmind, 1989) that varies slightly from fishery to fishery (Prescott et al., 1996; McGarvey et al., 1999; Ziegler et al., 2004). Furthermore, southern rock lobster fisheries in South Australia include a minimum legal size limit that is set high enough to protect the majority of immature animals after accounting for rates of growth (McGarvey et al. 1999; Linnane et al. 2008, 2017). Hence, for SZRLF's southern rock lobster the process of recruitment to the fishery can be considered to be primarily due to growth from undersize lobsters, instead of occurring as instantaneous and direct entries into the fishery over the legal size range. This latter observation is important for CSA and EDM-CSA (described below), given these fit to recruitment index data that are assumed to be proportional to the population of undersized animals.

EDM (Extended Depletion Model)

EDM was developed in Paper Three with the aim of allowing yearly recruitments, as well as start-year exploitable abundance to be estimated, using only total catch and CPUE in numbers of animals and a value for the natural mortality rate. It uses the Leslie-Davis depletion model's capacity to infer information on start-period abundance from data on within-year depletions, and combines this with the information on recruitment that is inherent in the between-year population dynamics, which is typical of delay-difference models. EDM needs to fit to CPUE for only part of each available fishing year during which it makes the same assumptions as the Leslie-Davis depletion model, and so for the rest of the fishing year it does not need data on CPUE or total fishing effort nor assumptions on catchability. EDM was applied to the SZRLF and the resulting recruitment and abundance estimates compared to those obtained from a more sophisticated, but data hungry, integrated stock assessment model (LenMod, see below).

The literature indicates that there have been relatively few models that estimate yearly recruitment with such minimal data as EDM. As noted further above, delay-difference models can achieve similar results, but in practice require either additional demographic information or need to be fit to auxiliary data sources as for example by CSA. Studies on alternative multi-year depletion models may deliver similar outcomes to EDM, but differ crucially in requiring variously two or more of the following conditions to exist for the full period of fishing within each year, namely stationary catchability parameters, CPUE or catch be fit, effort data to exist, or no recruitment to occur (Bailey and Elner, 1989; Polovina et al., 1995; Gonzalez-Yanez et al., 2006; Ehrhardt and Deleveaux, 2009; Robert et al., 2010; Babcock et al., 2015; Roa-Ureta, 2015). Robert et al. (2010) and Babcock et al. (2015) applied Bayesian multi-year depletion models that link catchability between years via drawing it from a random distribution specified by priors. Robert et al. (2010) modelled catchability as a random walk process to capture autocorrelations and gradual changes between years, but required *a priori* values for a vector of proportions to assign in-season recruitments from an estimated yearly recruitment parameter. More generally, under data-limited conditions Bayesian population dynamics models potentially suffer from insufficiently "informative" priors on catchability, and when this is the case maximum likelihood estimation should be used (Thorson and Cope, 2017).

Note that fitting the CPUE data simultaneously for all years means that EDM in common with biomass dynamics and delay-difference models, gains a more robust estimate of catchability than would be obtained from applying the Leslie-Davis model separately in each year. Hence, if for only a few years there is high observation error, weak population depletion (Magnusson and Hilborn, 2007), or within-year change in catchability, then the estimates of recruitment and abundance may still be reasonable in those years, assuming that catchability is well informed by the fits to the data in the other years. Conversely, if EDM is fit to only a few years of available data then its estimates must become more sensitive in the same manner as for Leslie-Davis models (Miller and Mohn, 1993; and further above). It is possible to estimate whether catchability changes over time by fitting EDM to subsets of the data, and using the likelihood ratio statistic as a test for significance of the variation. For the SZRLF fisheries-independent CPUE data exists and was used in Paper Three to help interpret estimates from EDM.

Two fundamental extensions of EDM were developed in Paper Three. One model is a modification to EDM so that it can fit to a recruitment index, with the resultant model named "EDM-CSA" to indicate it is a hybrid model between EDM and CSA. EDM-CSA thus potentially benefits from more information on a fishery than EDM, at the cost of estimating one additional parameter. However, unlike CSA it does not require an external constraint on the ratio of catchabilities. For the SZRLF the recruitment index was based on discarded undersize lobsters. Non-linear density-dependence of catch rates on abundance is a common and serious problem as described further above. A generalized form of EDM was developed that allows an additional parameter to be estimated in the CPUE-abundance relationship to account for a degree of non-linearity, namely "beta" as per section "Caveats on the estimation of catchability and abundance" in this Introduction.

Caveats on demographically aggregated models

The models described above involve population dynamics on a stock of animals aggregated across length and sex attributes. That is, the stock that is modelled over time is the exploitable abundance defined as the sum of the length-sex specific products of capture probability and abundance. An assumption of uniform, though not necessarily maximum, length-sex vulnerability is implicitly assumed by biomass dynamics, delay-difference, and depletion models to maintain a consistent definition of exploitable abundance over time. If this assumption is invalid then changes in the length-sex distribution of the population over time will change the net vulnerability of the population and consequently exploitable abundance. Hence, CPUE may change even if both the total abundance above legal size and the catchability do not change. That is, consider at time “t”, CPUE(t) = q(t)*N(t), where “q” is catchability that is independent of “N” which is the exploitable abundance, then the latter may change directly because of a change in demographic composition instead of a change in total catch or total numbers recruiting above legal size. In practice this means that in population models that are not resolved at a relevant demographic resolution, bias will be expressed in both catchability and abundance-related parameters. One attempt to address this problem is to include the “beta” form of non-linear CPUE observation equation described further above, but this will be inadequate unless the beta parameter could be linked to external demographic information. Note that these issues are separate to the problem described further above on caveats regarding the effects on CPUE of changing levels of fishing effort within a year, which may occur even if both length-sex vulnerability and length-sex population proportions remain uniform but for which the level of catchability differs within a year.

This suggests a weakness of fishery models that do not quantify demographic subcomponents of a population since the demography very likely does change over time as a result of heterogeneity in recruitment and growth processes. Hence, the exploitable abundance may change in ways not accounted for only by changing levels of total catch and recruitment, and further, such changes may differ from changes that occur to total abundance (Maunder et al., 2006).

Length-sex structured integrated models

Models that incorporate data on the length-sex demographic composition of the catch (in addition to total catch and CPUE) can represent and estimate at the resolution of length-sex for both total population and vulnerability. Hence, length-sex structured models can model changes in exploitable abundance more realistically over time by quantifying change in the length-sex structure of the population being fished (Punt et al., 2013). Provision of estimates of total abundance, instead of only exploitable abundance, may be of interest when constructing stock assessment indicators (Maunder et al., 2006; Linnane et al., 2017). However, unless a model is also spatially structured (i.e. models sub-regions of a fishing zone), it relies on an implicit assumption that the length-sex distribution of the population is homogeneous across the total area fished whenever the spatial distribution of fishing effort changes. Yet, even with inclusion of spatial sub-regions, when movement between the sub-regions is also modelled, there can be a substantial problem of parameter confounding between mortality and movement when associated parameters are estimated simultaneously (McGarvey et al., 2010).

Length-sex structure population models are examples of integrated models because they fit to several sources of data simultaneously (Maunder and Punt, 2013; Punt et al., 2013). In the case of length-sex structure models these include length-sex catch composition data that often are sourced from survey samples such as is the case for SZRLF (Linnane et al., 2017). These models, aside from accounting for mortality for individual length-sex classes, also incorporate growth among individual length-sex classes using transition matrices, and their population dynamics can be represented as (Punt et al., 2013): $N(t) = X(t-1)*S(t-1)*N(t-1) + R(t)$, where “N(t)” is a vector of total abundance (not exploitable abundance) by length-sex class at time “t”, “X” is a length transition matrix that may be sex-specific, “S” is a diagonal matrix of survival probabilities, and “R” is a vector of the number of recruiting animals. Total absolute abundance at time “t” is then represented by the sum over length-sex classes, restricted to legal size classes in "knife-edged" fisheries. In catch-conditioned models the “S” matrix may be implemented as the product of a natural survival factor (often fixed and non-specific by length-sex) multiplied by a matrix 1-H(t) where “H” is a diagonal matrix of harvest fraction by length-sex classes.

A component in stock assessment reporting for the SZRLF involves outputs, such as monthly total biomass above legal size and harvest fraction, from an integrated length-sex structured model of the type described above, the implementation of which is referred to here as “LenMod”. LenMod is based on the original model specifications as described by Punt and Kennedy (1997), and has since been used in scientific studies (McGarvey et al., 2010, 2015) and South Australian stock assessments (e.g. Linnane et al., 2017), undergoing various modifications over the years. LenMod is catch-conditioned on total catch weight that includes dead discarded lobsters and catch by the recreational fishery. The “X” length transition matrix is sex- and month-specific, with entries estimated externally using a growth model as described by McGarvey and Feenstra (2001). The SZRLF fishing season starts in October of each calendar year, and LenMod fits to monthly data available for each month over October-May aggregated over the entire fishing zone. The CPUE observation equation models linear proportionality to exploitable abundance, and separate catchability parameters are estimated for each of the eight months, with separate sets estimated for the period before and since inception of TACC (in season 1993). The version of LenMod that was used in Paper Three (appendix B of McGarvey et al., 2015; online supplementary material B for Paper Three),was non-spatial, estimated vulnerability by length-sex class as the product of a sex-specific logistic function of length class and a month-specific vulnerability proportion by sex. Parameter estimation is by maximum likelihood, and optimization was performed using Automatic Differentiation Model Builder (ADMB) which is a C++ software environment that is commonly used to optimize objective functions for fishery stock assessments in Australia and the world (Fournier et al., 2012; Punt et al., 2013; Dichmont et al., 2016a, 2016b).

Paper One

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Environmental influences on daily commercial catch rates of South Australia's southern rock lobster (*Jasus edwardsii*)

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ABSTRACT

The extent to which catchability of southern rock lobster (*Jasus edwardsii*) due to short-term environmental factors, rather than abundance, may be affecting legal-size catch rates from the South Australian Southern Zone rock lobster fishery was examined. Multivariate weighted linear regression was applied to daily aggregated commercial catch rates using several environmental covariates in addition to year and month. Model pruning via backward selection identified the following variables as being significantly related to catch rate: wave height and period, lagged wave height, bottom temperature, moon phase, and a spatial block index. These variables explained 7% of the total variance in log-transformed daily catch rates and another 84% was explained by month and year. A negative relationship was found between catch rate and each of bottom temperature and same-day wave height, while the relationships between catch rate and days prior to full moon, and average wave height over the past 3 days were positive.

Key words: catch rates, environmental variables, *Jasus edwardsii*, southern rock lobster, weighted regression

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INTRODUCTION

The southern rock lobster (*Jasus edwardsii*) fishery is the highest valued wild commercial fishery in South Australia being worth $81.3 million from 1557 tonnes of production for the 2010/2011 financial year (Knight and Tsolos, 2012). The fishery is divided into two management regions (Fig. 1), the Northern and Southern Zones (Linnane and Crosthwaite, 2009), the latter being the focus of this study. The zones are further sub-divided into Marine Fishing Areas (MFAs) for reporting purposes. The Southern Zone has provided around 80% of the total state rock lobster catch in recent years (Knight and Tsolos, 2012), the bulk of which was caught in MFAs 55, 56, and 58 (Fig. 1).

Both input and output controls are used to manage the Southern Zone fishery (Sloan and Crosthwaite, 2007). Fishing seasons extend from October to May of the following year (seasons are referred to here by start-of-season year) and lobsters below the minimum legal size of 98.5 mm carapace are returned to the water. Each fisher may own no more than 100 pots, and the total number of licences in the fishery is limited to 181. Since 1993, an annual total allowable commercial catch (TACC) system has been in place, with the TACC for the 2010 season set to 1250 tonnes (Linnane *et al.*, 2011). The current harvest strategy decision rule is designed to maintain exploitation rates at desired levels (Punt *et al.*, 2012). Catch per unit effort (catch rate) is used as the principal index of relative abundance in modelling and stock assessment for *J. edwardsii* fisheries in Australia and New Zealand. In South Australia, since 2011, the TACC quota for each fishing season is directly set via a tabular harvest control rule which takes, as input, nominal catch rate from the previous season. However, factors other than abundance may impact catch rates, and these are often assumed to act as a time-varying multiplicative factor on abundance, known as catchability (Arreguin-Sanchez, 1996).

Temperature is known to impact catch rates for many species of lobster. The most common result found in the literature is that of a positive association between catch rates (or catchability) and temperature for species such as *Homarus americanus* (McCleese and

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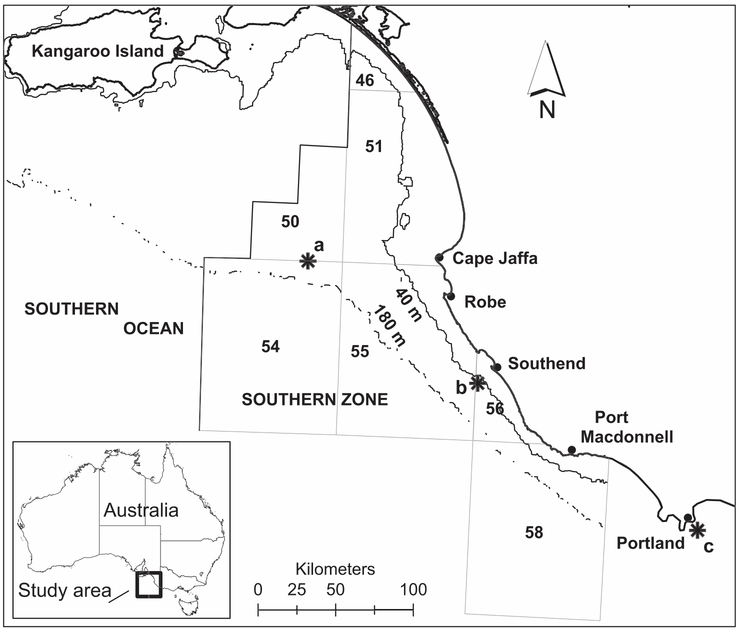


Figure 1. Fishery management region, MFAs, depth contours, and locations of main environmental data locations. Three sources of environmental data are indicated: (a) for waves, (b) for bottom temperature, and (c) for sea surface height (SSH) and wind.

Wilder, 1958; Drinkwater *et al.*, 2006), *Homarus gammarus* (Smith *et al.*, 1999; Schmalenbach, 2009), *Panulirus cygnus* (Morgan, 1974; de Lestang *et al.*, 2009), and *J. edwardsii* (Ziegler *et al.*, 2004). However, Courchene and Stokesbury (2011), who compared lobster trap catches with SCUBA dive surveys, reported a negative association between *H. americanus* catch rates and bottom temperature.

Ocean swell off the South Australian coast is associated with rapidly changing sea-states, including storm fronts that pass close to the coast (Middleton and Bye, 2007). Significant sediment re-suspension may occur along the continental shelf from high swells and bottom currents (Middleton and Bye, 2007). Fishers in Western Australia have reported that lobster daily catch rates were influenced by sea swell, wind strength, tidal movement and water turbidity (Morgan, 1974). In addition, sea swell on the days prior to fishing had a significant positive impact on catch rates of *P. cygnus* (Srisurichan *et al.*, 2005). A study of *Paribacus japonicus* catch rates also found a positive association with large swells (Yamakawa *et al.*, 1994). The literature on the relationship between ocean swell and catch rates for *J. edwardsii* is limited. However, South Australian rock lobster fishers anecdotally report improved catches on the days after a large swell.

The lunar cycle is reported to affect catch rates of other species of rock lobster, *P. cygnus* (Morgan, 1974; Srisurichan *et al.*, 2005) and *P. japonicus* (Yamakawa *et al.*, 1994), with higher catch rates generally linked to periods around the new moon. South Australian rock lobster fishers anecdotally report observations of improved catch rates in the days just prior to the full moon.

Wind-induced cold water upwelling is a regular feature of the South Australian Southern Zone fishery during November to March (Lewis, 1981; Schahinger, 1987), and may occur over periods of 3–10 days (Middleton and Bye, 2007). Known locally as the 'Bonney upwelling', upwelling reduces bottom temperatures and increases nutrient content, with oceanic water forced broadly up onto the relatively narrow continental shelf between Cape Jaffa and Portland (Fig. 1). In accordance with upwelling dynamics (Middleton *et al.*, 2007), correlations have been found among bottom temperatures, sea surface height (SSH), local alongshore winds, and alongshore currents for the Bonney Coast region, with lags ranging from 0 to 3 days (Schahinger, 1987).

The primary aim of this study was to examine the short-term catchability effects on daily catch rates, within the Southern Zone rock lobster fishery, of environmental variables including bottom temperature, waves, moon phase, wind, and SSH, with the outcomes also being of interest to the stock assessment of the fishery.

METHODS

Data

Commercial fishing data were recorded as daily totals by commercial fishers and entered into a daily logbook, submitted monthly. Compulsory reporting information includes fishing effort (daily potlifts) and landed catch in weight (kg) of live non-spawning legal-sized lobsters (Linnane *et al.*, 2011). Daily catch rates (kg potlift^{-1}) for the Southern Zone fishery were calculated for each day of fishing from October 1998 to May 2009, by first aggregating catch and effort over fishers for each day, and then dividing the total daily catch weight by the total daily potlifts.

Each fisher also reported daily depth, in the form of an average daily depth, and the principal MFA block where fishing took place. A spatial block index was computed to reflect the average MFA fished by all fishers on a given day, and similarly a single depth covariate was created by averaging the reported depths from all fishers. The spatial block index is a daily-aggregated quantity which was used to capture known biological trends, such as density and growth (McGarvey *et al.*, 1999), going from northwest to southeast along the coast in the study region. Integer values were assigned to each of the four main MFAs following sequentially along the coast, namely, 1 = 51, 2 = 55, 3 = 56, 4 = 58 (which make up >99% of the data), with the daily spatial block index calculated as the average of these integers over all fishers.

Environmental covariates included bottom temperature, wind, SSH, moon phase, and ocean wave (swell) information, with most data being at the sub-daily level of resolution. The period from midday to midday (midnight centred), rather than the more conventional midnight to midnight period, was used in the aggregation to the daily level. This period was selected because fishers set baited pots overnight and haul them in at first light over a 24-h period.

The wave data set was output from the WAVEWATCH III wind-wave model run by the US National Weather Service (http://polar.ncep.noaa.gov/). Outputs from the model were obtained for a location ~80 m deep (point ‘a’ in Fig. 1), from February 1997 to March 2010, and included wave height (m) and wave period (s).

Daily average bottom temperatures (°C) were compiled from hourly recordings from a TidBit bottom temperature logger, maintained by SARDI Aquatic Sciences, located at ~60 m depth off Southend (point ‘b’ in Fig. 1). These data extended from January 1999 to September 2009, although very few data exist between seasons 2003 and 2005 inclusive and for several months during seasons 1998, 2001, 2002, and 2006. Sea surface temperature (SST) was not used because, during summer, the water column is stratified by temperature (Lewis, 1981), and sharp upwelling events of cold bottom water flow onto the shelf that are not always shown in satellite SST photographs.

SSH (m) was sourced from a location along the coast at Portland (point ‘c’ in Fig. 1). The raw data, obtained from the Australian Bureau of Meteorology (BoM), were filtered to remove tidal effects and incoherent low energy fluctuations of little energy. Larger oceanic water movements such as coastally trapped waves and upwellings remained in the filtered SSH series. The data extended from February 1993 to March 2010, except January 1999, for which data was missing.

Wind data, also obtained from BoM, were sourced from Cashmore airport near Portland (point ‘c’ in Fig. 1). The data extended from January 1990 to September 2009, except for January 2000, which had no data. Components of the data include wind speed (m s^{-1}), wind direction (degrees True), and wind stress (Pascals) for total and alongshore directions (–45° True).

Moon phases were obtained by first accessing data on moon fraction illuminated at midnight from 1994 to 2009 from the US Naval Observatory website (http://aa.usno.navy.mil/data/docs/MoonFraction.php) for the Chamorro time zone which is 30 min ahead of the study region’s time zone. Eight discrete ordered moon phases were then created by defining eight periods per lunar cycle, each spanning a change of 25% in moon fraction illumination, with the first phase variable centred on 0% illumination describing the new moon period.

The number of days that could be used in the analysis was substantially reduced by the lack of data for some of the environmental covariates. Bottom temperature was the least available of all covariates which resulted in about a 50% reduction of sample days between 1998 and 2008. Days with data were also deleted if these would otherwise form very sparsely represented months or seasons. The final number of days in the model was 1258 (Table 1) with an overall geometric mean catch rate of 1.2 kg per potlift. Month values were defined from 1 to 8, in order from start to end of the fishing season (October to May), with month 9 being the off-season (June to September inclusive; May to September prior to 2003).

Model

The model assumes that lobster catch rate for day t, U_t, is a multiplicative function of K_t, daily catchability, and lobster abundance B_t, as follows:

Table 1. Number of days and geometric mean catch rate per fishing season and month, used in the modelling. Sn and Mn are the model fishing season and month.

	Mn 1 (October)	Mn 2 (November)	Mn 3 (December)	Mn 4 (January)	Mn 5 (February)	Mn 6 (March)	Mn 7 (April)	Mn 8 (May)	Off-season (June–September)	All
Sn 1998	0	0	0	9: 1.1	28: 1.0	27: 1.0	30: 0.8	0	0	94: 0.9
Sn 1999	30: 1.4	30: 1.5	29: 1.5	0	27: 1.3	27: 1.2	14: 1.4	0	0	157: 1.4
Sn 2000	30: 1.5	30: 1.6	29: 1.6	31: 1.7	28: 1.4	26: 1.4	9: 1.7	0	0	183: 1.5
Sn 2001	26: 1.6	30: 1.7	29: 1.9	29: 2.0	27: 1.6	0	0	0	0	141: 1.8
Sn 2002	0	0	0	24: 2.3	28: 1.7	29: 2.0	22: 1.9	0	0	103: 1.9
Sn 2003	0	0	0	0	0	0	0	0	0	0
Sn 2004	0	0	0	0	0	0	0	0	0	0
Sn 2005	0	0	0	0	0	0	0	0	0	0
Sn 2006	27: 1.4	27: 1.3	30: 1.4	19: 1.4	0	0	0	0	0	103: 1.4
Sn 2007	28: 1.2	30: 1.1	31: 1.1	31: 1.3	29: 1.1	31: 0.9	30: 0.7	31: 0.5	0	241: 1.0
Sn 2008	30: 0.7	30: 0.8	31: 0.8	30: 0.9	25: 0.8	31: 0.7	28: 0.4	31: 0.4	0	236: 0.6
All	171: 1.2	177: 1.3	179: 1.3	173: 1.5	192: 1.2	171: 1.1	133: 0.9	62: 0.4	0	1258: 1.2

$$U_t = K_t B_t \varepsilon_t, \tag{1}$$

where $\varepsilon_t \sim \mathrm{LN}(\lambda,\ \sigma_t^2)$ is the independently log-normally distributed observation error with distribution parameters $\lambda = 0$ and σ_t^2.

Equation 1 is linear when the catch rates are log-transformed (Venables and Dichmont, 2004):

$$y_t = \log(U_t) = \mu_t + e_t, \tag{2}$$

where y_t is a normally distributed response variable, with mean parameter $\mu_t = \mathrm{E}(y_t) = \log(K_t B_t)$, and variance parameter $\sigma_t^2 = \mathrm{Var}(y_t)$, with $e_t \sim \mathrm{N}(0,\ \sigma_t^2)$ being independently normally distributed errors. σ_t^2 is time-dependent to account for the existence of large variation in daily fishing effort (25th, 50th, and 75th percentiles of 2400, 7000, and 10 000 potlifts), and is modelled as $\sigma_t^2 = \sigma^2/\omega_t$, where ω_t is a variance weighting that is a function of potlifts (specified below). Multivariate linear regression was performed assuming a mean response $\mu_t = q_t + f_t$, where $q_t = \log(K_t)$ and $f_t = \log(B_t)$, with q_t and f_t linear combinations of environmental covariates and season-month terms, respectively. None of the days used in the analysis had a total daily catch weight of 0.

Regression weights

The unweighted ($\omega_t = 1$) regression exhibited a quantile–quantile (QQ) plot of standardised residuals (Fig. 2a) that indicated non-normality, and the plot of residuals versus daily potlifts (Fig. 2b) was non-homogeneous (right-skewed funnel shaped) with over-dispersion in residuals for days with low effort. Relative precision in catch rate was assumed to vary directly with fishing effort (daily potlifts), and a power function of potlifts was considered appropriate for the regression weights, $\omega_t = (\text{pots-lifted-on-day-t})^{1/m}$ ($m \geq 1$). A power function allows for a rapid monotonic increase (with daily potlifts) in the weighting over the lower range of potlifts and more slower increases among potlifts in the higher range. The larger the value of m, the less σ_t^2 is reduced for days with high potlifts relative to days with low potlifts. The condition $m > 1$ was suggested by cluster sampling considerations (Cochran, 1977), involving temporal change in inter-fisher variability and in spatial autocorrelation among catches of individual potlifts, as well as by the right-skewedness observed in Fig. 2b.

Analyses (results not shown) suggest that $m = 3$ was optimal by balancing outcomes from residual diagnostic plots and the small sample corrected Akaike's information criterion ($\mathrm{AIC_c}$). Compared with unweighted regression, $m = 3$ reduced both over-dispersion (Fig. 2d) and non-normality (Fig. 2c) in the residuals.

Model selection and implementation

The data were restricted to days for which all the covariates as well as fishery data were available, after which model pruning via backward selection was performed. Forward selection was not chosen as it potentially is more prone, than backward selection, to inappropriate exclusion of important subsets of covariates (Guyon and Elisseeff, 2003). $\mathrm{AIC_c}$ was used, as the ratio of number of days with data to the number of model parameters is small (<20) (Burnham and Anderson, 2002). At each step, the term deleted was the one resulting in the reduced model with the lowest $\mathrm{AIC_c}$, until deletion of any remaining terms decreased $\mathrm{AIC_c}$ by less than 2 units (Burnham and Anderson, 2002).

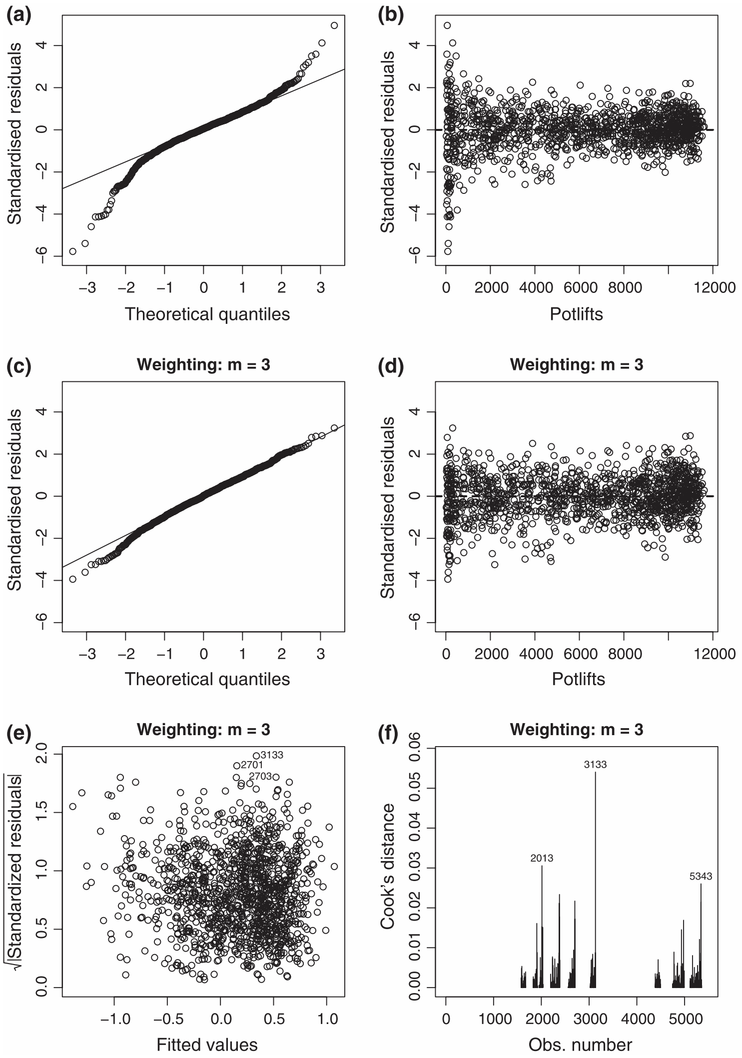


Figure 2. Final model diagnostic plots of standardised residuals. (a,b) QQ plot and dispersion versus daily potlifts plot, respectively, for the regression without weighting. (c,d) QQ and dispersion plots for the corresponding regression with weighting indexed by 'm' = 3. (e) Spread-location plot of the square root of absolute standardised residuals versus fitted values. (f) Influence plot of Cook's distances versus daily observation label.

After this a further step-wise selection process was performed by deleting, at each step, the term that decreased the weighted regression's adjusted proportion variance explained statistic (adjR^2) the least, until deletion of any remaining terms decreased adjR^2 by more than 0.25%. The adjR^2 criterion was applied to avoid retention of covariates that accounted for very little variability in the data (Maunder and Punt, 2004).

However, due to regression weighting the R^2 statistic does not exactly represent the proportion of variation explained in the log-transformed catch rates by the covariate data, but rather it is a measure of proportion of variation in weighted log-transformed catch rates that can be accounted for by the weighted covariates. This potentially results in a positive bias in R^2 because the weighted data are likely to be less noisy than the unweighted data (Willett and Singer, 1988).

The starting model included covariate main effects plus their bivariate interactions with fishing season and month. Included also were moving averages, lagged variously over 1–5 days, of wave height, bottom temperature, and alongshore wind stress, covariates thought, on *a priori* physical grounds, to be related in a potentially delayed way to catch rate. The initial model for the mean of log-transformed catch rates, to which were also added the interaction and lag terms, is as follows:

$$\mu_t = \mathrm{Sn} + \mathrm{Mn} + \mathrm{Sn} : \mathrm{Mn} + \mathrm{WaveH} + \mathrm{WaveP} + \mathrm{T} + \mathrm{Moon} + \mathrm{SSH} + \mathrm{Wtau} + \mathrm{WtauAS} + \mathrm{MFAi} + \mathrm{Depth}, \quad (3)$$

where *Sn* is fishing season (factor) and *Mn* is month (factor), hence Sn + Mn + Sn:Mn is a monthly time-trend component. *WaveH* is wave height, *WaveP* is wave period, *T* is bottom temperature, *Moon* is moon phase (factor), *SSH* is sea surface height, *Wtau* is total wind stress, *WtauAS* is alongshore wind stress, *MFAi* is average spatial block (index), and *Depth* is average depth.

The statistical software used for all the modelling was R [version 2.13.0 (2011-04-13) Copyright (C) 2011; The R Foundation for Statistical Computing ISBN 3-900051-07-0]. Standard diagnostic output plots of residuals were examined to identify influential data points, residual trends, and non-normality. The extent of autocorrelation in the residuals was also examined, which, for example, may exist due to data sampling being fisheries-dependent; this was done by plotting the autocorrelation and partial autocorrelation functions (ACF and PACF) of the residuals.

Inferences on catch rates

The ratio of mean catch rates was calculated to provide a relative measure of impact on estimated mean catch rate attributable to a given change in a particular covariate. The inter-quartile range (IQR) of each covariate quantifies the 50% range of observed daily values about the median, and provides a more meaningful comparison metric of change in covariates than unit change when different measurement scales are involved (e.g. 1 degree Celsius and 1 metre). Consider, for a given day t, the change in estimated mean catch rate, from $E(u_t)$ to $E(u'_t)$, due only to a change in the value of the ith covariate, $X_{t,i}$, when it is increased by an amount equal to its interquartile range, that is, $X'_{t,i} = X_{t,i} + \mathrm{IQR}_i$. The ratio of mean catch rates, $E(u'_t)/E(u_t)$, hence equals exp $(\mathrm{IQR}_i * \beta_i)$, where β_i is the estimated effect parameter, which follows from the definition of a log-normal mean, hypothetical constant levels of other covariates and fishing effort ($\sigma_t^2 = \sigma_t'^2$), for both catch rate models.

Since the logarithm is a monotonic function, and the probability distribution of β_i is approximately normal, the confidence interval for the ratio of mean catch rates, based on the standard errors of the estimated parameters involved and the IQR value, is given by

$$\exp(\mathrm{IQR}_i * \beta_i \pm t_{\alpha/2,n-k} * \mathrm{SE}(\beta_i) * \mathrm{IQR}_i), \quad (4)$$

where n is number of days, k is number of parameters, t is the t-statistic, and α is the significance level.

Data sensitivity models

Spatial heterogeneity in catch rates was explored by separately fitting the final model to aggregated catch and effort data divided either per inshore–offshore depth zone (<40 m and ≥40 m) or per MFA block (55, 56, and 58). Effects of spatial heterogeneity in bottom temperature were also investigated by separately fitting time-temperature sub-models (i.e., Sn + Mn + Sn: Mn + T) per MFA block (55, 56, and 58), using data from additional bottom temperature loggers at similar depth to the Southend logger (but with fewer data) situated off Robe (for MFA 55) and off Port Macdonnell (for MFA 58), in addition to the data from the Southend logger (for MFA 56). Two additional covariates were obtained from BoM for the purpose of examining causal influences for the moon phase effect; an 8 level cloud cover factor (0 for clear, 8 for totally overcast) and its interaction with moon phase were added to the final model, and another model involved substitution in place of moon phase the observed daily minimum sea level in metres above Tide Gauge Zero.

RESULTS

Final model

The model retained was

$$\begin{aligned}\mu_t = {} & \mathrm{Sn} + \mathrm{Mn} + \mathrm{Sn} : \mathrm{Mn} + \mathrm{WaveH} + \mathrm{WaveP} + \mathrm{T} \\ & + \mathrm{Moon} + \mathrm{MFAi} + \mathrm{Mn} : \mathrm{WaveH} + \mathrm{Sn} : \mathrm{T} \\ & + \mathrm{WaveHLagAvg}. \end{aligned} \quad (5)$$

The interaction terms Sn:T and Mn:WaveH were relative to 1998 and month 1, respectively. The only lagged covariate term selected was a moving average of wave height over a lag period involving the most recent 3 days (WaveHLagAvg). All retained terms were highly statistically significant. The total number of estimated parameters was 72.

Influential data points (Fig. 2f), violations of mean-variance homogeneity (Fig. 2e), and non-normality in residuals (Fig. 2c) were not detected, supporting the assumption of log-normally distributed observation errors for catch rates. Further diagnostic analyses (results not shown) indicated no high collinearity among covariates and no strong non-linearity in the response of log-transformed catch rates for any of the covariates, but residuals exhibited modest first-order autoregression (AR1 coefficient of 0.27). The latter outcome increased the magnitude of standard errors for effect parameters by between 4% and 21% in a generalised least squares formulation of the final model with a fixed AR1 covariance structure. Weakening the regression weights in the final model, by using 8 instead of 3 for m in ω_t, resulted in a decrease of 1.5% in adjR^2, while strong weighting by using an m value of 1 increased adjR^2 by 1.7%.

Variance explained by model terms

Each row in Table 2 provides statistics comparing a model that differs from the final model only by omission of the regression terms indicated. The (adjusted) proportion of total variance in log-transformed catch rates explained by all the terms (including time) in the final weighted regression model was 91.3%. Exclusion from the final model of all the covariates resulted in a loss of 7.0% explained variance, leaving 84.3% of total variance attributable to the time-trend with the season factor explaining more variance than the month factor. Exclusion of only all the wave covariates (height and period) indicated that these were the most important environmental covariates explaining in total 2.5% of variance. Similarly, 0.9%, 1%, and 1.3% of variance were explained by each of moon phase, temperature, and MFAi, respectively.

Table 2. Impact of excluding given combinations of terms from the final model.

Term excluded	Increase in AICc	Decrease in adjR^2	Estimated parameters
None (final model)	0	0	72
MFAi	176.5	0.013	71
Moon	117.7	0.009	65
Sn:T	29.5	0.003	65
T + Sn:T	121.1	0.010	64
WaveP	175.3	0.013	71
WaveHLagAvg	65.7	0.005	71
Mn:WaveH	70.2	0.006	65
WaveH + Mn:WaveH	193.5	0.015	64
WaveH + Mn:WaveH + WaveHLagAvg	223.0	0.018	63
WaveP + WaveH + Mn:WaveH + WaveHLagAvg	303.6	0.025	62
All covariate terms (time-only model)	709.4	0.070	46
Mn + Sn:Mn + Mn:WaveH	1067.0	0.125	27
Sn + Sn:Mn + Sn:T	2281.3	0.469	27

Waves

Table 3 provides the ratios of relative impact on mean catch rates from IQR increases in covariates, and the corresponding confidence intervals. Prediction intervals (uncertainty for catch rates per random individual day) were also calculated for all covariates, and these were an order of magnitude or more wider (results not shown) than the confidence intervals, reflecting high overall daily variability in catch rates. The estimated coefficients for same-day wave height were negative for months 3–8, but negligible for months 1 and 2, with coefficients of variation indicating high relative uncertainty. The largest effect was during month 8 when a 1.1 m increase in wave height resulted in an estimated reduction to mean catch rate of 14% (95% CI: −18 to −10). IQR did not vary much between months, meaning that an increase in wave height of 1.1 m (used for each month) is reasonably representative for any of the months.

Table 3. Coefficient estimates, coefficients of variation (CV), and effect impacts on mean daily catch rates for given interquartile range (IQR) increases in covariates. Provided also are 95% confidence (CI) interval limits. IQR column values in brackets refer to IQRs specific per time period but were not used in calculations.

Final model term	Estimate	CV	exp(IQR*Est.)	95% CI	IQR
WaveH + Mn1:WaveH	−0.013	0.88	0.98	0.96, 1.01	1.1 (1.1)
WaveH + Mn2:WaveH	0.010	1.27	1.01	0.98, 1.04	1.1 (1.1)
WaveH + Mn3:WaveH	−0.094	0.14	0.90	0.87, 0.93	1.1 (1.0)
WaveH + Mn4:WaveH	−0.094	0.14	0.90	0.87, 0.93	1.1 (1.1)
WaveH + Mn5:WaveH	−0.089	0.16	0.90	0.88, 0.93	1.1 (1.0)
WaveH + Mn6:WaveH	−0.059	0.23	0.94	0.91, 0.96	1.1 (1.1)
WaveH + Mn7:WaveH	−0.097	0.15	0.89	0.87, 0.92	1.1 (1.1)
WaveH + Mn8:WaveH	−0.133	0.16	0.86	0.82, 0.90	1.1 (1.3)
T + Sn1998:T	−0.101	0.18	0.80	0.74, 0.86	2.2 (2.2)
T + Sn1999:T	−0.020	0.61	0.96	0.91, 1.01	2.2 (1.6)
T + Sn2000:T	−0.069	0.13	0.86	0.83, 0.89	2.2 (2.0)
T + Sn2001:T	−0.021	0.51	0.95	0.91, 1.00	2.2 (1.9)
T + Sn2002:T	−0.123	0.21	0.76	0.68, 0.85	2.2 (0.6)
T + Sn2006:T	−0.090	0.26	0.82	0.74, 0.91	2.2 (1.3)
T + Sn2007:T	−0.038	0.33	0.92	0.87, 0.97	2.2 (2.5)
T + Sn2008:T	−0.027	0.34	0.94	0.90, 0.98	2.2 (2.2)
WaveHLagAvg	0.045	0.12	1.05	1.04, 1.06	1.0
WaveP	0.035	0.07	1.07	1.06, 1.08	1.9
MFAi	−0.250	0.07	0.95	0.94, 0.95	0.2

Wave period was estimated with a positive coefficient with mean catch rate increasing by 7% (95% CI: 6–8) for an increase of 1.9 s in period. Model selection indicated both wave period and wave height covariates helped explain the data, although there was minor positive correlation between these data sources (Pearson $r = 0.33$, $P < 0.001$).

A positive coefficient was estimated for average wave height over the previous 3 days, which implies that the larger the average swell over the last 3 days, the larger the estimated mean catch rate on the day of fishing. For an increase of 1.0 m in lagged average wave height, an increase in mean catch rate occurs of 5% (95% CI: 4–6). Lags of 3 and 4 days were determined most appropriate using AIC_c and adjR^2 (Fig. 3).

The final model applied separately to catch rate data restricted inshore and offshore indicated a stronger (particularly for same-day) result inshore than offshore, with exclusion of WaveH + Mn:WaveH offshore decreasing adjR^2 by only 0.2% (increasing AIC_c 7) but inshore decreasing adjR^2 by 3.4% (increasing AIC_c 329). The MFA-specific model did not show as strong a contrast in results, although exclusion of WaveH + Mn:WaveH in MFA 58 decreased adjR^2 by 3.2% (increasing AIC_c 312) compared with 0.9% (76) and 1.0% (109) for MFAs 55 and 56, respectively.

Temperature

A negative effect was estimated for all seasons in response to an increase in temperature. For example, an increase of 2.2 °C during fishing season 2000 was estimated to decrease mean catch rate by 14% (95% CI: −17 to −11) (Table 3). Temperature effects, all of which were negative, varied considerably among fishing seasons, with weakest impact during 1999 and 2001. IQR in temperature also varied substantially among fishing seasons (Table 3), implying that an increase in temperature of 2.2 °C is not equally likely for all seasons.

The same qualitative results were obtained by fitting the final model to inshore–offshore and MFA-specific catch rate data sets, and from the three MFA-specific temperature sub-models, indicating no major spatial differences. All these sensitivity models provided strong support (>10 increase in AIC_c and >0.5% decreases in adjR^2) for a negative temperature effect on catch rates.

Moon phase

The estimated effect of a change in moon phase on mean catch rate is approximately cyclic, increasing up to and including the phase prior to the full moon, at which a 10% increase on new moon mean catch rate is achieved (Fig. 4). Mean catch rate decreases steadily after full moon, to 4% below the new moon levels for phases between the full and new moons.

Separate models by inshore–offshore and MFA indicated trivial differences spatially in the moon phase effect. Inclusion of cloud cover increased AIC_c by 84 and contributed trivially to adjR^2. Excluding moon phase and adding either minimum tide levels or high-low tidal differences increased AIC_c by over 100,

Figure 3. AIC_c statistics for a range of models differing in the lagged moving average wave height covariate as a function of the lag averaging period.

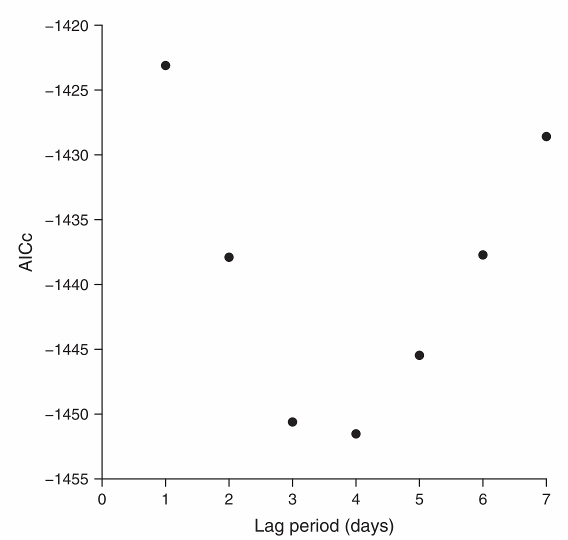
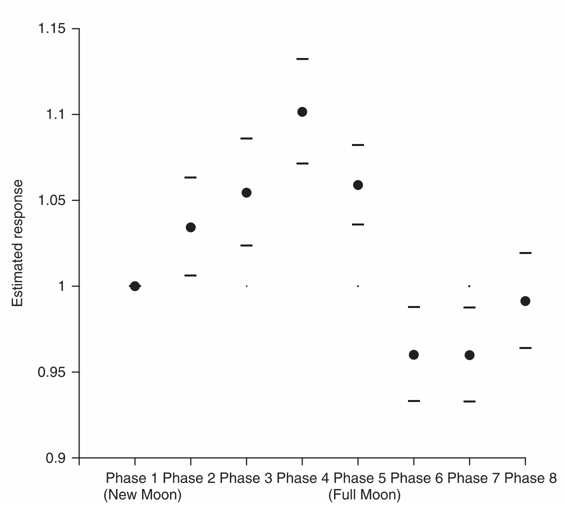


Figure 4. Final model estimated relative (to the new moon) mean catch rate response by moon phase and the 95% confidence intervals.



suggesting that these covariates, although related to moon phase, do not capture the process which impacts catch rates.

Spatial block index

The spatial block index covariate in the final model was estimated with a negative coefficient (Table 3), reflecting higher catch rates further north along the Bonney Coast. However, the inshore–offshore analysis revealed that this spatial block effect inshore was not supported. Exclusion of the term MFAi from the inshore model led to a reduction in AIC_c by 2.2 and trivial changes in adjR^2, compared with an increase in AIC_c of 160 and a decrease in adjR^2 of 1.7% for the offshore model.

DISCUSSION

This study identified several environmental variables which impact on the daily catch rates of *J. edwardsii* within the Southern Zone rock lobster fishery of South Australia. These variables were wave height and period, lagged wave height, bottom temperature, and moon phase. Given the specified regression weighting by potlifts, these variables, together with a spatial block index, explained 7.0% of total variance in log-transformed daily catch rates. Another 84.3% was explained by a time-trend involving season and month.

A similar outcome was obtained from an analysis which applied the methodology in this paper to a smaller but equivalent data set for the Western Zone rock lobster fishery of Victoria (results not shown). A negative relationship was found between catch rate and each of bottom temperature and same-day wave height, whereas the relationship to same-day wave period and average wave height over the past 3 days was positive, but moon phase was not retained in the final model.

The time–environment interaction terms Mn:WaveH and Sn:T may be influenced by longer term changes in catch rates, due to both abundance and catchability potentially varying on longer time scales, and between which the model cannot easily distinguish (Maunder and Punt, 2004). However, model sensitivity which excluded the time–-environment interaction terms provided similar environmental effect outcomes (results not shown) to those from the final model. A further sensitivity test was then conducted that excluded all interaction terms involving time (Mn:WaveH, Sn:T, and Sn:Mn) to obtain a less ambiguous time-trend index (Hinton and Maunder, 2004), which produced a yearly effect pattern (Fig. 5) exhibiting only minor differences from the pattern in the yearly log-transformed catch rate data.

To gauge the impact of using catch rate data at the fine scale of individual fisher records, a sensitivity model was run based on the final model that included a factor variable with fisher licence identifiers as levels, and which had term MFAi replaced with a factor variable with MFA block label as levels. For each of the covariates the qualitative outcome of this run was fully concordant (results not shown) with those from the daily aggregated analysis presented in this paper. Although all estimated terms were strongly retained according to AICc, the model only explained 57.5% of total variance in log-transformed fisher catch rates, with the time-trend involving season and month explaining 43.6% and environmental variables 2.9%. Maunder and Punt (2004) reported that the R^2 statistic would generally be greater for a coarser level of data aggregation than at a finer resolution. Note that the estimated MFA coefficients showed a negative linear trend with MFA block (Fig. 6), supporting the use of a single linear spatial coefficient (MFAi) in the final model. The year effect pattern (Sn), obtained from a version of this model that excluded all the interaction terms, also exhibited (Fig. 5) relatively minor differences with the pattern in the yearly log-transformed catch rate data. As the available environmental data were not measured per individual fisher, this paper used daily fisher-aggregated catch rates.

Figure 5. Estimated mean catch rate response (log-transformed) by fishing season for the final model excluding interactions (solid line), final model excluding interactions using individual fisher data (dashed line), and log-transformed data catch rate (empty squares). Data catch rates were calculated as season total catch/total potlifts, and model series were scaled to have an equal mean with the data series.

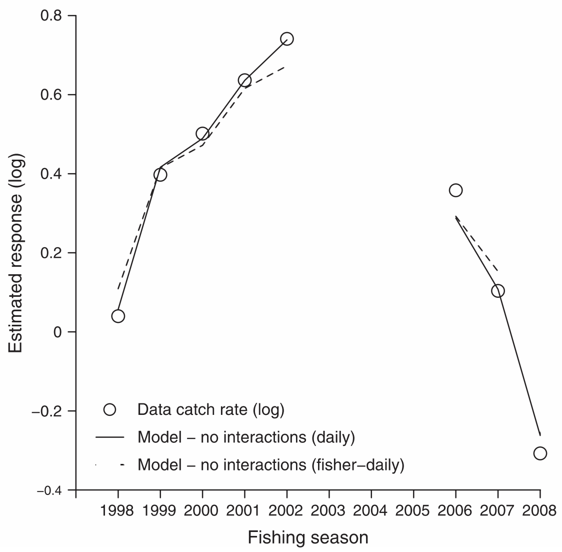
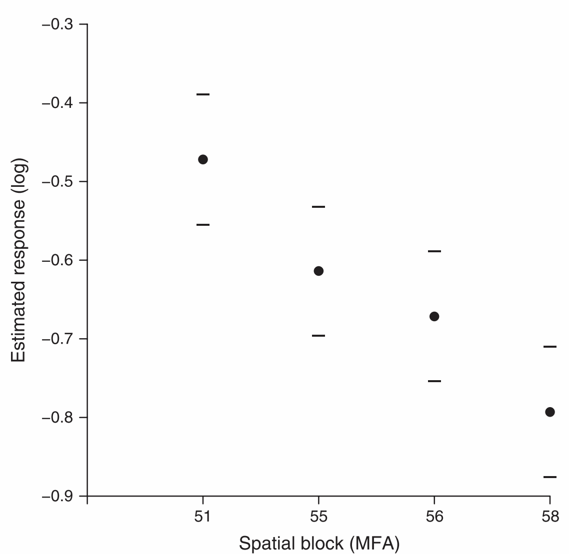


Figure 6. Estimated mean catch rate response (log-transformed) by coastal MFA block for the final model using individual fisher data and the 95% confidence intervals.



The impact on modelling outcomes of within-year smoothing of the time-trend was examined to help determine the extent of confounding influences on the estimation of environmental effects. The discrete monthly term Mn + Sn:Mn was replaced with a natural cubic spline smoothing function (Venables and Dichmont, 2004) for the final model but without the time-interaction terms. All of the environmental effects were strongly retained by AIC_c (>10), and signs of all estimated coefficients were unchanged for each of the three models (results not shown), defined by approximate levels of time-trend smoothing for weekly (adjR^2 = 92.6%, very flexible), monthly (90.5%, discrete monthly was also 90.5%), and linear (84.3%, least flexible) trend. The adjR^2 values in the same three models due to all environmental effects combined (and temperature, moon phase) were 4.6% (0.4%, 0.1%), 5.7% (0.6%, 0.9%), and 7.5% (2.3%, 0.9%), respectively. The weekly time-trend appeared very choppy, while also confounding with moon phase substantially (as expected). But the linear time-trend was too simple to account enough for longer term processes that occur throughout the fishing season (discussed below), as was indicated by a notable trend in the residuals across days within season (figure not shown).

Waves

The results indicate that daily mean catch rate is lower when waves are higher, but that mean catch rate is also lower when the average wave height over the previous 3–4 days was lower. Srisurichan *et al.* (2005) reported a similar outcome for *P. cygnus* concerning a positive response of legal-sized catch rate to lagged wave heights, and noted that swell may produce conditions favouring greater protection from predators by increasing bottom turbidity and food availability.

Weissburg and Zimmer-Faust (1993) found that predation by blue crabs (*Callinectes sapidus*) was optimal in slow-flowing water, and Cobb (1995) suggested that turbulence and greater fluid velocities make it harder for crustaceans to follow bait odour trails. Hence, the feeding ability of lobsters may be reduced during a swell when turbulence is greatest, leading to a reduction in same-day catch rates. The wave height effect was much stronger inshore, which may relate to greater turbulence when waves pass through shallower water.

It is not clear why the same-day wave height effect is insubstantial in October and November. An explanation for the positive effect of same-day wave period is also not clear, though this result does imply that mean catch rate increases when waves pass less frequently.

Temperature

Bottom temperature was found to have a negative effect on mean catch rate across season and spatial location, after taking into account the factor month, which incorporates some aspect of the temperature cycle. This finding is contrary to most studies in the literature on lobsters which report a positive association between catch rate and temperature (see Introduction). However, Courchene and Stokesbury (2011) reported a similar result for *H. americanus* comparing catch rates at optimal versus extreme temperatures, concluding that catchability was impacted via reduced lobster mobility at high temperatures, and noting also that increased lobster growth rates at such temperatures may result in avoidance of traps by moulting lobsters. But the modelling in our study did not indicate that the negative effect of temperature on catch rate was restricted to particular months such as those known for moulting or cold-water upwelling (term Mn:T was not retained). In addition, catch rates were observed to decline over quite a large temperature range of 12–17 °C (total range 9.5–17.6 °C, median 14.2 °C; figure not shown), although variables other than temperature also may have contributed to the noted decline.

Indeed, some confounding in the relationship between catch rates and environmental catchability variables is suggested due to the processes of population growth and population depletion by fishing pressure. For the Southern Zone fishery, bottom temperatures are low at the onset of summer (Lewis, 1981) and the legal-sized population is incremented by lobsters growing into legal-size during the previous (warmer) months of October–November (MacDiarmid, 1989), whereas for the rest of the season, bottom temperatures are higher and population depletion occurs due to continued fishing pressure. Hence during the early part of the season, temperatures are higher and catch rates lower than in summer with the highest catch rates and lowest temperatures, after which temperature rise and catch rates fall to lowest levels by end of season. This implies that the estimated negative effect on catch rate attributed to temperature may be confounded with the processes described above. Indeed, total variance explained by temperature increased to 5.1% for a main effects version of the final model that was without the month factor terms, but for which plots of residuals versus month (figure not shown) indicated a clear trend and suggests the existence of important unmeasured influences.

Moulting of *J. edwardsii* takes place over a period of several weeks (Musgrove, 2000), as does the impact on the region's population due to fishing, and these longer term processes are accounted for by the estimated monthly time-trend (Sn + Mn + Sn:Mn) component in the model. The results of the spline modelling (see above) showed that the difference in variance explained, due to temperature, between the linear and the monthly time-trend models was much greater than between the monthly and weekly models. Yet this may indicate remaining minor unmeasured confounding influences on the shorter time-scales or else that too much variability in log-transformed catch rate was smoothed out by the weekly time-trend (as was the case for moon phase). Note that the estimated temperature effect on catch rates may also be confounded on the time-scale of between seasons. Total variance explained by temperature was 5.9% for a main effects version of the final model that was without the season factor terms; this, however, also exhibited a trend in residuals versus season (figure not shown) that was close to the trend in data log-transformed catch rates, implying that unmeasured influences are likely to be dominant on this time-scale.

A metabolic index known as the aerobic scope for activity (SFA), which is a physiological measure of spare capacity to do sustained work (Crear and Forteath, 2000), suggests a potential mechanism influencing catch rates via dependence of SFA on ambient bottom temperature. The SFA expresses the relationship between active and standard respiratory consumption of an animal, impacting on motor performance and behaviour, and differs between species and within species spatially (Crear and Forteath, 2000; Lagerspetz and Vainio, 2006; Drinkwater *et al.*, 2010). All organisms have an optimal temperature range, and for laboratory-held intermoult *J. edwardsii, the* SFA was reported by Crear and Forteath (2000) as increasing from 5 °C up to a maximum at the acclimatised temperature of 13 °C, beyond which it dropped to 21 °C. Crear and Forteath (2000) noted that 13 °C is not an atypical ambient temperature for *J. edwardsii* in its natural environment (median of 14.2 °C in our study) and implied it may be near its preferred temperature. Maximum SFA frequently exists at the preferred temperature (Lagerspetz and Vainio, 2006), which, if as assumed, occurs around 13 °C, suggests that activities such as foraging, including the finding of bait, may be less effective above this temperature.

An alternative explanation is that temperature acts as a proxy index for another (unmeasured) variable impacting on catch rates. Changes in bottom temperature in the Bonney Coast region are linked with changes in other variables such as current velocity (Schahinger, 1987), salinity, dissolved oxygen, and nitrate concentrations (Lewis, 1981), which may impact on lobster catchability or activity (Morgan, 1974; Zimmer-Faust *et al.*, 1984; Cobb, 1995; Crear and Forteath, 2000).

Moon phase

Mean catch rate was estimated to be highest during the phase just prior to the full moon and lowest prior to the new moon, regardless of spatial location or cloud cover. This contrasts with a Tasmanian controlled field experiment study on size-dependent trapping inhibition of *J. edwardsii,* which found no significant difference in spring sublegal-sized catch rates (for either sex) between the new moon and full moon (Ihde *et al.*, 2006). The finding that catch rates for some other species of rock lobster are affected by moon phase is substantiated in the literature (Morgan, 1974; Yamakawa *et al.*, 1994; Srisurichan *et al.*, 2005), although these involved peak catch rates around the new moon. There exist studies on catch rates of other crustaceans that do indicate the same timing in relation to moon phase found in the present study. For example, Courtney *et al.* (1996) working on eastern king prawns (*Penaeus plebejus*) found that catch rates peaked shortly before the full moon and declined for about 7 days afterwards, especially for males, implicating potential sex-specific factors.

In terms of nightly movement activity of *J. edwardsii*, MacDiarmid *et al.* (1991) found no significant correlation between the proportion of lobsters active at night in New Zealand and the number of hours of moonlight. Similarly, Williams and Dean (1989) reported no increase in the length of the lobster active period when hours of darkness in summer were increased to match the winter length of darkness. The present finding concerning the pattern of timing connecting catch rates to moon phase, together with the above studies, suggest that a moon phase effect on catch rates is likely to involve more than a direct response to moon light levels alone, such as a degree of endogenous timing (Williams and Dean, 1989).

Spatial block index

An outcome of higher estimated catch rates further north along the Bonney Coast was found, and determined to apply mainly for offshore waters (>40 m depth). This appears not to be directly related to known higher mean lobster weight further north (McGarvey *et al.*, 1999), as exploratory data analyses provided little indication of a difference between inshore and offshore in mean weight trend with spatial block index. Alternatively, the number of lobsters offshore may be greater further northwest, and that inshore there is a more uniform spatial spread. Evidence for this comes from spatial mapping of catch rates of legal-sized lobster from fishery-independent sampling (Linnane and Crosthwaite, 2009; Linnane *et al.*, 2011), indicating patches of very high catch rates offshore and particularly further north.

Conclusions for stock assessment

Overall, the outcome is that of a real, but comparatively small, impact on daily catch rates of *J. edwardsii*, due to short-term environmental catchability effects, for South Australia's Southern Zone fishery. This study could not confirm that environmental variables were the likely cause, through catchability, of major changes in catch rates such as the steep decline observed over the period 2003 to 2009 (Linnane *et al.*, 2010). It should be noted that modelling did not explicitly incorporate longer term influences due to growth or fishing practices.

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Paper Two

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Statement of Authorship

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Name of Principal Author (Candidate)	John Feenstra
Contribution to the Paper	Performed and conceived the analysis, interpreted data, wrote manuscript, and acted as corresponding author.
Overall percentage (%)	90%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.
Signature	Date 15/08/2018

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Impacts on CPUE from vessel fleet composition changes in an Australian lobster (*Jasus edwardsii*) fishery.

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Impacts on CPUE from vessel fleet composition changes in an Australian lobster (*Jasus edwardsii*) fishery.

ABSTRACT

The Australian Victorian Western Zone rock lobster fishery is assessed using standardised catch-per-unit-effort (CPUE). Nominal CPUE declined over 1978-2009, but this underrepresents the estimated decline in abundance, while since 2009 standardised CPUE rose notably less than nominal CPUE. We identify vessel as a key factor that explains the discrepancy between nominal and standardised CPUE. The composition of the fleet changed since 2009, under the pressure of constraining total allowable catch quotas, with vessels exiting the fishery having substantially lower estimated catchability, which increased the average fishing power of the fleet. New diagnostic indices were constructed to quantify discrepancies between trends in nominal and standardised CPUE that assisted in identifying periods during which both catchability and vessel composition changed.

KEYWORDS: southern rock lobster, *Jasus edwardsii*, entry and exit of vessels, rising catchability, fleet dynamics, standardised CPUE

Introduction

In Victoria, Australia, the Western Zone rock lobster fishery (WZRLF) for *Jasus edwardsii* is divided into three regions for assessment purposes, extending east from the Victorian border with South Australia to Apollo Bay (Figure 1; Linnane et al. 2016). Commercial fishing is undertaken using baited pots that are generally set and hauled within 24 hours, with the fishing year extending from mid-November to mid-September (Linnane et al. 2016). Management measures include a minimum legal size, protection of ovigerous females and limited access, and since 2001, a Total Allowable Commercial Catch (TACC) based on individual transferable quota (ITQ) units, and restrictions on the number of licences and pots (VDPI 2009; VFA 2017).

Catch rates, or catch per unit of effort (CPUE), is taken as a relative index of biomass, and used to set annual TACCs in other *J. edwardsii* fisheries off southern Australia (DPIPWE 2015; McGarvey et al. 2016) and New Zealand (Breen et al. 2008; Breen et al. 2009). Nominal yearly CPUE, computed here as total reported yearly catch divided by total yearly effort, may deviate substantially from the true trend in biomass if catchability varies over time (Punt et al. 2013), in which case a process of "standardisation" is applied to obtain a more representative index of biomass trend (Maunder & Punt 2004). In the WZRLF, TACC-setting procedures have used standardised CPUE as a primary input (Linnane et al. 2016; VSG 2017; VFA 2017).

In reviewing the WZRLF harvest strategy (VFA 2017), it was observed that nominal CPUE rose more substantially than standardised CPUE since 2009. We examine the hypothesis that changes over 1978-2014 in the composition of the fleet led to changes in average catchability (c.f. Hilborn and Walters 1992), particularly since 2009 when vessels of low fishing power left the fishery. The aim of this study was to identify the most influential factors involved in the differences in trends between nominal and standardised CPUE, and to investigate the above hypothesis concerning the role of fleet entry and exit dynamics on catchability.

Materials and Methods

Daily commercial fishing data are fishery-dependent and since 1978 have been reported in mandatory logbooks that are submitted monthly (VDPI 2009, VFA 2017), as landed (live, legal sized, non-spawning) lobster catch (kg) and fishing effort expended (number of pot lifts). Since introduction of quota management in 2001, fishers are additionally required to weigh and report their catch within 20 minutes after landing via a telephone based interactive voice response system, and enter details in catch disposal records (VFA 2017). The covariates used in the standardisation of CPUE were fishing year (1978-2014), month (November to July individually, August-September combined), as well as available fisheries information that was assumed to potentially impact CPUE namely depth category (< 40 m, >= 40 m), region (Portland, Warrnambool, Apollo Bay; Figure 1), fisher identifier (237 fishers), and vessel identifier (500 vessels). The daily catch records were pre-processed, which involved removing records with incorrect or missing covariate data, followed by removal of fishers present in the fishery for less than 200 days in total or who fished during fewer than three fishing years (to reduce the influence of inexperienced fishers). Subsequently records were removed that had no catch (0.8%). Nominal yearly CPUE was then computed as the ratio of total annual catch to total effort.

A generalised linear model (GLM) was fitted to 347,259 data points, assuming a gamma error distribution and a log-link function (Maunder & Punt 2004):

$$CPUE \sim Year + Month + Region + Depth + Fisher + Vessel \qquad (1)$$

Alternative error models (gamma inverse, lognormal, normal), were tested, but did not result in improved residual diagnostics or AICc (results not shown). Also tested were three models with two-factor interactions, namely *Month:Depth*, *Month:Region*, and *Depth:Region*. These however, only explained an additional 0.14%, 0.17%, and 0.06% deviance and trivially impacted the estimated year trend (results not shown). Model fitting was conducted in R 3.3.2 (R Core Team, 2016) using function *glm* from package *stats*. Backward model selection was performed starting from the full model (Equation 1), and an increase of less than 2 units in AICc (Burnham & Anderson 2002) was used to identify redundant terms.

The standardised CPUE index was calculated as the exponential of the *Year* effect, which was assumed to indicate the yearly trend in lobster biomass. 95% confidence intervals were constructed for each year as the exponential of lower and upper limits of the 95% confidence intervals on *Year*. The index was scaled to have a mean (over 1978-2014) equal to that of the nominal CPUE. Given the focus of this study on analysing differences between nominal and standardised CPUE, an index, *V*, was constructed to more easily identify annual changes in these differences. *V* is a measure of annual relative change in nominal CPUE due to modelled factors unrelated to abundance (i.e. catchability and observation error), and is defined as follows:

$$V_y = \frac{(CPUE_y^N - CPUE_y^S) - (CPUE_{y-1}^N - CPUE_{y-1}^S)}{CPUE_y^{\mathrm{N}}} \qquad (2)$$

where $CPUE_y^{\mathrm{S}}$ is the standardised (and scaled) CPUE for year *y*, and $CPUE_y^{\mathrm{N}}$ is the nominal CPUE for year *y*.

A yearly "influence" index for the *Vessel* effect was calculated following the approach of Bentley et al. (2012), as the exponential of the weighted (by record count) mean *Vessel* coefficient (normalised to a value of 1 over 1978-2014). The net impact on yearly CPUE also depends on sources of catchability other than *Vessel*, and hence two additional influence indices were constructed to assist analysis: the product of influence values for all non-year covariates other than *Vessel*, and the product of influence values over all the non-year covariates (total catchability).

The consequences of changes in fleet composition were examined in more detail using influence indices for three subsets of the fleet in each year: vessels that make their initial entry into the fishery ("Entering"), vessels that leave the fishery ("Exiting"), and all other vessels ("Remaining"). These three influence indices were calculated for vessels that were in the fishery for more than one year, and as the exponential of the weighted (by record count) mean vessel coefficient, divided by the exponential of the weighted mean over all vessels ("Entering", "Exiting", and "Remaining" combined) and years (1978-2014), followed by smoothing to improve visualisation of trends using a second-order moving average.

Results

Each of the covariates was retained in the final model, which explained 46.8% of the deviance. Residual diagnostic plots did not suggest any substantial model violations, although some departure from normality was evident in the standardised deviance residuals at the extreme ends of the theoretical quantile range (Figure S1). *Year* explained relatively little deviance compared to either *Vessel* and *Fisher* combined or *Month*, while there was significant anti-correlation between estimated coefficients for *Vessel* and *Fisher* (Pearson -0.49, Spearman -0.47, over fitted data points), with these covariates not explaining much of the deviance on their own (Table 1). Removal of either *Vessel* or *Month* from the model led to a change in the trend of standardised CPUE towards that of nominal CPUE, with the effect of *Vessel* being greater than that of *Month* (Figure S2). Removing each of *Fisher, Depth*, or *Region* had only minor effects on the trend (Figure S2). These outcomes suggest that *Vessel* most directly impacts on nominal CPUE.

Nominal CPUE underrepresents the decline in estimated abundance inferred from standardised CPUE during 1979-1987 and 1991-1998, while exaggerating a rise in abundance during 2009-2013, the extent of which is indicated by positive values of V (Figure 2). The nominal CPUE series presented in Figure 2 is based on a ratio estimator, which was compared with nominal CPUE calculated as a geometric mean revealing a similar trend with the latter approximately 5% lower over 1978-1981 and 6% higher over 2010-2013 after rescaling to a common mean (Figure S3).

Figure 3A shows a marked increasing trend in the *Vessel* influence during 1979-1987, when the non-vessel influence was more stable. In contrast, both *Vessel* and non-vessel influences exhibit an upward trend during 2010-2012, which led to increasing catchability over this period. Catchability declines during 1988-1991 because even though *Vessel* influence rises over these years, this is more than offset by the decline in non-vessel influence. *Fisher* influence increased markedly over 1991-1998 (Figure S4), contributing to a rise in catchability due to non-vessel influences (Figure 3A). Nominal CPUE remains relatively stable during 1992-1995 while standardised CPUE declines (Figure 2), which is driven by a rapid increase in total catchability that is due more strongly to the rise in *Vessel* influence than by the rise in non-vessel influences (Figure 3A).

Influence values of vessels that permanently exit from the fishery in most years is well below that of the rest of the fleet (Figure 3B). Vessels leave during a period when total vessel influence increases (Figure 3A). For example, the exiting vessels have consistently lower fishing power than the other vessels before 1987 and during 2009-2012 (Figure 3B). In contrast, the magnitude of the discrepancy in fishing power between entering and exiting vessels during 2005-2009 was small, with exiting vessels having slightly more power (Figure 3B), and total vessel influence was relatively flat (Figure 3A). However, catchability decreased substantially during 2005-2009 due to decreasing influence from non-vessel sources of catchability (Figure 3A), and nominal CPUE decreased more rapidly over this period than standardised CPUE (Figure 2).

Although the yearly vessel entry-exit dynamics is volatile, fleet size grew until 1989, and declined steadily thereafter (Figure 4). Since 1998, the number of vessels exiting the fishery is notably higher than the number entering (Figure 4), with the latter declining rapidly just prior to introduction of TACC in 2001 and again during 2006-2009 when the fishery restructured and the level of TACC dropped substantially (VFA 2017).

The dynamics of changing fleet composition over time in the WZRLF was evaluated further by plotting for each year a kernel density function of the exponential of *Vessel* coefficients based on the count of daily fishing records per vessel (Figure 5). Three pertinent trends in these distributions were evident for the period 2001-2014: (1) lower total number of days fished since 2009 (less area inside each violin distribution); (2) a smaller proportion of vessels with low fishing power since 2009; (3) no evidence of new vessels increasing the maximum fishing power.

Discussion

There are notable periods of increasing divergence between nominal and standardised CPUE over 1978-2014 (Figure 2), linked with periods of increasing or decreasing catchability determined predominantly by the *Vessel* effect with periods of increasing catchability more prevalent including during 2009-2013 (Figures 2, 3A). A greater proportion of vessels in 2010-2013 had higher fishing power compared to vessels in 2001-2009 (Figure 5), which was driven primarily by less efficient vessels exiting the fishery after 2009 rather than more efficient vessels entering the fishery as quantified in figures 3B and 4.

The trend in standardised CPUE will be biased upwards by technology “creep” over time in individual vessels (Ye and Dennis 2009). However, this study cannot draw conclusions regarding impacts of technology upgrades on individual vessels because changes in fleet composition relate to differences in catchability among vessels, but we lack data on vessel characteristics (e.g. terrain detection equipment, plotter software) required to model changes in fishing power by vessel (Ye and Dennis 2009; Hoyle and Okamoto 2011).

Studies on other fisheries have drawn similar conclusions regarding an upward trend in catchability of CPUE having been substantially induced by less effective vessels leaving the fishery. These include O’Neill and Leigh (2007) and Braccini et al. (2012) for Australian eastern king prawn (*Melicertus plebejus*), Hoyle et al. (2010) for bigeye tuna (*Thunnus obesus*), Hoyle and Okamoto (2011) for bigeye and yellowfin (*Thunnus albacares*) tunas in the Western and Central Pacific Ocean, Eigaard and Munch-Petersen (2011) for Danish northern shrimp (*Pandalus borealis*), Bentley et al. (2012) for New Zealand trevally (*Caranx lutescens*), and Holdsworth and Kendrick (2012) for New Zealand striped marlin (*Kajikia audax*). However, Starr et al. (2013) reported that for New Zealand southern rock lobster stocks (areas CRA7/8) vessel effect explained a substantial amount of model deviance despite it marginally impacting the trend in standardised CPUE. This result, together with our findings, underscores that more generally, proportion of deviance explained by a non-year covariate effect is not always related to its influence on year trend of standardised CPUE (c.f. Bentley et al. 2012).

Although the fleet size has been decreasing since inception of TACC in 2001 (Figure 4), the level of TACC only reduced over period 2006-2009 (from 450 to 240 t), after which it remained relatively stable (VFA 2017). The TACC had not substantially constrained the fishery until after 2009 (VFA 2017), with the ability of the fishery to catch the TACC being inversely proportional to the level of TACC and directly proportional to the available fishable biomass. However, when TACC reduces it may become uneconomic to fish with vessels of lower fishing power (Pascoe et al. 2013), which suggests a potential explanation for the outcome from our study that vessels with particularly low fishing power exiting the fishery during 2009-2012 (Figure 3B). More generally, studies on other fisheries and species have reported that fleet restructuring and setting of TACC can induce the exiting of vessels with low fishing power (Marchal et al. 2013; Pascoe et al. 2013; Solís et al. 2014).

Conclusion

Rising catchability can be mediated by a range of processes. However, here we have demonstrated that the dynamics of vessel entry and exit into a fishery can be a dominant process. Thus, in the case of the WZRLF, even for a period when the technology of fishing may not be advancing, selective changes in fleet composition due to exiting of less efficient operators under conditions of sufficiently low TACC, can result in nominal CPUE overstating rises in stock abundance. GLM standardisation, combined with appropriate catchability metrics such as those used in this study, provide a simple and direct mechanism for detecting and analysing fleet compositional effects.

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Figures

Figure 1. Map of the Western Zone rock lobster fishery (WZRLF) of Victoria, Australia, showing the three reporting regions (Portland, Warrnambool, Apollo Bay) and the 40 m depth contour boundary.

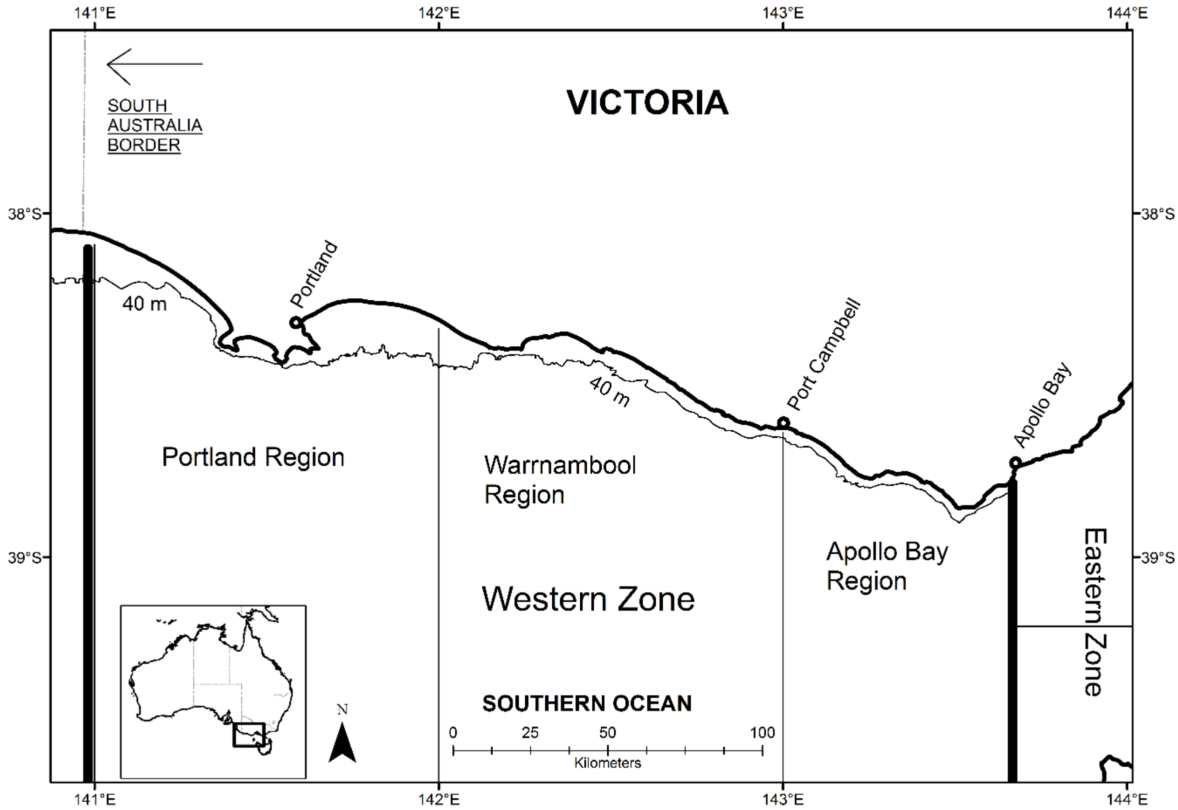


Figure 2. CPUE indices and the CPUE annual discrepancy index by fishing year for the WZRLF of Victoria, Australia. Left axis: Nominal CPUE (filled circle line) and standardised CPUE (open circle line). The standardised CPUE series, shown with bars indicating 95% confidence intervals, was rescaled to have a mean equal to that of the nominal series. Right axis: v_y (Equation 2), representing the percent change in nominal CPUE due to catchability and observation error.

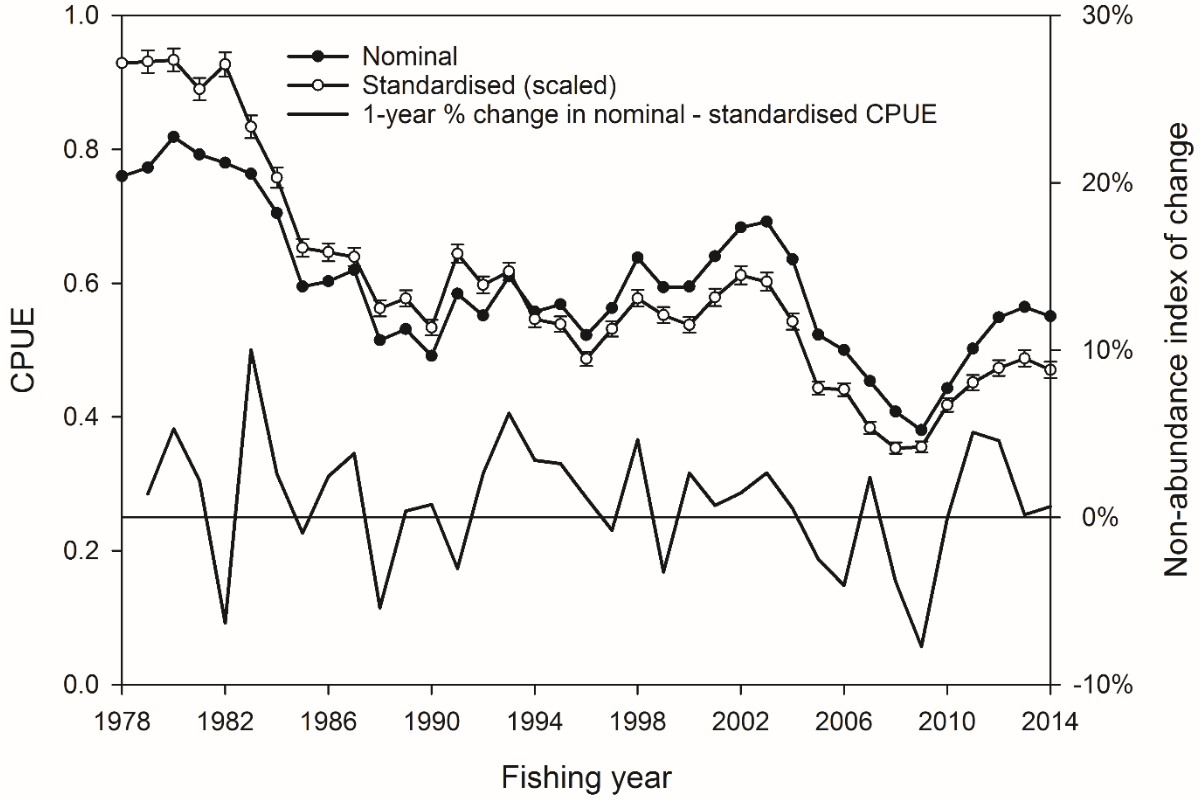


Figure 3. Indices of catchability by fishing year based on terms estimated in Equation 1, for the WZRLF of Victoria, Australia. **A**, Influence values shown for all non-year covariate effects combined (continuous line), for *Vessel* (open circle line), and all non-year effects combined except for *Vessel* (open triangle line); **B**, Influence values for each of vessels (fishing > 1 year) entering the fishery (dashed), exiting (dotted), or remaining (solid), smoothed using a second-order moving average.

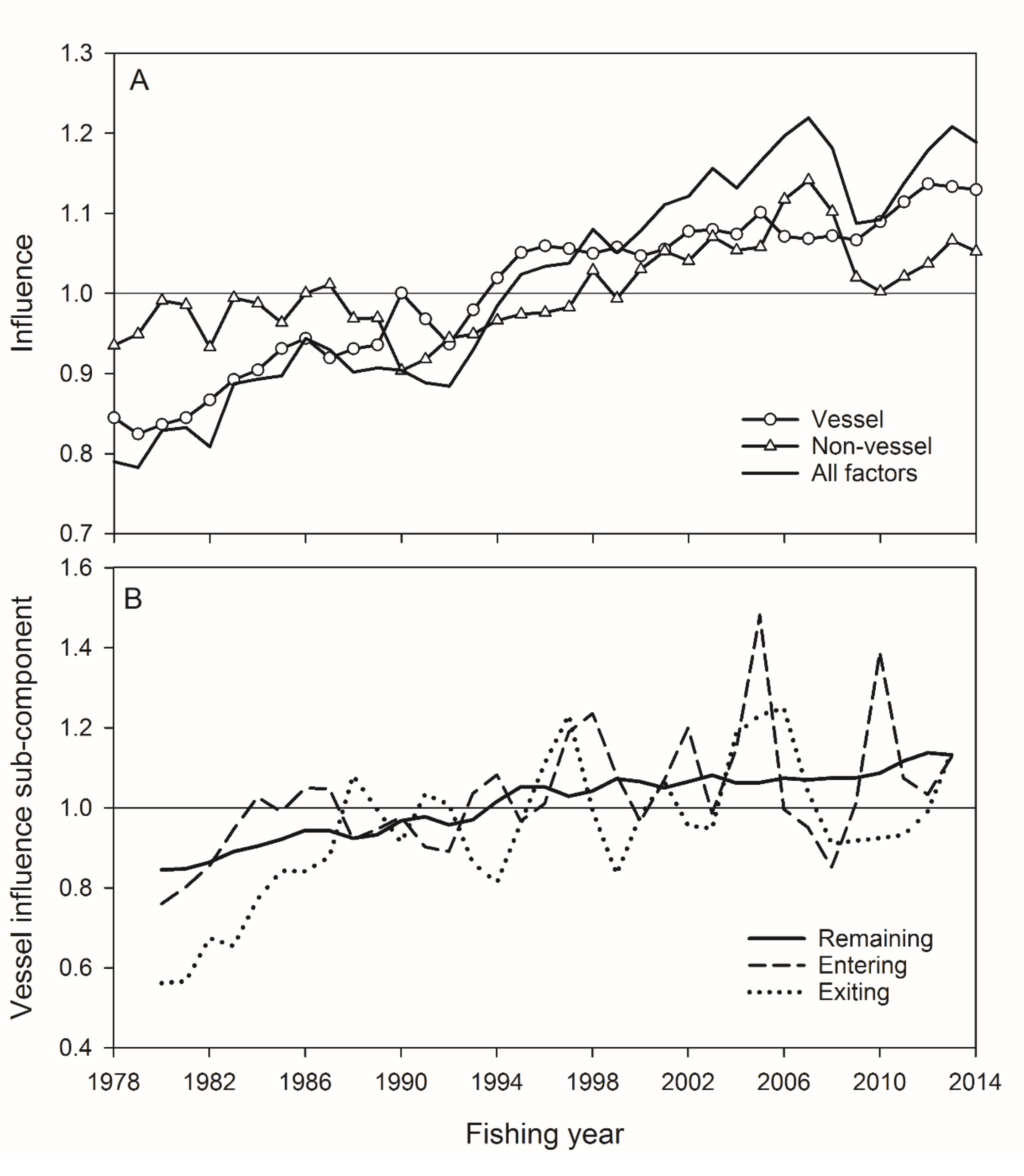


Figure 4. Vessel fleet statistics by fishing year for the WZRLF of Victoria, Australia. Left axis: Proportion of all vessels entering (dashed line) or exiting (dotted line) the fishery. Right axis: Count of all vessels in the fishery by fishing year (continuous line). Vessels in the fishery for only one year were excluded for both axes.

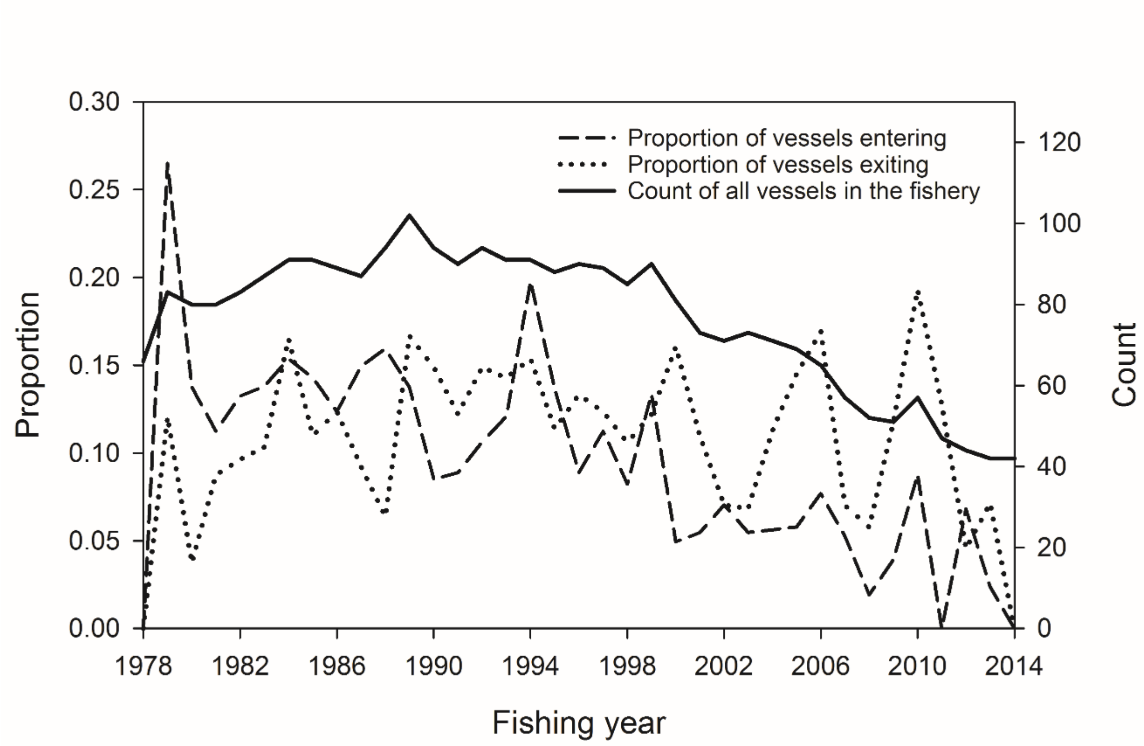
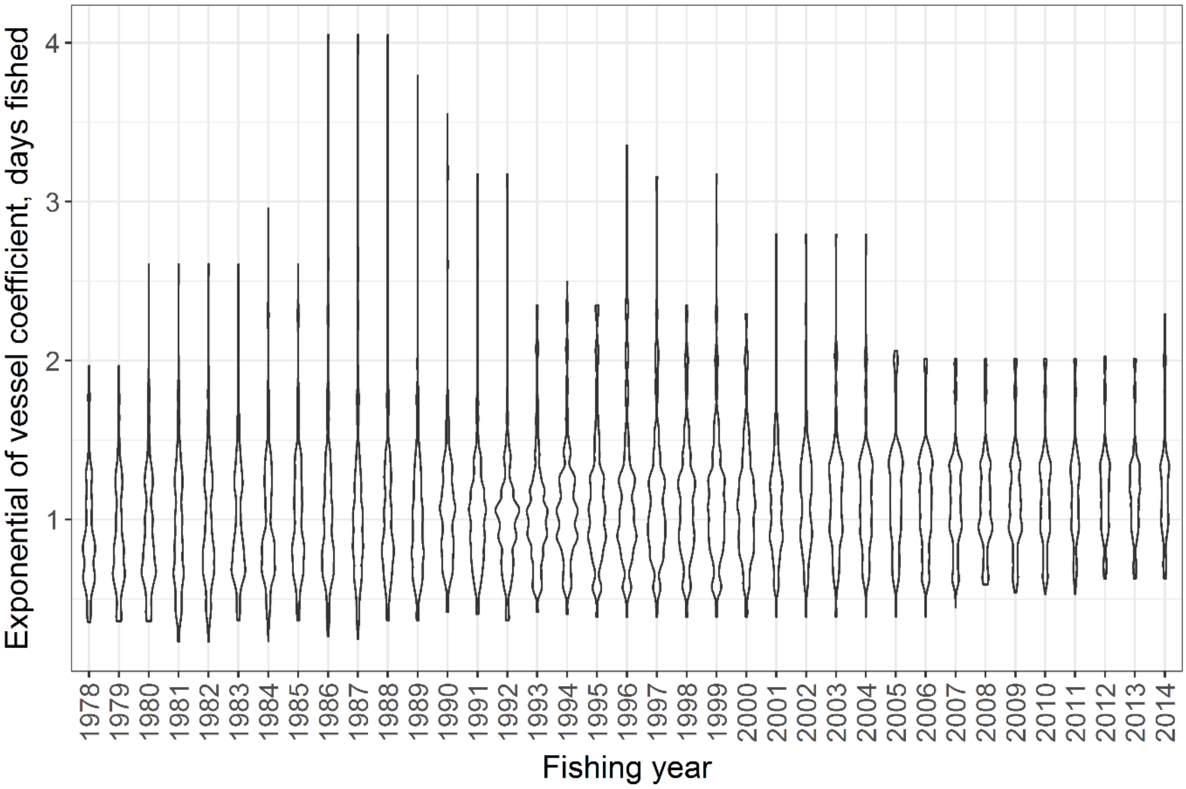


Figure 5. Kernel density functions by fishing year of the exponential of *Vessel* coefficients estimated in Equation 1, for the WZRLF of Victoria, Australia. The area of the density function in a year is scaled to the total number of days fished by all vessels in that year.



Tables

Table 1. Impact of excluding one or more covariate terms from the final model, quantified by AICc (the sample size corrected AIC) and adjusted R^2 (the deviance explained proportion). The number of data points is 347,259.

Model covariate excluded	Increase in AICc	Decrease in adjusted R^2	Estimated parameters
None (final model)	0	0	732
Region	1719	0.3%	730
Depth	2942	0.4%	731
Fisher	12552	1.9%	549
Vessel	18297	2.8%	286
Year	19549	2.9%	696
Month	86588	14.3%	723
Vessel and *Fisher*	89341	14.9%	49
All except *Year* and *Month*	122884	21.4%	46
All except *Year*	211500	41.5%	37

Paper Three

This paper was published.

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Principal Author

Name of Principal Author (Candidate)	John Feenstra
Contribution to the Paper	Performed and conceived the analysis, interpreted data, wrote manuscript, and acted as corresponding author.
Overall percentage (%)	90%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.
Signature	Date 15/08/2018

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Inferring absolute recruitment and legal size population numbers of southern rock lobster (*Jasus edwardsii*) in South Australia's Southern Zone fishery using extended forms of depletion modelling

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ABSTRACT

An extended depletion model (EDM) is presented that estimates both a time-series of the number of animals recruiting to legal size as well as start-year exploitable population size. EDM requires total catch in numbers for all months, but fits only to monthly catch rates of legal size lobsters over a restricted period during each year, aggregating catch and recruitment over the remaining months. Applied to a South Australian southern rock lobster (*Jasus edwardsii*) fishery over 1994–2014, catch rates for January, February, and March were fit under assumptions of no recruitment and equal catchability during these months of high catches. No assumptions are made about catchability during April–December. A hybrid model, EDM-CSA, combines EDM and catch-survey analysis (CSA), by additionally fitting to a recruitment index. Comparisons were made with estimates from a length-based integrated stock assessment model (LenMod). All parameter estimation was by maximum likelihood. Mean estimates of recruitment from the models differed by no more than 3% and of population size by no more than 12%. Trends in recruitment and population size were similar among models. A likelihood ratio test using EDM detected a significant increase in catchability from 2011 to 2012, which was sustained during 2012–2014, and that was corroborated by fisheries-independent survey data. Hyperstability in fishery catch-rates was also supported.

1. Introduction

The commercial fishery for southern rock lobster (*Jasus edwardsii*) in South Australia's Southern Zone (SZ) (Fig. 1) was valued at AU$88.9 million for the 2013/14 financial year, based on a production of 1247 tonnes (EconSearch, 2015). The sea-floor in the region consists of a mainly homogeneous patch of limestone reef, which is a suitable habitat for the southern rock lobster (Lewis, 1981; Linnane et al., 2015). Fishing gear has changed little over time, consisting of steel-framed baited pots that are set individually overnight and hauled at first light. The dimensions of lobster pots, including mesh and escape gap size, are regulated, along with many other aspects of the fishery (Sloan and Crosthwaite, 2007; PIRSA, 2013), including since 1983 a minimum legal size (MLS) of 98.5 mm carapace length and a prohibition on the retention of egg-bearing female lobsters. Since 1993, total allowable commercial catches (TACCs) have been in place, implemented as individual transferable quotas. A yearly quota setting harvest control rule involving the targeting of a constant exploitation rate was implemented in 2011 and refined in 2013 (PIRSA, 2013; McGarvey et al., 2016).

Leslie–DeLury depletion models (Leslie and Davis, 1939; De Lury, 1947), sometimes simply referred to as depletion models, in their basic form involve estimation of an initial abundance level of a closed population subject to a series of successive depletions informed by a combination of two of the following three data sources: (a) the absolute numbers of animals removed, (b) effort statistics on the removal process, and (c) relative capture rates. Recently, several methods have emerged that explicitly incorporate recruitment into the exploitable population in depletion models. Species to which these methods have been applied include spiny lobster *Panulirus argus* (Gonzalez-Yanez et al., 2006; Ehrhardt and Deleveaux, 2009; Babcock et al., 2015), octopus *Octopus vulgaris* (Robert et al., 2010), squid *Loligo gahi* (Roa-Ureta, 2012), and

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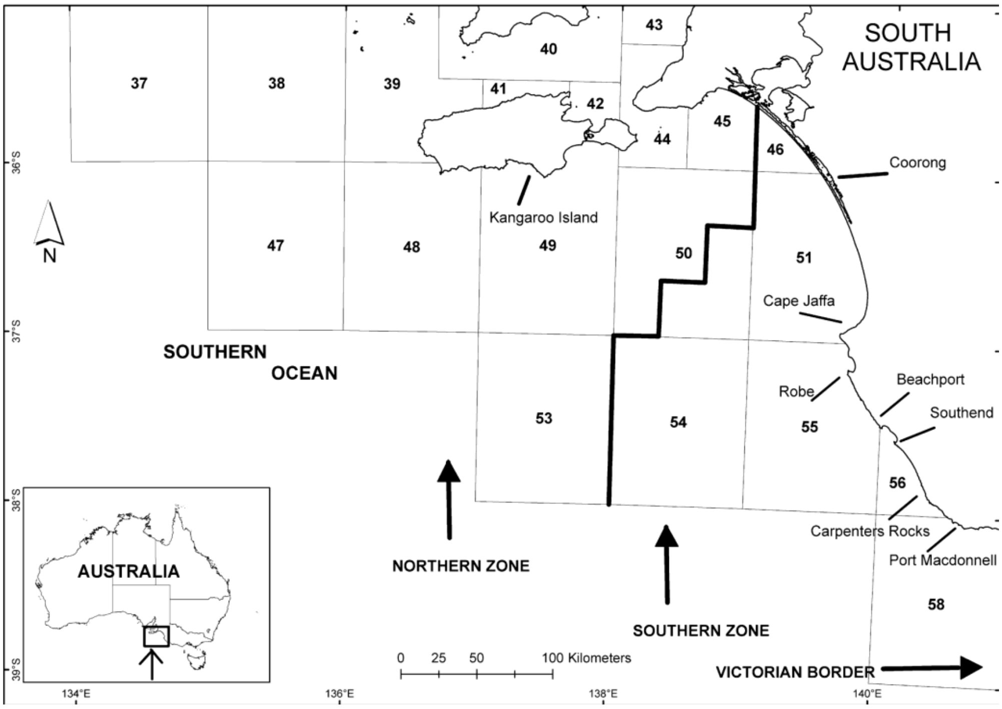

Fig. 1. Southern Zone (and part Northern Zone) rock lobster fisheries of South Australia, with numbers showing marine fishing area blocks.

Spanish mackerel *Scomberomorus commerson* (Roa-Ureta, 2015). Maynou (2015) applied the multi-annual generalised depletion model of Roa-Ureta (2015) to striped red mullet *Mullus surmuletus* and cuttlefish *Sepia officinalis*. These methods involve catch and effort data for the legally exploitable component of the population. They do not utilise data on animals recruiting to the fishery.

Catch-survey analysis (CSA) is a modified form of depletion modelling that involves a yearly time-step and infers the annual numbers and the trend of recruiting animals into a legal size exploitable population by fitting to a catch rate data series on the recruiting animals, referred to here as a pre-recruit index ("PRI"), as well as to catch rates for the fully recruited exploitable population (Collie and Sissenwine, 1983). CSA has been applied to several species, including American lobster *Homarus americanus* (Conser and Idoine, 1992), blue king crab *Paralithodes platypus* (Zheng et al., 1997; Collie et al., 2005), blue crab *callinectes sapidus* (Kahn and Helser, 2005), shrimp *Pandalus borealis* (Cadrin et al., 1999; Cadrin, 2000), while Conser (1995) applied it to Icelandic cod *Gadus morhua*, Icelandic Haddock *Melanogrammus aeglefinus*, redfish *Sebastes marinus*, and the Canadian redfishes *Sebastes fasciatus* and *Sebastes mentella*. Information on catchability is typically provided by pre-specifying the ratio of catchability for newly recruiting animals to that for fully recruited animals. Absolute abundance estimates from CSA are very sensitive to this ratio (Mesnil, 2003, 2005).

The SZ southern rock lobster fishery is relatively data-rich and has attracted substantial modelling efforts over time to monitor the status of the stock, including application of an integrated population dynamics model (here denoted "LenMod") (Punt and Kennedy, 1997; Hobday and Punt, 2001; Punt, 2003; McGarvey et al., 2010; Linnane et al., 2015; McGarvey et al., 2015) that represents the population by length and sex, and fits to catch rates and survey-derived data on monthly length-sex compositions. This paper compares estimates of start-January population size for 1994–2014 and yearly recruitment for 1994–2013, between LenMod, which allows catchability to differ by month and includes factors for population vulnerability (to fishing) by month and sex, and two multi-annual depletion models referred to as EDM and EDM-CSA. EDM is an extended depletion model that simultaneously estimates all recruitment parameters together with a single catchability parameter, and fits to monthly catch rate data over a restricted period during the year, accounting for both catch and recruitment aggregated over the remaining period of the year. EDM-CSA is a combination of EDM and CSA which also fits to PRI data and estimates an extra catchability parameter for recruiting animals. Sensitivity of EDM to catchability assumptions is examined, and a statistical test based on EDM is adapted to detect yearly changes in catchability. The implications of the depletion modelling are discussed.

2. Materials and methods

2.1. Data

Daily totals of catch and effort are recorded by commercial fishers in logbooks, submitted monthly. Compulsory information collected include fishing effort (potlifts), landed catch in weight (kg) and in numbers of live non-spawning legal size lobsters, as well as voluntary data on discarded catch such as numbers of dead, undersize, and spawning lobsters (Linnane et al., 2015). The mean depth and main marine fishing area blocks fished are also recorded. The reporting blocks making up South Australia's SZ fishery are 46, 50, 51, 54, 55, 56, and 58 (Fig. 1), with the bulk of the data coming from blocks 55, 56, and 58. The fishing season starts in October and ends in May of the following year (April for years prior to 2004).

EDM fits to monthly catch rate data constructed as the sum of commercial landed catch in numbers divided by the sum of commercial potlift counts, for each of January to March and for each calendar year during 1994–2014. EDM is conditioned on total monthly catch in numbers consisting of commercial landed catch inflated by a factor of 1 plus the ratio of dead discard catch in numbers divided by landed catch in numbers, and by a factor of 1 plus the ratio of recreational catch in weight divided by commercial landed catch in weight, the latter based on extrapolations from recreational fishing surveys since 1998. The mean across 1994–2014 of the inflation factors for commercial dead discard catch are respectively 1.08, 1.07, and 1.06 for January–March, and those for the recreational factors are 1.06, 1.05, and 1.12. EDM-CSA additionally requires an index that is directly proportional to the number of lobsters recruiting across the MLS. The PRI data series is based on monthly counts of discarded undersized lobsters divided by potlifts (Linnane et al., 2015). Reporting of discarded undersized lobsters is on a voluntary basis since season 2000, and for PRI, effort is calculated only for fishers who recorded data on counts of undersized lobsters.

LenMod is conditioned on monthly total catch in weight (kg), and for fishing seasons 1983–2013 fits to the following data: monthly commercial landed catch rates constructed as the sum of commercial landed catch in weight (kg) divided by the sum of commercial potlift counts, monthly commercial landed catch in numbers, monthly catch rates for numbers of discarded spawning lobsters, and for 1991 onwards counts of lobsters by sex and 4 mm length bins (lowest bin of 82.5–86.5 mm). The latter counts were obtained from a volunteer fisher catch sampling program that measures up to 30,000 lobsters annually (Linnane et al., 2015). Additionally, LenMod fits to catch rate data on live non-spawning lobsters of legal size from fishery-independent monitoring surveys (FIMS) for two or three months per year from 2006 onwards (Linnane et al., 2015).

The catch sampling program mainly consists of volunteer fishers reporting on up to three of their pots set during a fishing trip and which can also involve research staff as onboard observers (Linnane et al., 2015). The sampling protocols for this program have varied over time, along with the proportion of vessels that participate (as high as 40% in season 2007 to as low as 15% in season 2013; Linnane et al., 2011, 2015). The aggregate count of potlifts across January-March per season is predominantly less than 1% of commercial logbook fishing effort (Supplementary Fig. S1(a)). There is no clear trend over time or among MFAs, but sampling for the northern area (MFAs 51 and 55) is typically reported at a greater proportion of commercial effort compared to the southern area (MFAs 56 and 58) (Supplementary Fig. S1(a)). Similarly, the relative amount of reported effort involving undersized lobster information on commercial logbooks since 2000 was 80% or above for MFAs 51 and 55, which is greater than for MFAs 56 and 58 by factors of between 1.3 and 2 (Supplementary Fig. S1(b)). Total commercial fishing effort for the main northern area (MFA 55) fluctuates, but for most years is near or above the level for MFAs 56 and 58 (Supplementary Fig. S1(c)).

Table 1 summarises the data sources and time periods for each of EDM, EDM-CSA, LenMod, and the EDM sensitivity models (details provided below).

2.2. EDM

A key assumption of depletion models is that within-year catchability is constant over the period of depletion during which data are fit. Moulting for southern rock lobster is considered to occur mainly during two periods of the year, October to November for males and April–June for females (MacDiarmid, 1989), although there is some indication of spatial variability in this timing, with it occurring earlier in Tasmania (Ziegler et al., 2004) and later in South Australia (Prescott et al., 1996; McGarvey et al., 1999). Differences between the sexes in the timing of moulting can result in substantial variation in catchability (Ziegler et al., 2004). Substantial numbers of female lobsters are found in spawning condition during October and November in the SZ fishery (Linnane et al., 2015), and this leads to a change across part of the year in the composition of the population that is accessible by the fishery since spawning females are required to be returned to the water. Feenstra et al. (2014) found relatively minor effects of environmental impacts on catchability for the SZ fishery. Movement of lobsters in or out of the SZ fishery is considered negligible, with movements predominantly being of relatively small extent and consisting of the inshore-offshore kind (Linnane et al., 2005). Hence January to March inclusive was considered as the most reasonable period for which to assume a uniformly exploitable population, no recruitment, and constant catchability. The suitability of January to March in meeting these assumptions is explored by sensitivity analysis (Section 3.2).

The model year is defined as starting in January and ending in December, but with catch rate data fit only for January to March inclusive, which we will denote as the “fitted depletion period” or simply the “depletion period”. Remaining catch and all recruitment during the rest of the year are modelled using a single time-step that will be denoted as the “amalgamated period”. The start-January exploitable (available and vulnerable) population, defined as the number of live, non-spawning, legal size lobsters, $N_{t,0}$ for year t (‘0’ = January), is modelled for T (21) years from 1994 to 2014 inclusive. We now describe the ‘base’ form of EDM that assumes a single catchability coefficient over January to March and all years modelled.

Start-month exploitable population $N_{t,m}$ for February to April (m = 1, 2, 3) of year t, assuming natural mortality occurs continuously during each month, and catch is taken instantaneously mid-month is:

$$N_{t,m} = e^{-\sum_{j=0}^{m-1} M_j} N_{t,0} - \sum_{i=0}^{m-1} e^{-0.5M_i - \sum_{j=i}^{m-1} (j-i)M_j} C_{t,i} \tag{1}$$

where $C_{t,i}$ is the total catch in numbers (landed commercial, recreational, and dead discards) for month i of year t, and M_i is the instantaneous rate of natural mortality during month i. Eq. (1) can be derived from expansion and collection of terms in the basic recursive equation $N_{t,m} = (e^{-0.5M_{m-1}} N_{t,m-1} - C_{t,m-1})e^{-0.5M_{m-1}}$. Values for M_i were determined from a value for yearly natural mortality rate, M of 0.1 y^{-1} according to the proportion of days per year for each month i.

The recruitment to the legal-size exploitable population, and the total catch across the amalgamated period, for each year t, are assumed to have been taken instantaneously fractions Tr_t and Tc_t into this period respectively. The exploitable population at the start of year $t+1$, $N_{t+1,0}$, is hence defined by the equation

$$N_{t+1,0} = N_{t,m_{sa}} e^{-M_{am}} + R_t e^{-(1-Tr_t)M_{am}} - e^{-(1-Tc_t)M_{am}} \sum_{i=m_{sa}}^{11} C_{t,i} \tag{2}$$

where m_{sa} equals 3 (April) and so $N_{t,m_{sa}}$ is the exploitable population size at the start of the amalgamated period and during which $M_{am} = \left(M - \sum_{j=0}^{m_{sa}-1} M_j \right)$ is the natural mortality rate and R_t is the number of lobsters growing into legal size, Tc_t ranges between 0.800 and 0.855, calculated as the point at which half of the total catch during the amalgamated period was taken, and Tr_t

Table 1
Models used in the study and their data requirements. Note: "Legal size" refers to live non-spawning lobsters of legal size, and "season" refers to period October to May identified by the calendar year in October.

Model	Data
EDM (base)	Total catch (legal size numbers) and commercial catch rate (legal size numbers/potlifts) for each of months January, February, and March over calendar years 1994–2014. Total catch (legal size numbers) aggregated over April–December.
EDM-sensitivity:	
EDM (base) fit separately for subsets of months.	Dec.–Jan., Jan.–Feb., Feb.–Mar., Mar.–Apr.
EDM (base) fit separately for subsets of years.	1994–2007, 2008–2014
EDM (base) fit separately for smaller subsets of years.	1994–1997, 1998–2001, 2002–2005, 2006–2009, 2010–2014; and 1994–1995, 1996–1999, 2000–2003, 2004–2007, 2008–2011, 2012–2014.
EDM (base) fit separately for subsets of years + yearly catchability.	1994–2007, 2008–2014, 1994–2014
EDM (base) fit separately for subsets of years + yearly catchability and sigma; fully-yearly resolved model.	1994–2007, 2008–2014, 1994–2014
EDM (base) with natural mortality estimated.	Same as base.
EDM (base) with β estimated.	Same as base.
EDM (base) with β estimated separately for subsets of months.	Dec.–Jan., Jan.–Feb., Feb.–Mar., Mar.–Apr.
EDM-CSA	As for EDM (base), but additionally requires data on commercial PRI (undersize discard numbers/potlifts) over years 1994–2013.
LenMod	Total legal size catch (both in numbers and in weight) and commercial catch rate (legal size weight/potlifts), for each month during seasons 1983–2013. Commercial catch rates for numbers of discarded spawning lobsters for October–December during 1983–2013. FIMS catch rates (legal size weight/potlifts) for up to three months a season since 2006. Counts of lobsters per sex and 4 mm length bins from the volunteer fisher catch sampling program, for each month during seasons 1991–2013.

equals 0.472 based on the half-way point between the midpoints of two assumed periods of growth namely 15 May and 1 November (MacDiarmid, 1989).

The monthly catch rate data, for each of the months January to March and the T years, are fit using maximum likelihood, assuming independent and identical log-normally distributed observation errors, for which the negative log-likelihood function (excluding additive constants) is

$$NLL_{EDM} = \sum_{m=0}^{m_{sa}-1} \sum_{t=1994}^{1994+T-1} \left(0.5 \frac{(\log(Cpue_{t,m}) - \log(q_l N_{t,m+0.5}))^2}{\sigma^2} + \log(\sigma) \right) \quad (3)$$

where $N_{t,m+0.5} = 0.5(N_{t,m} + N_{t,m+1})$ is the mean of start-month population size for months m and $m+1$ of year t, $Cpue_{t,m}$ is the commercial landed catch rate (number of lobsters/potlifts) for month m and year t, which is assumed to be linearly proportional to $N_{t,m+0.5}$, q_l is the legal size catchability parameter, and σ is the standard deviation of the observation error on $\log(Cpue_{t,m})$. In addition to q_l and σ, the other directly estimated parameters are $N_{1994,0}$ and R_t for each of T-1 years. The value for σ is constant across months and years, which implies that the level of precision for each of the monthly catch rate is the same. The period before TACC (1984–1993) is not modelled because this would necessitate separate catchability parameters for before and after TACC (1994+) introduction, and effectively the running of two structurally identical EDM models.

2.3. EDM sensitivity

The sensitivity of the outputs from EDM was explored to changes in the months defining the depletion period (January–March for the base model). EDM fits were performed for four alternative two-month periods: December to January, January to February, February to March, and March to April. For each two-month period, the yearly extent involved 1994–2013 inclusive, with 2014 left out for consistency, given data for December 2014 to January 2015 were not available.

Base EDM was also applied separately to subsets of consecutive years to examine the sensitivity of the outputs to assumed stationarity of catchability (q_l) among years. Two non-overlapping divisions of the period 1994–2014 were analysed, namely {1994–1997, 1998–2001, 2002–2005, 2006–2009, 2010–2014} and {1994–1995, 1996–1999, 2000–2003, 2004–2007, 2008–2011, 2012–2014}, to obtain an indication of the effect of choice of year grouping on outcomes. Further insights were then sought by applying, for each of periods 1994–2007, 2008–2014, 1994–2014, both the base EDM and also a fully yearly-resolved form of the base EDM that has parameters σ and q_l varying by year. Trends in estimated start-month population size from the base and yearly-resolved forms of EDM were compared with trends in (landed) catch rates for the commercial fishery and the FIMS, for summer months with FIMS sampling, namely January of 2010, 2011, 2012, and February of 2008, 2009, 2013, and 2014.

The likelihood ratio test (LRT) was used to evaluate the assumption of constant catchability among years given that the base EDM is a nested sub-model of the yearly-resolved EDM. It was also used to compare the base EDM against a model that varied only q_l (instead of both σ and q_l) among years, in order to test the effect of freeing catchability by year when observation error was assumed to be time-invariant.

The possibility of estimating natural mortality was investigated. A likelihood profile was constructed for natural mortality based on a range of values considered as potentially reasonable for rock lobsters in general namely 0.05–0.25 y^{-1} (Johnston and Bergh, 1993).

Hyperstability in fishery catch rates (Hilborn and Walters, 1992; Wilberg et al., 2010) was examined since this has been reported for other southern rock lobster stocks, in Tasmania (Ziegler et al., 2003), New Zealand (Haist et al., 2009), and South Australia (Linnane et al., 2010). Hyperstability was modelled using two approaches, one involving a new EDM run ("free-beta EDM") in which catchability is modelled as $q_l N_{t,m+0.5}^{\beta-1}$ where β is the extent to which catch-rates change non-linearly with abundance. The second approach (Supplementary material A) aims to estimate β by regressing fishery catch rate on FIMS catch rate, assuming the latter is representative of true population size. The first approach has been applied by Haist et al. (2009), Roa-Ureta (2012, 2015), and Maynou (2015), while the second approach has been applied to many marine species including by Harley et al. (2001), Hansen et al. (2005), Erisman et al. (2011), and Ward et al. (2013), with the bulk of all aforementioned studies reporting hyperstability ($\beta < 1$) rather than hyperdepletion ($\beta > 1$). If hyperstability is present in this fishery then free-beta EDM should more accurately model population dynamics, but potentially at the cost of lower estimation precision (Thorson and Berkson, 2010). The regression approach typically suffers from measurement errors (Fuller, 1987) in the fishery-independent data, which in this study was examined using the SIMEX method (Gould et al., 1997, 1999; Supplementary material A). Determination of hyperstability is important since ignoring it (i.e., assuming $\beta = 1$) when present leads to overestimation of population size especially when true population is low.

2.4. EDM-CSA

The population dynamics model for EDM-CSA is identical to that for EDM. However, an additional data source is fit, the PRI series, and one new parameter, the recruitment catchability (q_r), is estimated along with the legal size catchability parameter (q_l) and the other parameters in EDM. CSA, unlike EDM-CSA, parameterises q_r as the product of q_l times q_l/q_r, with the latter fixed at a pre-determined value since q_l and q_r/q_l are in practice highly negatively correlated (Conser, 1994). PRI data based on commercial fishery logbooks are considered more reliable from November to March (Linnane et al., 2015), and so the index is formed as the mean of November and December PRI.

The number of lobsters recruiting across the MLS each year is implicitly assumed to consist of a constant proportion (p) of the undersize population, and PRI is assumed to be directly proportional to the number of undersized animals, and hence recruitment is modelled to be directly proportional to PRI in expectation, since $q_r = q_s/p$ where q_s is the catchability of the undersize population. The proportions of the total number of sampled undersized lobsters among the four 4 mm length bins below the MLS vary relatively little among seasons, though during 1993–1999 the highest undersize length bin (94.5–98.5) proportion was consistently below that during 2000–2013 except for 2009 (Supplementary Table S1). Aside from relative length frequencies Supplementary Table S1 also contains information on undersize length selectivity and growth which together were used to obtain an approximation (calculations not shown) for the total yearly proportion of undersized lobsters that grow to above MLS, namely 78%. This suggests that, aside from data quality aspects regarding the voluntary data, the SZ fishery PRI data series may reasonably be expected to be representative of relative changes in yearly recruitment into the fishery.

The negative log-likelihood function for EDM-CSA is NLL_{EDM} plus a term for PRI, which is as follows assuming independent log-normally distributed observation errors for the PRI data (excluding additive constants):

$$NLL_{EDM-CSA} = NLL_{EDM} + \sum_{t=1994}^{1994+T-2} \left(0.5\frac{(\log(PRI_t) - \log(q_r R_t))^2}{\lambda\sigma^2} + \log(\lambda^{0.5}\sigma) \right) \quad (4)$$

where PRI_t is the PRI index datum for year t, and the variance of the observation error on $\log(PRI_t)$ is assumed to equal σ^2 multiplied by a pre-specified multiplier constant (λ). The value for λ was set to 1 given the absence of quantitative information on the relative level of precision of the PRI data. The recruitment for the last year is not estimated, but may be approximated using PRI data for that year.

2.5. LenMod

The implementation of LenMod currently used as part of South Australian stock assessments involves a population structured by season, month (October to May), sex and 4-mm length categories (Linnane et al., 2015). Fishing mortality is accounted for via removal from the population of the total catch each month. Yearly natural mortality is fixed at 0.1 y^{-1}. Growth is captured using size-transition matrices modelled separately per sex at the end of December and at the end of May (McGarvey and Feenstra, 2001). The smallest length-class has a lower limit of 82.5 mm.

LenMod was fit over fishing seasons 1983–2013 to monthly data as described in Section 2.1, allowing estimation of yearly settlement (new mainly undersized animals), recruitment to legal size, monthly sex-specific vulnerability, monthly catchability, and length selectivity, using maximum likelihood. Separate catchability parameters were estimated for the pre-TACC and TACC periods (seasons 1993+). The exploitable, or vulnerable, population (i.e., accessible to the fishing gear, and which is compared to EDM-estimated numbers) at the start of each month is computed as the sum-product of lobster numbers in each length bin of legal size and sex multiplied by factors for length-selectivity and monthly sex vulnerability. See Supplementary material B for more details.

2.6. Retrospective analysis

The sensitivity of model estimates of exploitable population size in January of the terminal year was examined to successive data set reductions by removing the last year of fitted data back to terminal year 2006 (which is the first year of FIMS data fit by LenMod), and was performed for base EDM, EDM-CSA, LenMod, and free-beta EDM. Mohn's rho (Mohn, 1999) was calculated for each of the models, using the formula and associated comparative rule-of-thumb (for long lived species) developed by Hurtado-Ferro et al. (2014). Hence if Mohn's rho is outside of the interval −0.15 to +0.20 it potentially (Hurtado-Ferro et al., 2014) indicates bias due to unsuitable structural model assumptions such as time-constant catchability (Mohn, 1999). Time series of start-January exploitable population size were plotted and compared for each of model and data set fit.

3. Results

3.1. Base models

Both commercial catch rates and total catch decline steeply across January–March (Fig. 2), which is consistent with an initial population that is reasonably depleted by fishing and may indicate a fishing history that is sufficiently informative for use by depletion methods (Magnusson and Hilborn, 2007). Overall, the EDM fit appears adequate as indicated by the residual diagnostic plots (Supplementary Fig. S2). However, the residual spread among years (Supplementary Fig. S2(f)) indicates relatively high imprecision for 2012–2014, which is also suggested by Figs. 2 and 3. The catch rate data points decline against cumulative catch in a reasonably linear manner for 2008–2014, unlike the period pre-2008 which involves some years where one month is out of alignment with the other two months (Fig. 3). This non-linearity in monthly patterns of catch rate data pre-2008 may be due to several reasons such as observation error in catch rates, ephemeral timing in recruitment, hyperstability–hyperdepletion, or arbitrary changes in catchability but between which it is difficult to distinguish without auxiliary

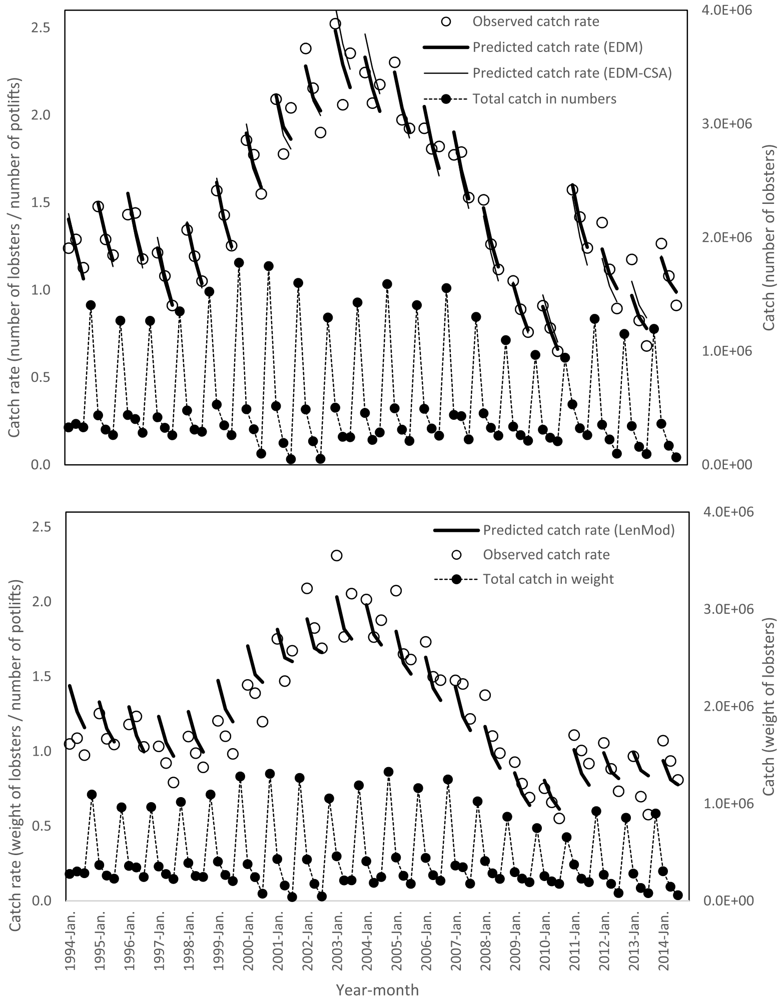

Fig. 2. Top: Time series of predicted catch rates (number of lobsters/number of potlifts) by EDM and EDM-CSA, observed commercial catch rate, and total catch in number of lobsters (commercial, dead, recreational) by calendar year by EDM time periods: January, February, March, and April–December amalgamated (only catch). Bottom: The LenMod equivalent time series displayed only for time steps in common with EDM (January–March) and calendar years 1994–2014, noting that LenMod catch and catch rate are in terms of catch in weight.

information (Miller and Mohn, 1993). EDM underestimates January catch rates and overestimates those for March for years 2012–2014, whereas this is not evident for pre-2008 for which January tends to be overestimated (Fig. 3).

EDM-CSA estimation is less precise post-2003 than pre-2003 for both catch rate (Supplementary Fig. S3(f)) and particularly PRI (Supplementary Fig. S4(f)). Catch rate is worst fit in 2012 and 2013 while PRI is worst fit in 2010 and 2012. An apparent declining trend in the residuals of PRI over the low to intermediate range of predicted PRI (Supplementary Fig. S4(c)) is associated with clustering of residuals post-2003, involving overestimation for 2004–2007 and, except for 2010, underestimation for 2008–2013 (Supplementary Fig. S4(f)).

LenMod tends to underestimate catch rate at high values of 1.70 and above (Supplementary Fig. S5(d)) due to underestimation in the peak catch rate period of calendar years 2002–2006 for January–March (Fig. 2) and December (results not shown), while catch-rates are overestimated between 1994 and 2001 (Fig. 2). There is a large difference for 1992–1993 in residuals (Supplementary Fig. S5(f)) that may be reflective mostly of LenMod estimating a different set of monthly catchability parameters for 1983–1992 and for 1993–2013. There is also a long-term trend in the residuals for years involving considerable overestimation in season 1993, which gradually changes to underestimation in 2003 and subsequently diminishes across 2003–2009 (Supplementary Fig. S5(f)). The reason for this long-term trend in the residuals is not readily discernable, though in comparison to EDM more months of the year and more types of data are fit (Table 1, Section 2), and so a potential factor could be spatio-temporal heterogeneity in the levels of sampling within and between data sources. Similarly, the trend in the residuals observed for EDM-CSA may perhaps be related to data quality issues in the PRI series. For example, both catch sampling and voluntary reporting of undersized lobsters on logbooks disproportionately sample the northern area of the fishery (Supplementary Fig. S1(a) and (b)) which contain lower densities of undersize lobsters (Linnane et al., 2015). However, reassuringly the mean estimated yearly recruitment levels from EDM and EDM-CSA

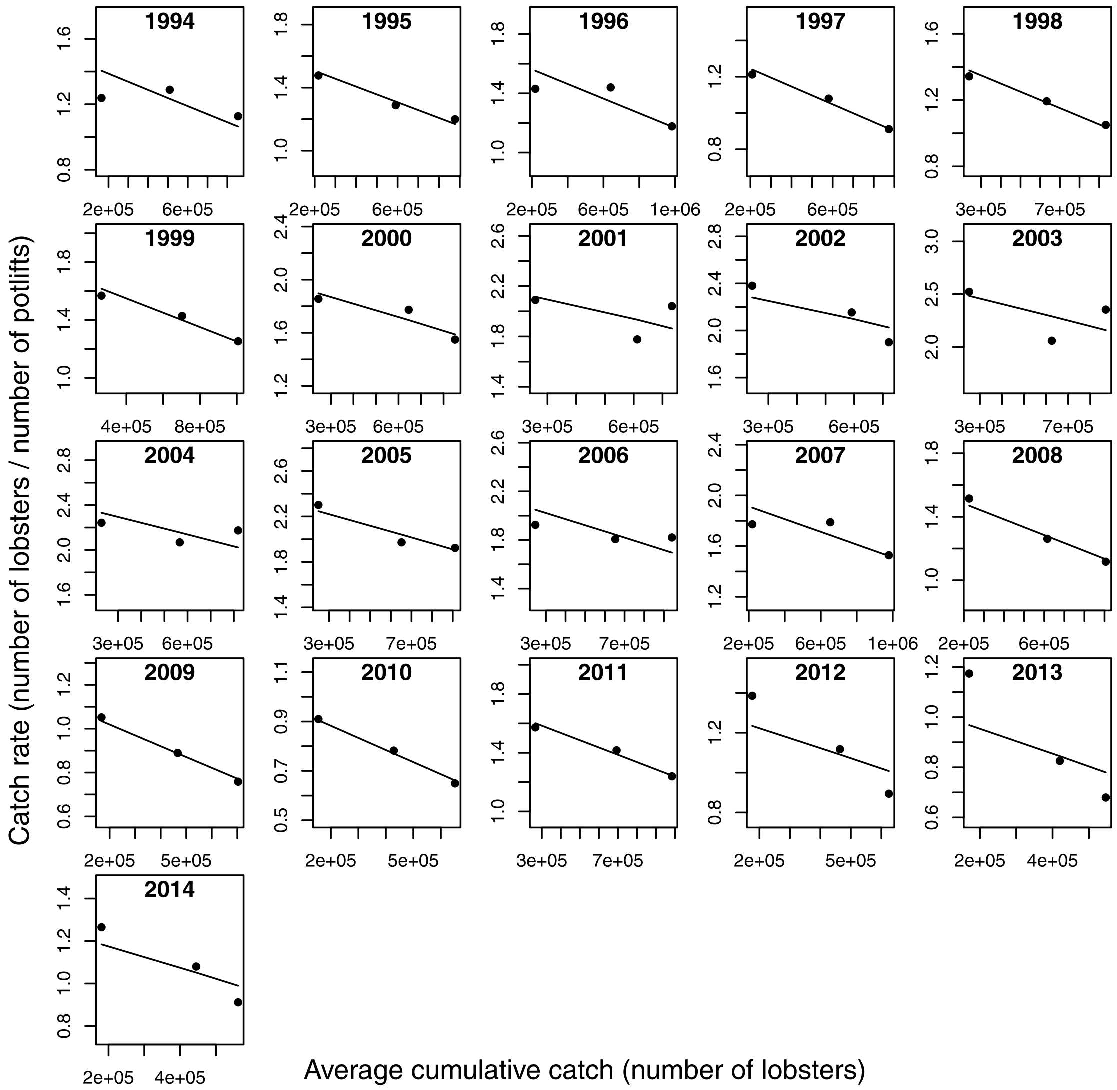

Fig. 3. Predicted catch rate (number of lobsters/number of potlifts) by EDM (base) as lines, and observed commercial catch rate as points, versus cumulative total catch in number of lobsters (commercial, dead, recreational) across the fitted depletion period of January to March in each year. The cumulative catch shown is the mean of the cumulative total catch for the current and previous months, which is compatible with predicted catch rate since that is defined to be proportional to mid-month population (see Section 2).

were respectively only 3% and 2% higher than from LenMod, and trends in recruitment from all three models were similar (Fig. 4). For 2009–2013 the 95% confidence intervals[1] for the EDM estimates narrowed (i.e. were more precise), while discrepancy with LenMod estimates increased (Fig. 4) and the 95% confidence intervals of EDM and LenMod show minimal or no overlap (Table 2). Overall the EDM estimates of recruitment were less precise than for EDM-CSA, especially since 2001, with the LenMod estimates most precise as indicated by CV levels (Table 2). Concordance with PRI appears greater for EDM-CSA than for EDM (Fig. 4 (bottom) and Fig. 5 (top)), and a close association is evident between recruitment estimates from EDM and EDM-CSA relative to LenMod at all levels of recruitment (Fig. 5 (bottom)).

Estimates of start-January exploitable population numbers do not differ substantially in trend nor in absolute level between EDM, EDM-CSA, and LenMod, except that LenMod estimates a moderately higher level prior to 2002 (Fig. 4). The mean estimated yearly population levels from EDM and EDM-CSA respectively during 1994–2014 were 4% and 12% below the mean from LenMod. Table 2 indicates that both EDM and EDM-CSA estimates of population size are approximately half as precise as those from LenMod which has a mean CV of 3.6%. The influence of the FIMS catch rate data on LenMod estimates of population size is minor, as determined from

[1] The confidence intervals were calculated based on the likelihood surface about the optimum parameter estimates, using the delta method to obtain approximate standard errors for the population quantities, with the parameter estimation and standard errors for EDM, EDM-CSA, and LenMod calculated using ADMB (version 11.1 for MS Visual C++ 2010 Express 64 bit). See Fournier et al. (2012) for information on ADMB algorithms.

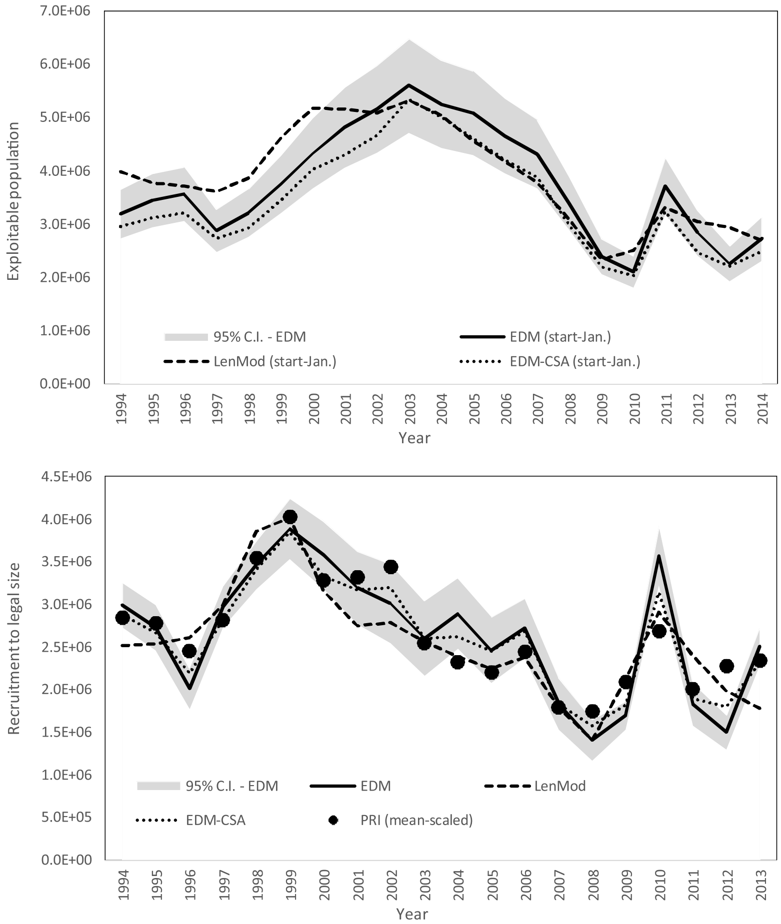

Fig. 4. Time series of estimated start-January exploitable population numbers (top) and recruitment to legal size (bottom) series from EDM, LenMod, and EDM-CSA. The maximum likelihood 95% confidence intervals for the EDM estimates are the shaded areas. Pre-recruit index (PRI) data points (mean of November–December) are added to the recruitment figure and are scaled so that the mean equals that of the EDM estimated recruitment series.

comparison to estimates from LenMod when the FIMS data were removed (results not shown).

Estimates of catchability for January–March from LenMod and EDM are similar, but the LenMod 95% confidence intervals are narrower (Table 3). Also evident from Table 3 (and Fig. 2) is that EDM fits the catch rates in numbers better than LenMod fits the catch rates in weight, which may in part be due to LenMod being required to balance multiple data sets in addition to commercial catch rates (Table 1). Finally, LenMod estimates qualitatively different female population vulnerability factors (accessibility to fishing) for October–November compared to April–May for which females are substantially less vulnerable by about 70%, while for the period in common with EDM of January–March it estimates females to be 20–25% less vulnerable (Table 3).

3.2. Sensitivity analyses

Catchability from EDM differed substantially among several of the alternative two-month fitted depletion periods (Fig. 6). The catchability estimate for depletion period December–January was 73% less than that of January–February, for March–April was 150% greater than that of February–March, while January–February was 16% less than that of February–March (Fig. 6). The catchability estimates from base EDM for the period January–March fell well within the 95% confidence intervals of EDM for depletion periods January–February and February–March, unlike EDM estimates for depletion periods December–January and March–April (Fig. 6).

Base EDM when applied separately to subsets of years estimated the catchability prior to 2008 to be lower than that after 2008, and for 2012–2014 the estimated catchability was 2.35 times that estimated for 1994–2014, the latter lying well outside of the 95% confidence intervals for the 2012–2014 estimate (Fig. 7). Significantly large catchability estimates for individual years 2012, 2013, and 2014 is also indicated by Fig. 8 (lower panel). Yearly-resolved EDM fits to data for 1994–2014 resulted in very imprecise ($CV > 50\%$; results not shown) catchability estimates for several years during 1994–2007, while catchability for years during 2008–2014 were estimated with lower levels of uncertainty ($CV < 15\%$; Fig. 8 (bottom)). An apparent increasing trend over 1994–2009 in catchability (Fig. 7) may be spurious due to the level of observation error. The LRT p-values for tests comparing base EDM fits across 1994–2007, 2008–2014, and 1994–2014 against the corresponding yearly-resolved model fits were respectively 0.00723, <1.0E−7, and <1.0E−7, providing evidence for temporal variation in catchability over 1994–2007, which is more strongly indicated

Table 2
Coefficient of variation (CV) and 95% confidence intervals (CI) for estimates of yearly recruitment and start-January exploitable population numbers from EDM (base), EDM-CSA, and LenMod. Cell values consist of CV% with 95% CI in parentheses in units of millions.

Year	Recruitment			Exploitable population numbers		
	EDM	EDM-CSA	LenMod	EDM	EDM-CSA	LenMod
1994	4.5% (2.7–3.3)	4.9% (2.6–3.2)	4.4% (2.3–2.7)	7.4% (2.7–3.6)	7.9% (2.5–3.4)	3.6% (3.7–4.3)
1995	5.0% (2.5–3)	4.9% (2.4–2.9)	4.8% (2.3–2.8)	7.4% (2.9–3.9)	7.5% (2.7–3.6)	3.6% (3.5–4)
1996	6.1% (1.8–2.3)	5.3% (2–2.4)	4.4% (2.4–2.8)	7.3% (3.1–4.1)	7.1% (2.8–3.7)	3.6% (3.5–4)
1997	4.1% (2.7–3.2)	4.5% (2.6–3.1)	4.1% (2.8–3.2)	7.1% (2.5–3.3)	7.7% (2.3–3.1)	3.7% (3.3–3.9)
1998	4.2% (3.2–3.7)	4.6% (3.1–3.7)	3.4% (3.6–4.1)	7.1% (2.8–3.7)	7.5% (2.5–3.4)	3.5% (3.6–4.1)
1999	4.7% (3.5–4.2)	5.0% (3.5–4.2)	3.6% (3.7–4.3)	7.3% (3.2–4.3)	7.6% (2.9–4)	3.3% (4.3–4.9)
2000	5.7% (3.2–4)	5.6% (3–3.7)	4.2% (2.9–3.4)	7.7% (3.7–5)	8.1% (3.4–4.7)	3.4% (4.8–5.5)
2001	6.9% (2.8–3.6)	6.0% (2.8–3.5)	4.3% (2.5–3)	8.0% (4.1–5.6)	8.1% (3.6–5)	3.5% (4.8–5.5)
2002	7.8% (2.5–3.5)	6.3% (2.8–3.6)	4.7% (2.5–3)	8.1% (4.3–6)	8.2% (3.9–5.4)	3.4% (4.7–5.4)
2003	8.7% (2.2–3)	6.7% (2.3–2.9)	4.8% (2.3–2.8)	8.0% (4.7–6.5)	7.9% (4.5–6.2)	3.3% (5–5.7)
2004	7.4% (2.5–3.3)	6.5% (2.3–3)	4.7% (2.2–2.6)	8.0% (4.4–6.1)	8.1% (4.2–5.8)	3.3% (4.7–5.4)
2005	8.0% (2.1–2.8)	6.5% (2.1–2.8)	4.3% (2.1–2.4)	7.9% (4.3–5.9)	7.9% (3.9–5.3)	3.3% (4.3–4.9)
2006	6.6% (2.4–3.1)	5.7% (2.4–3)	4.0% (2.2–2.6)	7.7% (4–5.4)	7.7% (3.6–4.8)	3.2% (3.9–4.4)
2007	8.5% (1.5–2.1)	6.5% (1.6–2.1)	4.4% (1.6–1.9)	7.6% (3.7–5)	7.0% (3.3–4.4)	3.2% (3.5–4)
2008	8.6% (1.2–1.6)	5.8% (1.4–1.8)	4.5% (1.3–1.5)	7.3% (2.9–3.9)	7.0% (2.6–3.4)	3.4% (2.9–3.3)
2009	4.9% (1.5–1.9)	4.9% (1.6–2)	3.3% (2–2.3)	7.2% (2.1–2.7)	7.8% (1.9–2.5)	3.7% (2.2–2.5)
2010	4.9% (3.2–3.9)	4.2% (2.9–3.4)	2.8% (2.7–3.1)	7.1% (1.8–2.4)	8.1% (1.7–2.4)	3.4% (2.3–2.7)
2011	7.1% (1.6–2.1)	5.6% (1.7–2.1)	3.7% (2.2–2.6)	7.3% (3.2–4.2)	6.6% (2.8–3.7)	3.2% (3.1–3.5)
2012	6.8% (1.3–1.7)	5.2% (1.6–2)	4.5% (1.8–2.2)	7.6% (2.4–3.3)	7.6% (2.1–2.8)	3.7% (2.8–3.3)
2013	4.5% (2.3–2.7)	4.9% (2.1–2.5)	7.4% (1.5–2)	7.5% (1.9–2.6)	8.4% (1.8–2.6)	4.1% (2.7–3.2)
2014				7.7% (2.3–3.1)	8.0% (2.1–2.9)	6.0% (2.4–3)
Mean CV%	6.2%	5.5%	4.3%	7.5%	7.7%	3.6%

Table 3
Monthly values of estimated catchability from LenMod with 95% confidence intervals and maximum likelihood estimates of monthly observation error standard deviation (sigma) for 1993–2013, relative female vulnerability (male = 1), and corresponding EDM (base) estimated catchability with 95% confidence intervals and sigma.

	October	November	December	January	February	March	April	May
LenMod – Catchability $\times 10^{-7}$	2.83	3.00	4.31	4.45	4.32	4.47	4.18	4.31
- 95% C.I. – lower	2.62	2.79	4.04	4.20	4.04	4.14	3.77	3.87
- 95% C.I. – upper	3.04	3.20	4.57	4.70	4.61	4.79	4.60	4.74
EDM – catchability				4.67	4.67	4.67		
- 95% C.I. – lower				3.90	3.90	3.90		
- 95% C.I. – upper				5.43	5.43	5.43		
LenMod – sigma	0.18	0.12	0.08	0.18	0.21	0.18	0.28	0.30
EDM – sigma				0.06	0.06	0.06		
LenMod – female vulnerability	1.20	1.44	1.05	0.79	0.78	0.75	0.54	0.28

for 2008–2014. Similarly, comparing base EDM and a model freeing only catchability parameters across years resulted in LRT p-values of <1.0E−7 for both 2008–2014 and 1994–2014, but the p-value was 0.317 for 1994–2007.

Fig. 8 (top) indicates similar trends in estimates of population size for base EDM and yearly-resolved EDM during 2008–2011, but during 2012–2014 the base EDM estimates remained around 2008–2011 levels or above while yearly-resolved EDM estimates declined substantially. Differences in trends between the commercial logbook and FIMS catch rates closely mirror differences between the population estimates from base EDM and yearly-resolved EDM except for 2011 (Fig. 8 (top)). Note that there is an element of confounding in Fig. 8 due to 2010–2012 involving January while the other years involve February, but nevertheless the more rapid decline inferred by yearly-resolved EDM estimates remains when Januaries 2010–2012 are ignored.

The estimate of M was 0.18 y^{-1} which is within a range of previously reported values for a broad range of rock lobster species (Johnston and Bergh, 1993), but the CV was 232% and all pairwise parameter correlations were above 0.95 in magnitude (between catchability and M it was 99.99%). The CV on catchability was 33%, which is an increase on that from base EDM of 8%. The profile likelihood for M (Supplementary Fig. S6) further supports these conclusions, indicating little change in the log-likelihood over a wide range of values for M. A value for M of 0.1 y^{-1} was assumed reasonable based on a range of 0.05–0.13 y^{-1} for *Jasus lalandii* reported by Johnston and Bergh (1993).

The estimate of β was 0.529 (95% CI 0.371–0.687) for the free-beta EDM run, which supports the hyperstability hypothesis given that $\beta = 1$ is well above the upper 95% limit. However, β and q_l are highly correlated (−99.95%), although a likelihood profile for β supports the narrow confidence interval determined for β (Supplementary Fig. S7), and similarly EDM with β estimated is favoured over base EDM as indicated by an LRT p-value of 0.001995. The mean estimated population size from free-beta EDM was 29% less than base EDM, but mean recruitment was only 4% less. When population size is low (and catchability high) the discrepancy with base EDM estimates is greatest (Supplementary Fig. S8), while interestingly estimated levels over 2012–2014 are close to those from yearly-resolved EDM (Fig. 8 (top)). Free-beta EDM displays a similar pattern of susceptibility to very strong deviations in catchability when applied outside of January–March (Fig. 6).

The estimate of β from regressing logged commercial fishery catch rate on logged FIMS catch rate was 0.395 (95% CI 0.067–0.722), and this differed little from the results from using SIMEX (Supplementary material A). This provides further support to the hyperstability hypothesis. Note that, aside from the measurement error aspect, estimating β using regression may perform poorly when there is insufficient contrast in the data (Harley et al., 2001), but for this study contrast was adequate given the ratio of maximum to minimum catch rate values for the fishery data was 2.3 and for FIMS was 5.8.

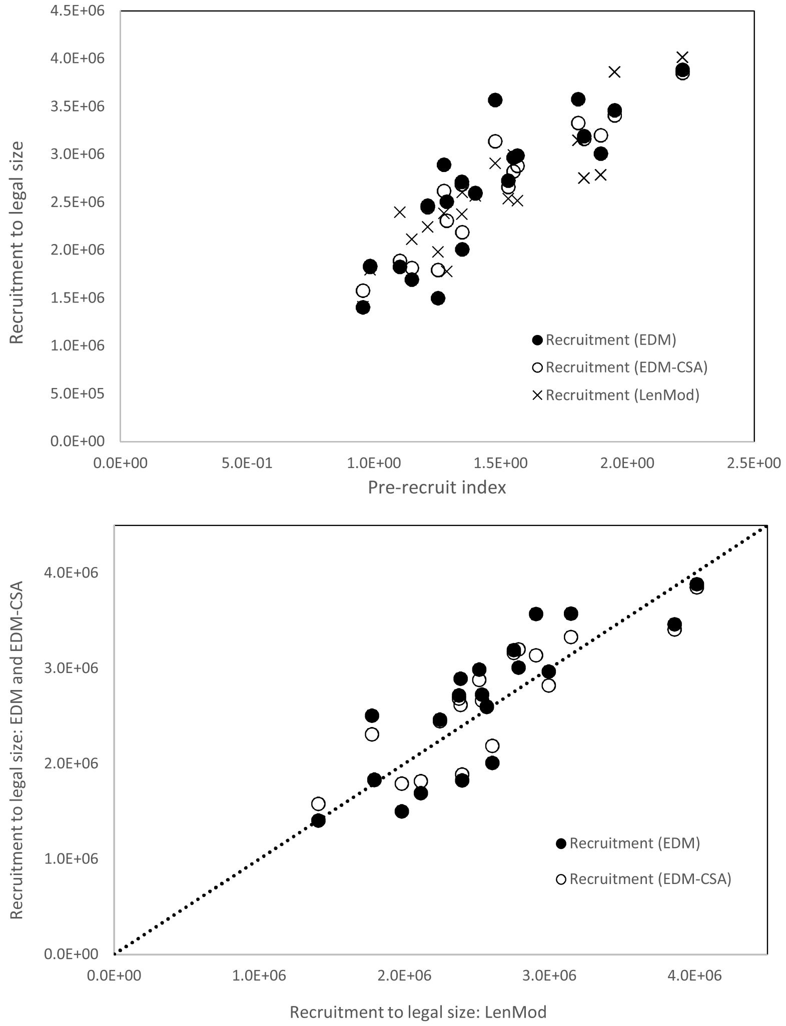

Fig. 5. Scatter plot of (top) EDM, EDM-CSA, and LenMod estimated recruitment to legal size versus pre-recruit index (PRI), and a scatter plot (bottom) of EDM and EDM-CSA estimated recruitment versus corresponding LenMod estimates with a diagonal (dotted) guideline indicating perfect agreement.

3.3. Retrospective analysis

The value of Mohn's rho for each of base EDM, free-beta EDM, EDM-CSA, and LenMod were +0.19, +0.33, +0.22, and +0.07 respectively. This suggests that for all models, the trend in estimated population size is revised downwards as more data are added, and which is consistent with the hypothesis of a rise in true catchability over the years. Applying the Mohn's rho interval rule-of-thumb strictly suggests that this indication of bias may be classed as substantial only for free-beta EDM and EDM-CSA. The retrospective time series plots (Fig. 9) confirm that there is downward revision of population estimates with more data fit, and that for all models this was most severe for the pre-2008 period. Over 2008–2014 free-beta EDM was more impacted than EDM and EDM-CSA. LenMod displays the least overall bias and does so mainly in the terminal year whereas the other models were impacted for most of the time series.

4. Discussion

4.1. Outcomes

There was close agreement between the three base models in the long-term trends and mean absolute levels of both estimated exploitable population numbers and recruitment to legal size (Fig. 4). The PRI data were highly correlated with recruitment estimates from EDM-CSA (Pearson $r = 94\%$), free-beta EDM (92%), LenMod (89%), and EDM (85%), which for the two EDM models is noteworthy considering these do not fit to data that directly inform recruitment (Table 1). The level of precision of the estimated population numbers and recruitment from the three base models was high ($CV < 10\%$, Table 2), as was the free-beta EDM except for 2008–2014 for which CVs were roughly double those from EDM (Supplementary Table S2). LenMod estimates were most precise, which perhaps is related to the much larger number of data

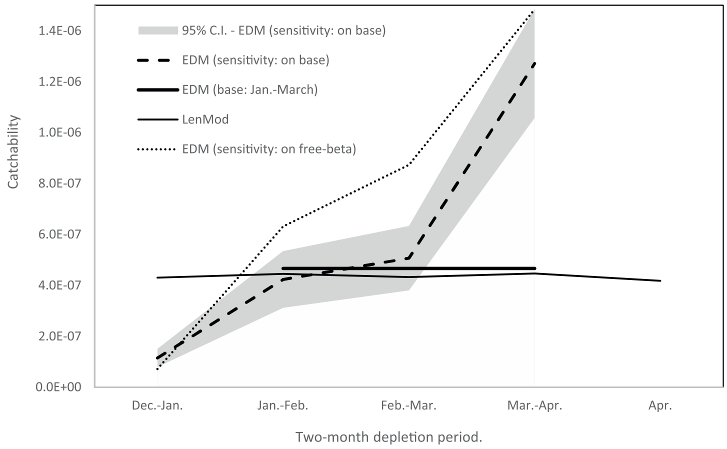

Fig. 6. Catchability values estimated by EDM (base) and free-beta EDM applied separately for different fitted depletion periods of January–March, December–January, January–February, February–March, and March–April. The 95% confidence intervals for each of the EDM estimates are the shaded areas. The LenMod estimates for December to April are also shown.

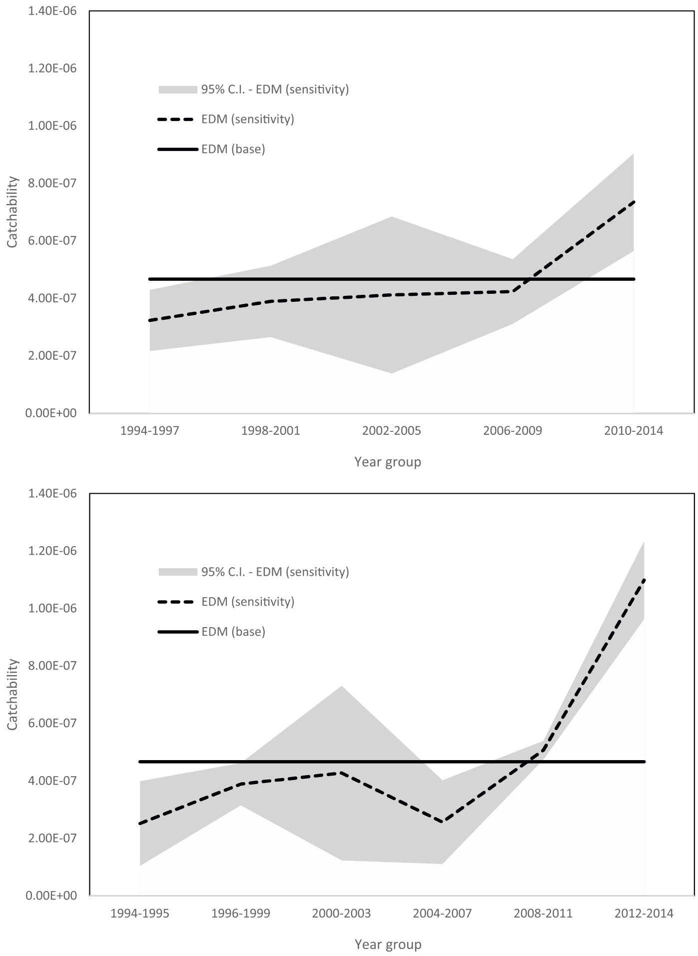

Fig. 7. Catchability estimated by EDM fit separately over different consecutive groups of calendar years with 95% confidence intervals, and EDM (base) applied over 1994–2014.

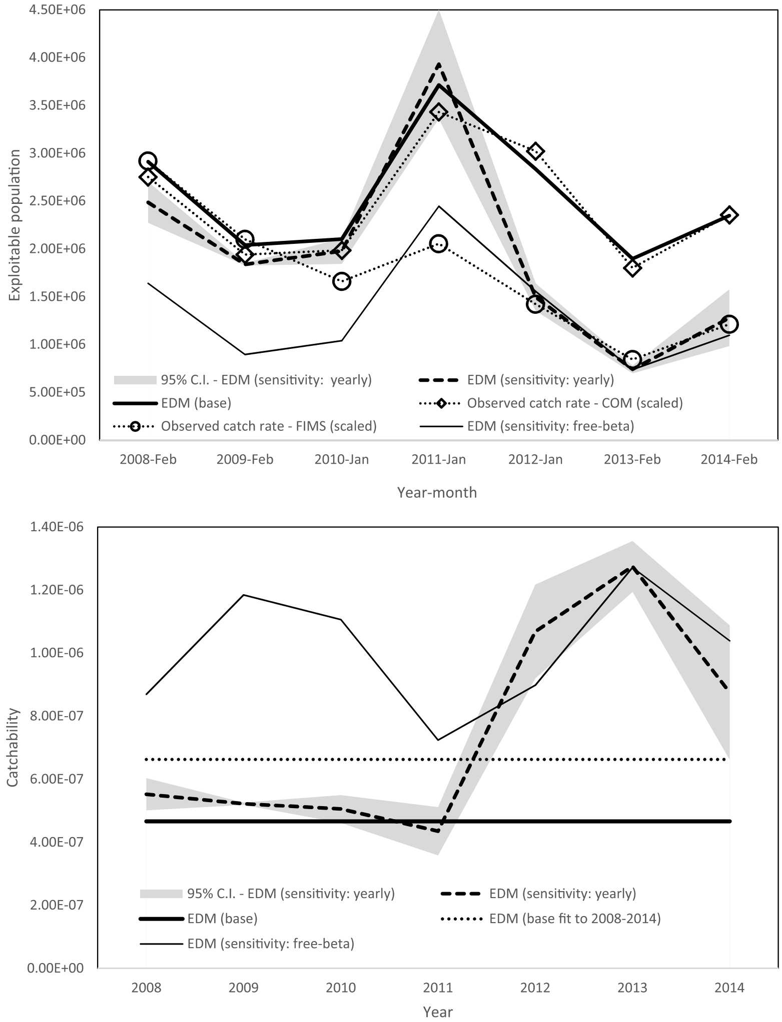

Fig. 8. Top: Time series over summer months involving FIMS sampling (January–February surveys) for calendar years 2008–2014 of commercial logbook and FIMS catch rate data series, absolute exploitable population numbers estimated by EDM (base) and free-beta EDM fit over all years 1993–2014, and by EDM (yearly) fit separately to each of years 2008–2014 and the 95% confidence intervals. Catch rates were scaled to the mean of the two EDM population series over 2008–2010. Bottom: Time series over calendar years 2008–2014 showing the estimated catchability values estimated by EDM (base) and EDM (free-beta) fit over all years 1993–2014, by EDM as base but fit only over years 2008–2014, and by EDM (yearly) fit separately to each of years 2008–2014 and the 95% confidence intervals.

points (Table 1) for only a small number of additional parameters. The EDM-CSA estimated parameters q_l and q_r were well determined (CV of 8% and 2%) and not highly correlated with each other (r = 31%), which suggests no need to fix q_l/q_r, as is typically the case for CSA. The models are similar in so far as they are catch conditioned and include fitting of catch rates, and hence all critically depend to some extent on population depletion between moulting times.

The sensitivity of base and free-beta EDM to changes in the timing of the fitted depletion period did not indicate serious problems with the assumptions of no recruitment and constant catchability across January–March (Fig. 6). The strongly contrasting results by EDM when applied to December–January and March–April (Fig. 6), potentially indicate violation of assumptions, given that some recruitment is known to occur during December (Prescott et al., 1996; McGarvey et al., 1999) and female availability to fishing in April is reduced due to the approach of the moulting period (MacDiarmid, 1989) as lobsters are then less likely to forage actively (Miller, 1990; Ziegler et al., 2004). These hypotheses regarding bias are supported by Miller and Mohn (1993) who found that depletion models would overestimate start-period abundance when recruitment occurred during the assumed depletion periods, and that decreasing catchability during depletion periods resulted in underestimation of abundance.

Depletion modelling in which a common catchability parameter is estimated across all years allows for more robust estimates of abundance for the years with higher observation errors, and it allows situations with few data points per fitted depletion period to be utilised given sufficient years of data. However, catchability can in reality change over time and one approach is to model such change by an assumed form of non-linearity for catchability (e.g. free-beta EDM). Another approach described by Wilberg et al. (2010) is to model catchability as a step function of year (e.g. yearly-resolved EDM). The retrospective analysis results are con-

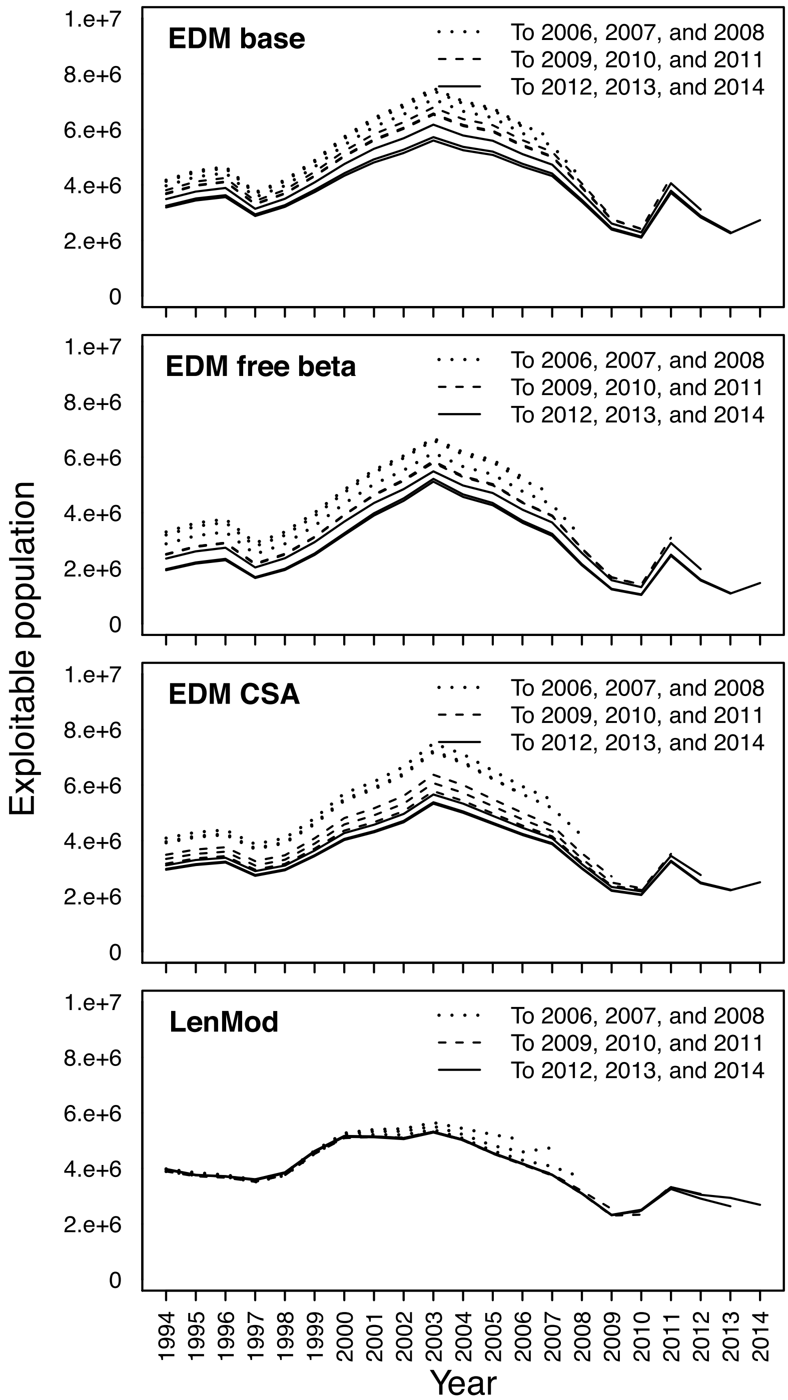

Fig. 9. Retrospective time series of start-January exploitable population size in the terminal year, for each of years 2006–2014. Top to bottom: EDM (base), free-beta EDM, EDM-CSA, and LenMod respectively.

sistent with the possibility of an increase in catchability having occurred since 2008 (Fig. 9), which is also suggested by estimates of catchability from yearly-resolved EDM (Fig. 8 (bottom)), particularly over 2011–2012. Likelihood ratio tests on EDM strongly reject (p-value < 1.0E−7) the null hypothesis of constant catchability during 2008–2014. Independent corroboration of a change in catchability during 2008–2014 comes from the divergence in trends between fishery catch rates and FIMS catch rates (Fig. 8), with the latter considered to be less biased as an indicator of true population trend (Linnane et al., 2015).

A hypothesis concerning changing catchability is that of hyperstability in the fishery catch rates (see Results). Linnane et al. (2015) report a spatial shift in fishing effort within the SZ fishery over recent seasons, which could induce hyperstability if the shift was towards higher density areas (Hilborn and Walters, 1992; Wilberg et al., 2010; Erisman et al., 2011; Ward et al., 2013). Fishers may target areas of higher catch rates (Linnane et al., 2015) or chase concentrations of higher priced smaller lobsters (Linnane and Crosthwaite, 2009). The latter behaviour could result in either hyperstability or hyperdepletion (localised depletion) depending on fleet and stock dynamics (Wilberg et al., 2010), although this study has found support for hyperstability in the regression of fishery catch rates on FIMS catch rates. However, over 2008–2014 the trend in estimated population size from free-beta EDM does not match that of the FIMS catch rates (Fig. 8). Thorson and Berkson (2010) report from simulation studies that the presence of both a separate yearly trend in catchability (e.g. due to technological improvements) and density-dependence can be difficult to model without auxiliary information and may lead to biases.

4.2. Modelling

EDM is similar to the multi-annual depletion models of Ehrhardt and Deleveaux (2009) and Roa-Ureta (2015) in the sense that those models simultaneously estimate all annual recruitment parameters using a monthly population dynamic equation. However, unlike EDM, the generalised depletion model of Roa-Ureta (2015) is conditioned on complete and exact fishing effort during the year, although it allows catchability to vary non-linearly with abundance and effort but with the associated parameters (e.g. β) assumed constant across all months of fishing. The models developed by Ehrhardt and Deleveaux (2009) and Bailey and Elner (1989) constrain annual recruitment to an amalgamated period, but their amalgamated period is strictly the fishery closed season. In principle, EDM requires no data on fishery-scale total effort, providing representative catch rates can be obtained from surveys over the fitted depletion period.

Royer et al. (2002) and Young et al. (2004) have also developed sub-yearly time-step depletion models that included use of indices of recruitment which were assumed to be without error, and each year was modelled separately with no inter-annual population dynamics. Similarly, Medley and Ninnes (1997) applied a daily depletion model to catch and effort data to obtain a relative index of yearly recruitment that was then assumed to be without error inside a yearly depletion model. However, EDM-CSA, in common with CSA studies, directly estimates yearly absolute recruitment levels by fitting to PRI data. The uncertainty in abundance estimates for CSA will be underestimated using maximum likelihood or bootstrapping of the data if uncertainty involving the fixed value for q_r/q_l is ignored (Brooks and Deroba, 2015).

4.3. Conclusions

This paper has shown that estimates from EDM compare reasonably with those from LenMod as applied to the SZ southern rock lobster fishery. More generally, EDM may be of use in single-stock fisheries in which data are limited, or as an auxiliary tool in more data-rich fisheries, where total catch in numbers are available (or inferable from mean weight) and a suitable fitted depletion period exists over a part of the fishing season. Similarly, EDM-CSA may be of use when pre-recruit index data are also available, regardless of whether there exist external constraints on catchability. The EDM estimation framework can detect significant arbitrary changes in catchability between years and complement inferences from fishery independent surveys. Overall, results from this study suggest that the assumption of constant catchability in lobster fishery models requires further consideration, particularly where catch rate hyperstability poses a risk to accurate stock assessment.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.02.019.

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Conclusion

Brief summary of contributions

This thesis has sought to provide outcomes for concerning the southern rock lobster (*Jasus edwardsii*) stocks of the SZRLF and the WZRLF in terms of identifying influences that impact on nominal catch rate through the mechanism of catchability. Identifying such influences on catch rate is important, aside from a purely scientific viewpoint, as catch rate forms a fundamental part of lobster stock assessments, which are conducted annually to monitor the sustainability of the stocks. In this thesis, studies were conducted that reported new findings on the nature of catchability of southern rock lobster due to the influence of abiotic environmental factors. However, it was further found that the quantitative impact on nominal catch rate by these environmental factors was relatively minor, and that a fishery factor, namely the entry/exit dynamics of fishing vessels, influenced the yearly trend of nominal catch rate more substantially. Another objective of the thesis was to develop and apply a novel method to estimate absolute exploitable abundance and recruitment given only data on catch and catch rate. This was achieved, and the method was applied to the data for the SZRLF, with results compared against those from an integrated population dynamics model used for stock assessment.

Outcomes and implications

In Paper One it was found that for the SZRLF the environmental covariates did not contribute substantially to either the trend or variance in CPUE. However, several covariates were retained after model selection, and Paper One details their effects on CPUE and compares them with results reported in the literature. The impact of moon phase was non-linear over the cycle of the moon, predicting an increase in mean CPUE of 10% at full moon compared to new moon, and a decrease of 4% compared to new moon for phases between the full and new moon. Wave period, and wave height lagged at three days, had an estimated positive influence on mean CPUE, while bottom temperature and (contemporary) wave height had a negative influence. The outcomes for full moon and lagged wave height are consistent with the anecdotal reports by some fishermen. Interestingly, the negative impact on CPUE by wave height was much stronger when the model was restricted to data for the inshore (< 40 m) than when it was restricted to the offshore (> 40 m), which suggests turbulence as a direct mechanism impacting on catchability. However, there was no significant contrast indicated between the inshore and offshore models for the estimated moon phase effect, supporting hypotheses involving endogenous timing. The same methodology was applied to the WZRLF, except sensitivity analyses were not conducted, which found similar qualitative outcomes and magnitudes to the SZRLF study, but moon phase was not supported as a significant influence. Inferences and implications were provided in Paper One, but below follows further discussion.

Paper One also determined that wind and sea surface height were not influential predictors for CPUE of the SZRLF and the WZRLF. This is potentially due to these covariates being naturally connected to bottom temperature (Drinkwater et al. 2006; Koeller, 1999; Schahinger, 1987), so they may provide no additional information on catchability that is not reflected in bottom temperature given the latter is probably a more direct influence in a lobster's immediate environment. Koeller (1999), studying the influence on American lobster catch of wind and temperature, urged caution when interpreting causal relationships between these three quantities over smaller (< 100 km) spatial scales and sub-yearly steps, due to potential confounding with changes in effort at different fishing locations driven by changing winds.

Unlike the snow crab fishery studied by Zisserson and Cook (2017), for the SZRLF over 1998-2008 no catastrophic impacts on CPUE are known to have occurred through the direct influence of temperature on mortality. The results from Paper One show that for the SZRLF, temperature does impact catchability, but only to a small extent. Southern rock lobster in the SZRLF appear resistant to the rapid drops in bottom temperature that occur several times over November-March in most years as a result of the "Bonney upwelling". This may suggest that the physiological mechanism of thermal acclimatization (Lagerspetz and Vainio, 2006) operates on southern rock lobsters by determining an appropriate preferred temperature and aerobic scope for activity (SFA) response curve (Crear and Forteath, 2000) conditioned on the range of temperatures they experience. One explanation for the estimated negative response of mean CPUE to temperature is based on the SFA hypothesis for catchability developed in Paper One. Suppose that the temperature for optimal SFA for the lobster stock is below the median value of the temperatures used in Paper One (14.2 °C), then the aerobic activity involved in foraging for food (and bait) will be increasingly inefficient at temperatures above the SFA optimal temperature. The possibility that within-year growth and depletion is confounded with temperature-driven catchability was investigated in Paper One by replacing the month factor covariate with spline functions of time smoothed to approximately weekly, monthly, or linear levels, which indicated only minor confounding at the sub-monthly scale.

In Paper Two the effects of vessel identifier was studied for the WZRLF by including it as a covariate in the CPUE standardization, along with fisher identifier, month, depth, and spatial block. The results indicated that changes occurred in the vessel composition of the fleet for much of 1978-2014, which contributed substantially to an increasing trend in net yearly catchability, meaning that the trend in standardized CPUE is more pessimistic than for nominal CPUE. In particular, it was found that the increases in estimated net catchability occurred predominantly for periods when the average catchability of exiting vessels was well below that of the rest of the fleet. Analysis in Paper Two was improved by contrasting the influence index ("I") of vessels with that of the combined non-vessel factors in the CPUE standardization, along with the index "V" that quantified discrepancies between nominal and standardized CPUE in terms of the magnitude of annual changes in total catchability. Moreover, the average annual increase in "I" for vessels over 1978-1995 for the WZRLF was 1.3%, which falls well within limits estimated for increases in fishing power reported from studies on the western rock lobster (*Panulirus cygnus*) fisheries in Western Australian that utilized time series of on-board equipment data (Fernandez et al., 1997; de Lestang et al., 2009). However, inferences drawn about catchability increases are limited in relation to improvements in vessel technologies for the WZRLF, given the lack of a time series of vessel data on changes in on-board equipment.

Catchability for the WZRLF is more complex than a simple upward influence on catchability due to vessel effects since introduction of TACC in 2001. The fleet contracted over 2000-2014 (Figure 4 in Paper Two), but an upward trend in vessel influence on catchability over that period was only estimated over 2000-2003 and 2009-2012. The literature on the function of TACC/ITQ in fisheries suggests that fleet reductions are associated with less efficient owners selling their quota to more efficient owners (e.g. Branch et al., 2006; Pascoe et al., 2013). Concerning 2009-2012 Paper Two suggested that this may have occurred due to the level of both TACC and lobster biomass by then having fallen sufficiently low to make it uneconomic to fish with vessels of low catchability. In contrast, Leon et al. (2015) found that for the Tasmanian TACC/ITQ lobster fishery, changes in permanent quota ownership were linked not to technical efficiency of the operators but to their financial capacity and that exiting of vessels was associated with operators of lower financial capacity, with this occurring only during periods of increasing biomass. However, the results reported here for the WZRLF, indicate that standardized CPUE respectively increased, decreased, and increased during 2000-2003, 2004-2008, and 2009-2012, and that these periods involve respectively low, high, and low fishing efficiency of exiting vessels. The link between periods of stock growth and vessel efficiency for the WZRLF is not observed for the period prior to TACC inception.

In Paper Three the novel multi-year depletion models EDM and EDM-CSA were applied to data for the SZRLF estimating yearly absolute recruitment numbers and start-January exploitable abundance for 1994-2014. The depletion period was January-March, over which no recruitment or change in catchability was assumed to occur. Aside from biological considerations, this was supported by sensitivity analyses testing alternative two-month depletion periods, which indicated that only over January-February and February-March did estimates of catchability not differ significantly (Fig. 6 of Paper Three). EDM and EDM-CSA estimates agreed reasonably well with those estimated by LenMod for both the mean level of estimated recruitment (within 3%) and abundance (within 12%). The density-dependent “free-beta” version of EDM indicated the presence of a significant degree of hyperstability (beta of 0.529, 95% CI 0.371–0.687) for CPUE of the SZRLF. Hyperstability was also supported by another analysis conducted in Paper Three that regressed commercial fishery CPUE on the CPUE from fishery-independent monitoring surveys (FIMS), following the approach of Harley et al. (2001).

Paper Three included an investigation into why the trend in the FIMS CPUE was more pessimistic than that in commercial fishery CPUE over calendar years 2008-2014 for the SZRLF. EDM was fit separately to data sets per individual year, revealing that estimated catchability roughly doubled over 2012-2014 compared to the common catchability estimate from EDM fit simultaneously to 1994-2014 (“base EDM”). Moreover, the trend in FIMS CPUE over 2008-2014 is closer to that exhibited by the abundance estimates from yearly fit EDM than to the trends in either the abundance estimates from base EDM, free-beta EDM, or commercial fishery CPUE. More generally, comparison of yearly-applied and base EDM estimates of catchability could be very beneficial for fisheries with no FIMS CPUE data by indicating the presence and direction of a change in catchability among years. However, a caveat exists on the detection of a change between years in catchability when that is associated with a change to catchability within the fitted depletion period of EDM (Miller and Mohn, 1993).

Ideas for Further Research

- The CPUE standardization and diagnostic analyses for the WZRLF could be repeated for the SZRLF. CPUE standardization was recently conducted for the SZRLF that showed only a minor difference in trend between standardized and nominal CPUE, but that did not include a covariate for vessel identifier as there was none. However, it may be feasible to construct a proxy index for vessel identifier that is unique and consistent through time, based on information that is external to the research catch-effort database. If this proves successful, CPUE standardization for the SZRLF will be better informed than it is currently by accounting for changes in catchability induced by changes in vessel fleet composition.
- The WZRLF analysis should be extended by adding a term for interactions between year and vessel effects to the CPUE standardization model. This would effectively model a separate relative abundance index per vessel (Maunder and Punt, 2004). However, interpretation of the results of this analysis would need careful consideration, since although adding such interaction terms may provide a proxy method to test for effects of technology upgrades to on-board vessel equipment, it may also confound with other factors (Maunder and Punt, 2004). The influence (“I”) indices described in Paper Two would also need modification.

- The EDM model framework could be further developed to provide a diagnostic indicator on the consistency of catchability between years that is implicitly assumed in the interpretation of yearly CPUE statistics as a measure of relative abundance. This could be important given that yearly CPUE is a fundamental input into the SZRLF's harvest strategy algorithm which determines the level of TACC each year (Linnane et al., 2017). For example, exploratory data analysis suggests that a substantial shift in the within-season distribution of fishing effort occurred away from January-March to earlier in the fishing season (October-December) going from season 2010 to 2011. This potentially implies a change in net catchability during these periods as a result of changing lobster vulnerability and fishery factors. The nature of such changes in catchability would need further investigation. Note also that improved CPUE standardization of the kind suggested further above may also be beneficial.
- EDM may be able to provide valid start-January exploitable biomass and catchability estimates, given catch and CPUE are also reported by the SZRLF in weight of animals caught (instead of numbers of animals). However, this would overestimate recruiting biomass given that growth among legal sized lobsters during the amalgamated period (April-December) would be included in the estimates. In order to obtain both valid estimates of recruitment as well as biomass, it may be possible to develop the EDM population dynamics model by adding a term for growth of contemporary biomass using growth parameterization such as that described for delay-difference models by Smith and Addison (2003).
- Running the various forms of EDM (base, EDM-CSA, free-beta EDM, and yearly EDM) with data extended to calendar year 2017 may be worthwhile. Similarly, it would be interesting to simulation test EDM fitted to data generated under varying regimes of (assumed) true length-sex vulnerability, using data simulated from a length-sex fishery model such as LenMod. Other aspects such as the sensitivity of EDM to hyperstability in CPUE could also be examined. One motivation for these suggested tasks is that the version of LenMod that was used as part of the SZRLF stock assessment at the time the analysis was performed for the EDM analysis in Paper Three, modelled the same length vulnerability function for all months within a season. Since then LenMod sensitivity modelling work (on data to season 2016) was conducted that involved varying length vulnerability within a season, and which resulted in lower estimated net length-sex vulnerability than was estimated by the previous version of LenMod.

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Supplementary material for Paper Two

Figure S1

Residual diagnostic plots of the main model as per equation 1 of the main text.

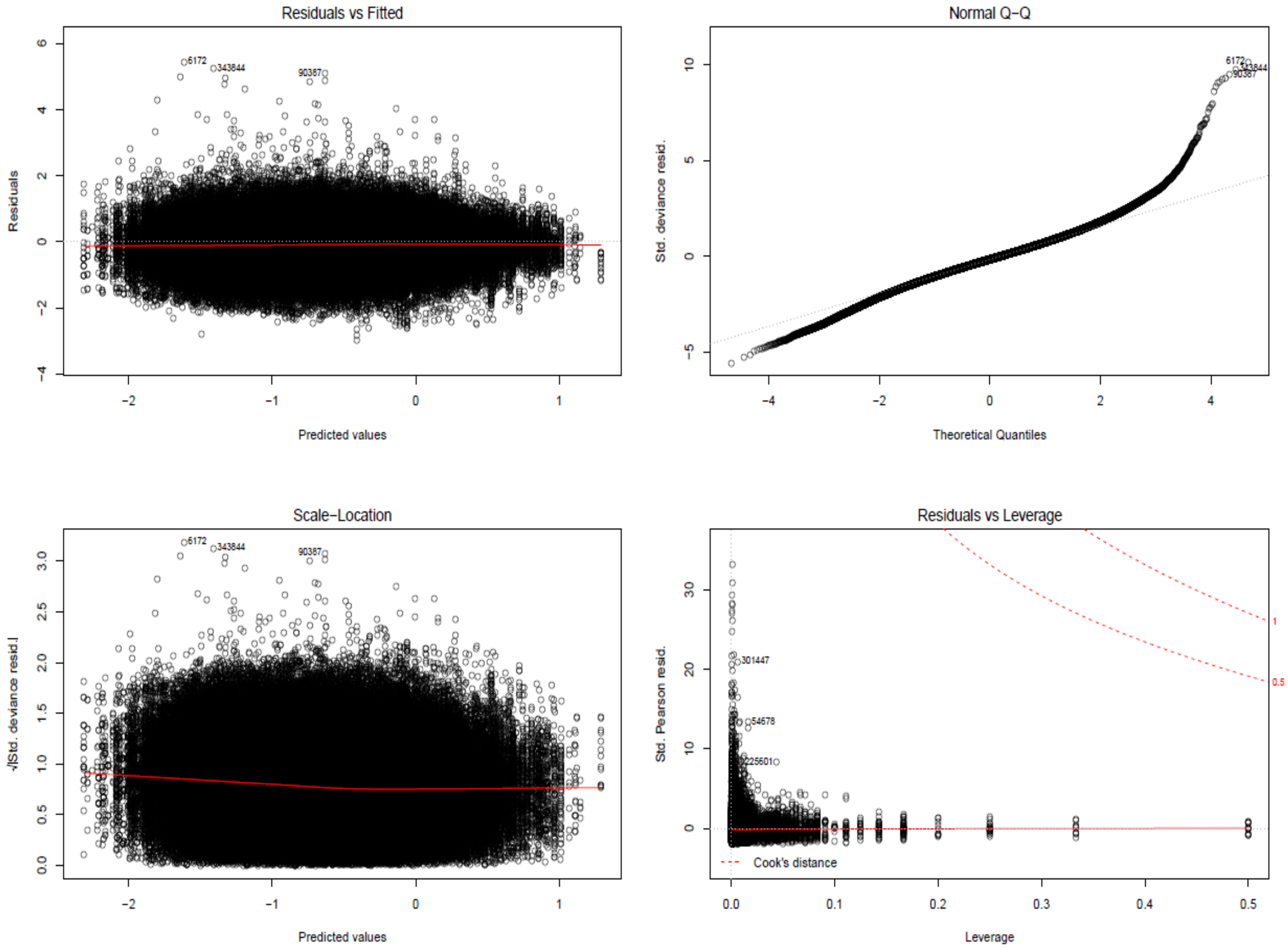
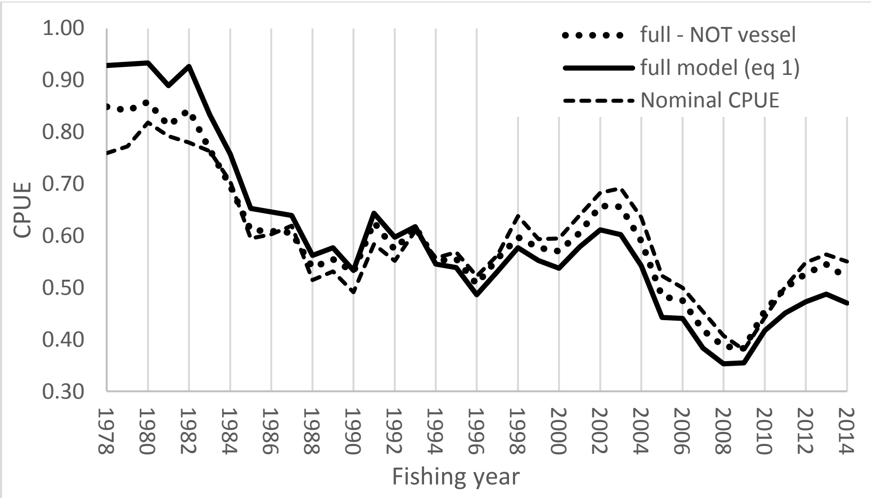
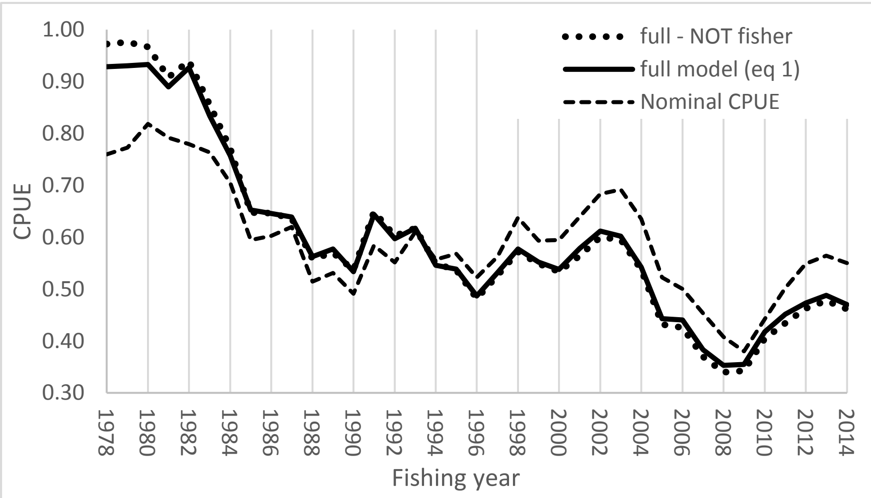
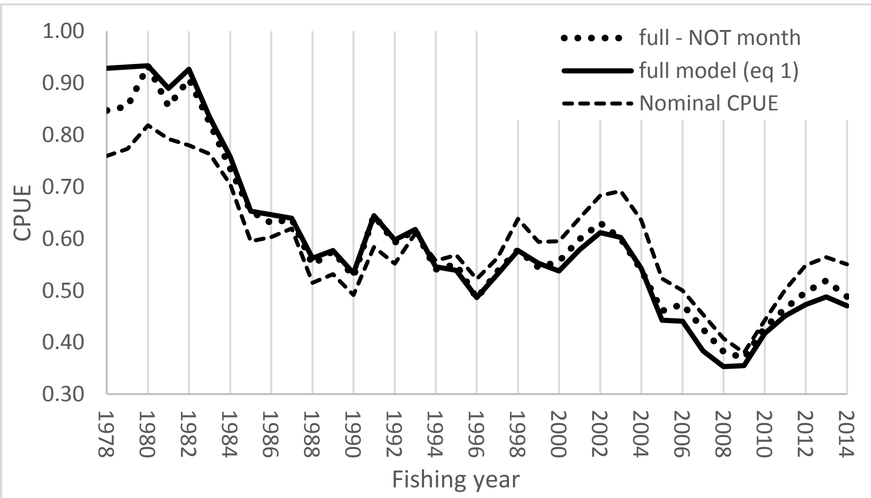


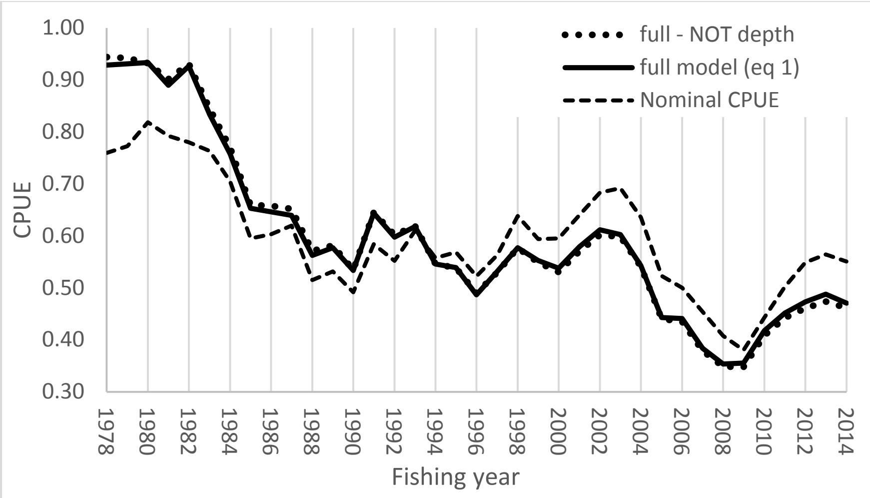
Figure S2

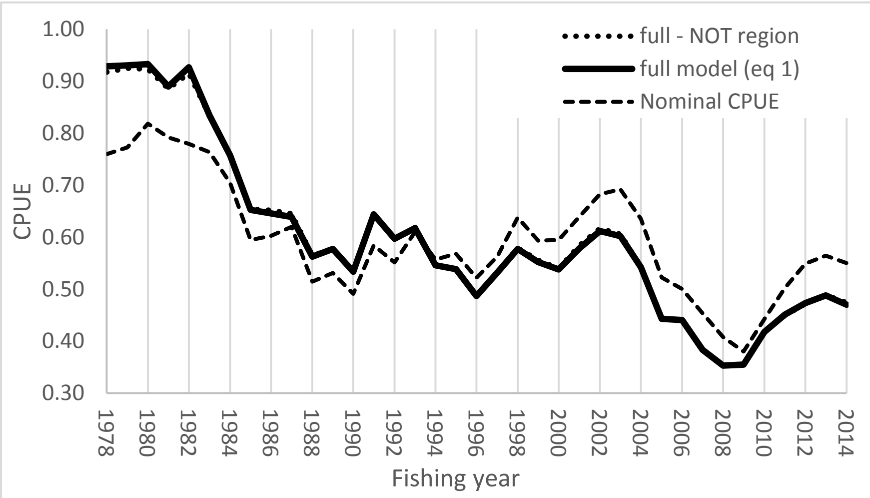
Standardised CPUE (mean scaled to nominal CPUE) for models as equation 1 in Methods of the text but with single terms excluded.








full - NOT depth
full model (eq 1)
Nominal CPUE
CPUE
Fishing year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Nominal CPUE
CPUE
Fishing year

Figure S3

Comparison between nominal CPUE trends: via the ratio estimator (as per Methods in the text) and via the geometric mean.

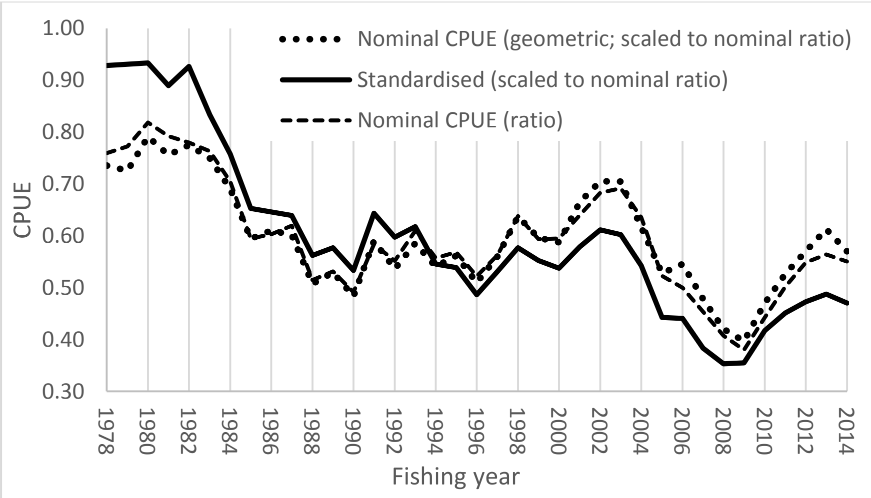
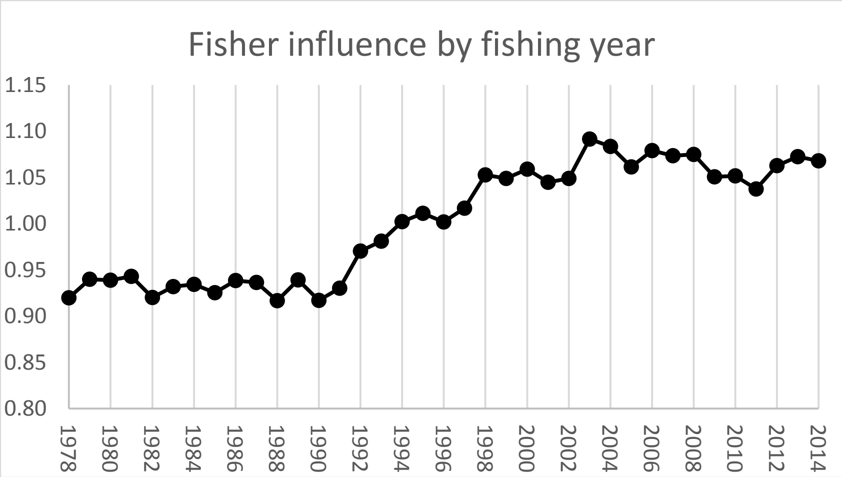
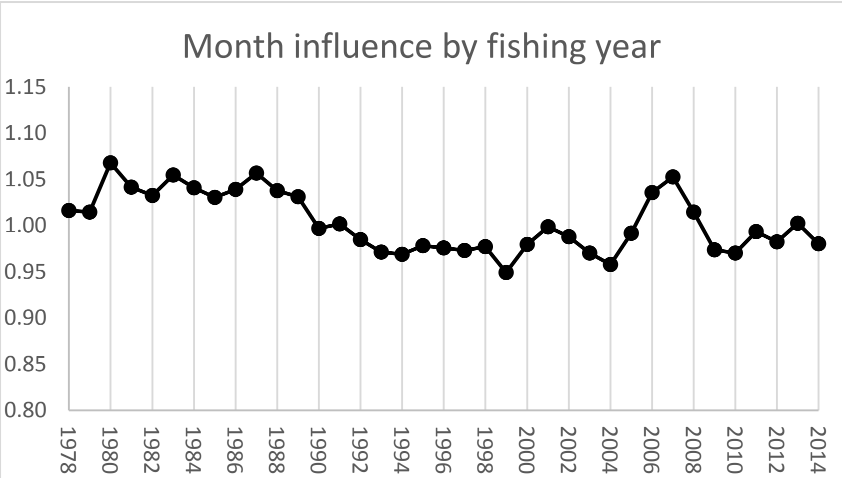
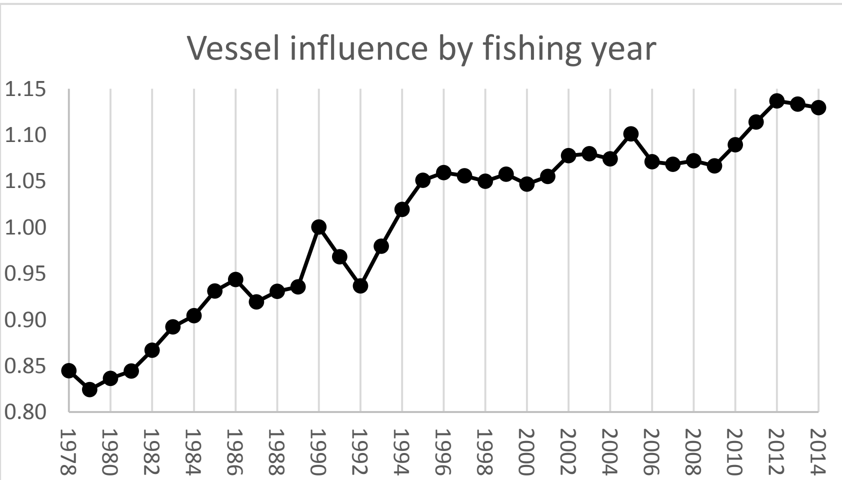


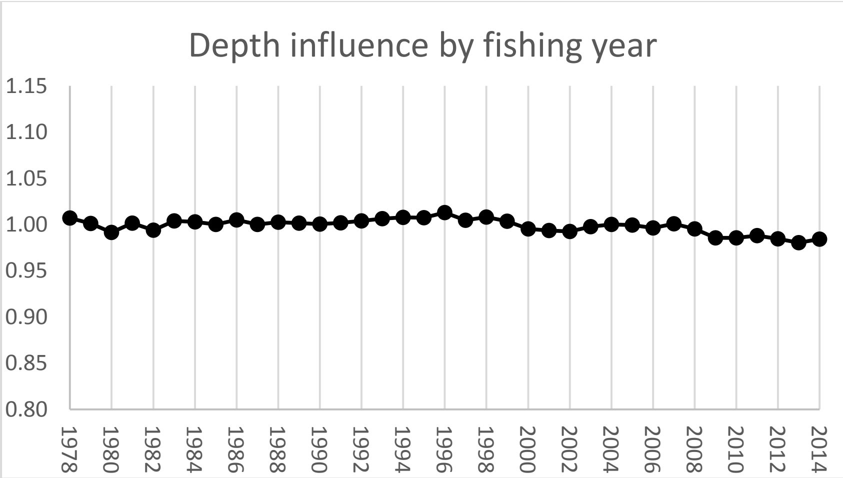
Figure S4

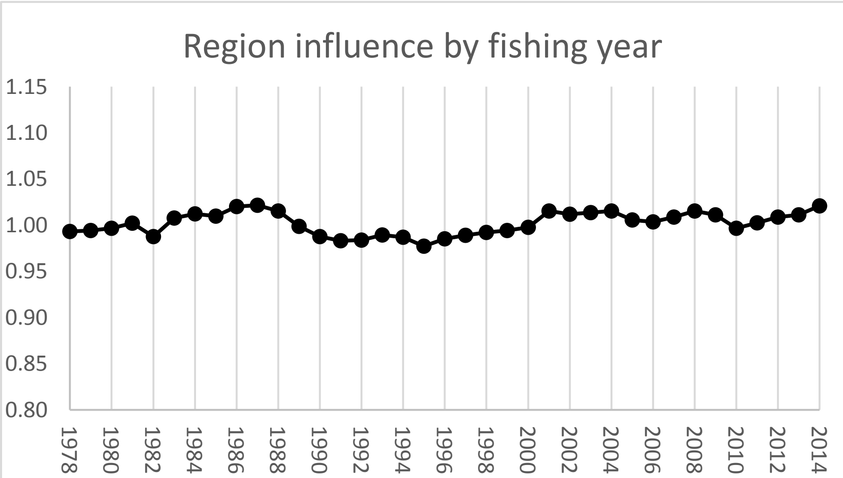
Influence" statistics by year for each of the non-year terms in the GLM equation 1 described in Methods of the text.








Depth influence by fishing year
1.15
1.10
1.05
1.00
0.95
0.90
0.85
0.80
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014


Region influence by fishing year
1.15
1.10
1.05
1.00
0.95
0.90
0.85
0.80
1978
1980
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1984
1986
1988
1990
1992
1994
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2012
2014

Supplementary material for Paper Three

A. Relationship between fishery catch rates and FIMS catch rates.

The power parameter, β, in the hypothesized power relationship between commercial fishery logbook catch rates and FIMS catch rates was estimated using log-log regression. The results (Fig. A.1) showed no pathology in residual diagnostics (results not shown). The estimate of β was 0.395 (95% CI 0.067-0.722), which would indicate statistically significant hyperstability.

However, measurement error in the FIMS catch-rates would negatively bias β in direct proportion to the ratio of the variance in the log of fishery catch rates to the sum of the variances in the log of the fishery catch rates and the log of the FIMS catch rates (Fuller, 1987). Hence the size of the potential bias will depend on the (unknown) level of error in the fishery catch rates as well as the error in the FIMS catch rates. Hence a simulation-extrapolation method (SIMEX: Gould et al., 1997, 1999) was applied using measurement error variances for the FIMS catch rates. Variances for the FIMS catch rates since season 2006 have recently been calculated (personal communication) using a method designed for systematic sample means and which account for the spatial autocorrelation typical of clustering species. The CV% values for legal size catch rates for each of the summer FIMS surveys for calendar years 2007-2014 inclusive (seasons 2006-2013) ranged between 5% and 10%, and a value for summer FIMS survey of calendar year 2006 was assumed to equal that of the 2007 survey. The original FIMS data series together with the survey variances were then used to generate a simulated data set of 10,000 replicate FIMS catch rate series, with each replicate series produced by adding a given level of normally distributed error to the original FIMS data values. This was repeated for several sets of 10,000 replicates, with each set differing by assuming a different multiplier constant (lambda) of the variance defining the normal distribution of errors. Log-log regressions of the original fishery catch rates on each of the replicate FIMS catch rate data series were then performed, and for each simulated data set a sample mean (across 10,000 values) of β was computed. Then, following the SIMEX methodology, an unbiased estimate was obtained by plotting each mean β value versus lambda that indicated a linear relationship, and that was then used to extrapolate to where lambda equals -1 to obtain the SIMEX estimate for β.

The resulting extrapolated value for β equaled 0.401 (Fig A.2), and implies only a minor amount of negative bias in the log-log regression estimate. Similarly, the sample standard deviation of the 10,000 β values for the simulation with lambda equal to 1 was 0.028, and this lead to the standard error on β increasing from 0.138 (original regression) to 0.141, suggesting only minor underestimation of the total error on β.

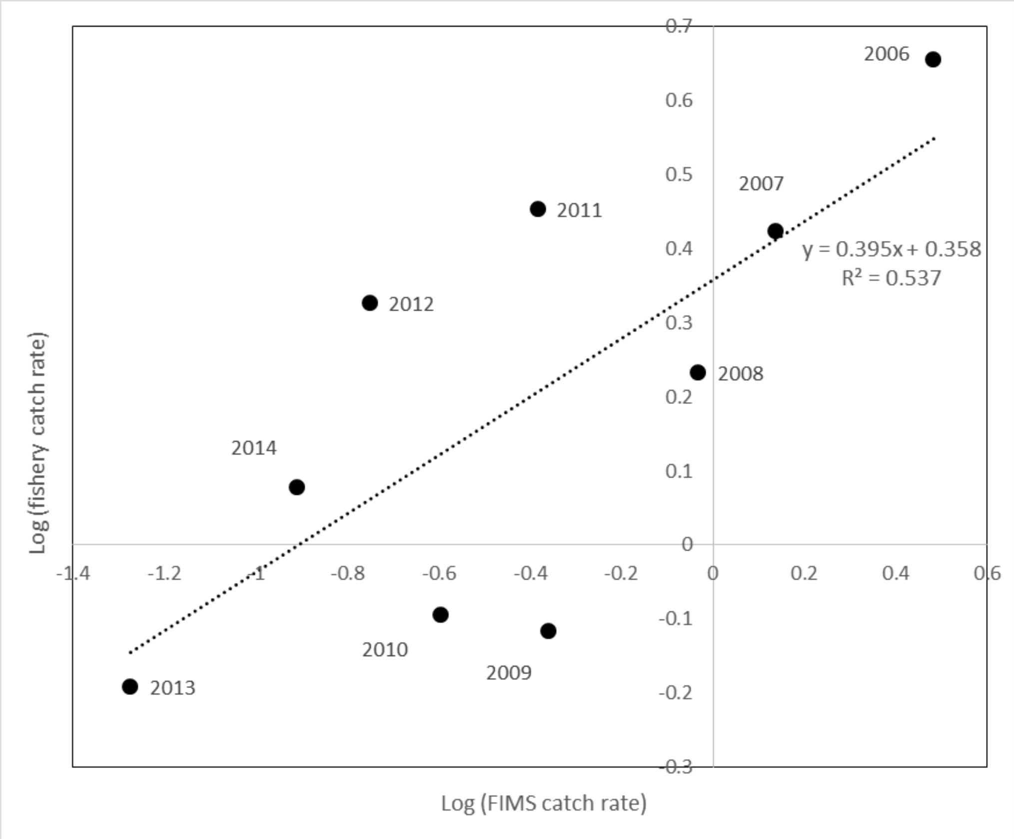

Fig. A.1 Linear regression of logged commercial logbook catch rate (numbers of lobsters / number of potlifts) on logged FIMS catch rate (numbers of lobsters / number of potlifts). The catch rates are those for summer months involving FIMS sampling (January-February surveys) for calendar years 2006-2014.

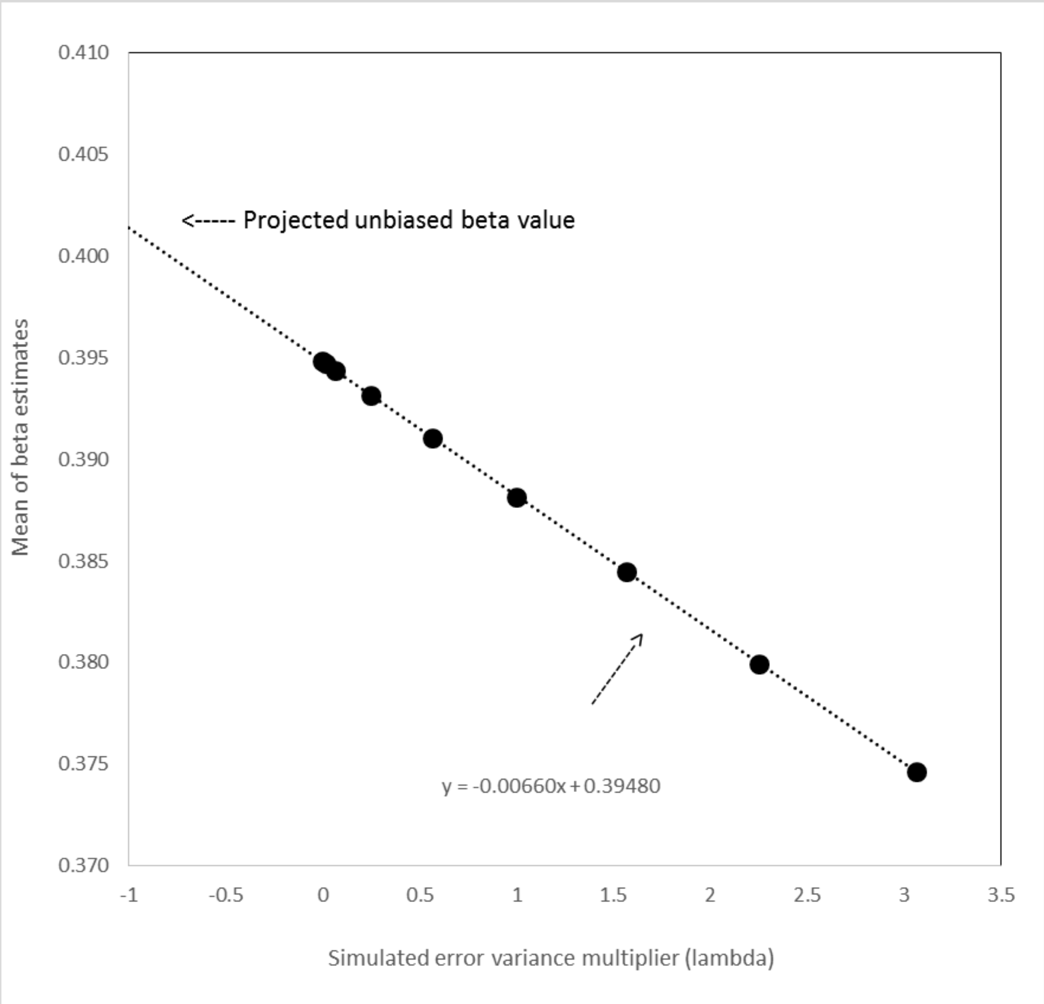

Fig. A.2 Trend in sample mean estimates of β from 10,000 replicates for each of several levels of simulated observation error in the FIMS catch rates as a function of error variance multiplier, according to the SIMEX method.

B. Specifications of the length-structured model (LenMod).

Overview

Various versions of the initial model formulation (Punt and Kennedy, 1997) have formed part of stock assessments for southern rock lobster off Tasmania, Victoria and South Australia for many years (e.g., Punt and Kennedy, 1997; Hobday and Punt, 2001; Punt, 2003; McGarvey et al., 2010; Linnane et al., 2015). The model is known as "LenMod" in South Australia, and a condensed form of model specifications can be found in McGarvey et al. (2015), while this present specification is a more detailed form that is as found in Linnane et al. (2015) but for a small number of modifications. LenMod is a population dynamics model that operates on a fishing season defined over, for the Southern Zone Rock Lobster Fishery, T = 9 time-steps (months), starting with the opening of the fishing season in October (i=1) to May (i=8), with a multi-month June-September (i=9) time step covering each closed winter season. The duration of the i^{th} time-step (i=1,..,T) in units of years is denoted t_i. Lobster size-classes are in 4 mm bins, the lowest length bin defined as 82.5-86.5 mm CL, with 29 bins for males and 21 for females. The model population array, $N^s_{y,i,l}$, is the number of lobsters by length bin (l), sex (s), fishing season (y; hereafter referred to as year), and month (i).

The population dynamics model

Basic dynamics

The equation that specifies $N^s_{y,i,l}$ takes account of natural mortality M (instantaneous yearly rate), fishing mortality, growth, and settlement under the assumption that harvest occurs before growth and settlement:

$$N^s_{y,i+1,l} = \sum_{l'} X^s_{l',l,i}\, N^s_{y,i,l'}\, e^{-Mt_i} \{1 - \tilde{H}^s_{y,i,l'}\} + \Omega^s_i \Phi^s_l\, R_y \qquad (1)$$

where:

$X^s_{l',l,i}$ is the fraction of the animals of sex s in size-class l' that grow into size-class l during time-step i; Ω^s_i is the fraction of the settlement that occurs to sex s during time-step i ($\sum_s \sum_i \Omega^s_i = 1$); Φ^s_l is the proportion of the settlement of animals of sex s that occurs to size-class l;

$\tilde{H}^s_{y,i,l'}$ is the exploitation rate on animals of sex s in size-class l' at the start of time-step i of year y over all fleets; and

R_y is the settlement of animals during year y:

$$R_y = \bar{R}\; e^{\varepsilon_y - (\sigma_{R,y})^2/2} \qquad (2)$$

where: $\bar{R}$ is mean settlement, ε_y is the "settlement residual" for year y, $\sigma_{R,y}$ is the standard deviation of the random fluctuations in settlement for year y:

$$\sigma_{R,y}^2 = \begin{cases} \tilde{\sigma}_R^2\, \tilde{\tau}^{(y_{\text{start}}-y)} & \text{if } y \le y_{start} \\ \tilde{\sigma}_R^2 & \text{otherwise} \end{cases} \tag{3}$$

$\tilde{\sigma}_R$ is the extent of variation in settlement for years after y_{start}, and $\tilde{\tau}$ determines the extent to which $\sigma_{R,y}$ changes with time ($\tilde{\tau} < 1$ means that the settlement will be closer to the mean settlement for the years before y_{start}).

Egg production is given by the following equation for the case in which spawning is assumed to occur at the start of time-step i_m of year *y*:

$$\tilde{B}_y = \sum_l Q_l \; N^{\text{f}}_{y,i_m,l} \tag{4}$$

where Q_l is the expected number of eggs produced by a mature female in size-class *l*, and i_m is the time-step in which spawning occurs (month 1) and $N^{\text{f}}_{y,i_m,l}$ being the total number of such females.

Catches

$C^f_{y,i}$ which is the landed catch in weight data by fleet *f* during time-step *i* of year *y*. In addition to landed catch, commercial data includes information on spawning lobsters and those brought up dead in the pots, while four surveys (1998, 2001, 2004, and 2007) are used as the basis to estimate catches for the recreational fleet. $C^f_{y,i}$ is used in defining the fully-selected exploitation rate for fleet *f* during time-step *i* of year *y*, $F^f_{y,i}$, is calculated as follows:

$$F^f_{y,i} = \frac{(1+d^f_{y,i})C^f_{y,i}}{\sum_l \sum_s \tilde{S}^{s,f}_{y,i,l}\,(1-\tilde{p}^s_{i,l})V^s_i\, W^s_l\; N^s_{y,i,l}e^{-Mt_i/2}} \tag{5}$$

where

$d^f_{y,i}$ is the ratio of the discarded dead catch to the legal-size catch for fleet *f* (only for commercials, and is 0 for recreationals);

V^s_i is the relative vulnerability of males to females during time-step *i* (V^s_i =1 for males);

$\tilde{p}^s_{i,l}$ is the proportion of mature animals of sex *s* in length-class *l* which are returned live during time-step *i* because they are spawning (0 for males); and

$\tilde{S}^s_{y,i,l}$ is the vulnerability by length for the gear used on animals of sex *s* in size-class *l* during time-step *i* of year *y* incorporates the legal minimum size as:

$$\tilde{S}^s_{y,i,l} = \begin{cases} 0 & \text{if } L^s_l + \Delta L^s_l \le \text{LML}_y \\ S^s_{y,i,l} & \text{if } L^s_l \ge \text{LML}_y \\ S^s_{y,i,l}(L^s_l + \Delta L^s_l - \text{LML}_y) / \Delta L^s_l & \text{otherwise} \end{cases} \tag{6}$$

$\tilde{S}^{s,f}_{y,i,l} = \tilde{S}^s_{y,i,l}$, as the same gear is assumed for commercial and recreational fishers.

L_l^s is the lower limit of size-class *l* for sex *s*, ΔL_l^s is the width of a size-class *l* for sex *s* (4 mm), LML_y is the legal minimum size during year *y*, $S_{y,i,l}^s$ is the vulnerability of the gear used on animals of sex *s* in size-class *l*. (There were no changes in LML_y, which is 98.5 mm carapace length, over the whole time series for the Southern Zone Rock Lobster Fishery.)

$F_{y,i}^f$, is used to define $\tilde{H}_{y,i,l'}^s$ as follows:

$$\tilde{H}_{y,i,l}^s = \sum_f \tilde{S}_{y,i,l}^s (1 - \tilde{p}_{i,l}^s) V_i^s F_{y,i}^f \qquad (7)$$

Initial conditions

It is impossible to project this model from unexploited equilibrium owing to a lack of historical catch records for the entire period of exploitation. Instead, it is assumed that the population was in equilibrium with respect to the average catch over the first five years for which catches are available in year $y_{start} - 20$. This approach to specifying the initial state of the stock differs from that traditionally adopted for assessments of rock lobster off Tasmania and Victoria (Punt and Kennedy 1997; Hobday and Punt 2001) in that no attempt is made to estimate an initial exploitation rate. The settlements for years $y_{start} - 20$ to $y_{start} - 1$ are treated as estimable so that the model is not in equilibrium at the start of year y_{start}.

The objective function

The objective function summarises the information collected from the fishery and contains contributions from four data sources:

a) Commercial catch and independent catch rates,
b) length-sex frequency data from sampling of commercial pot lifts, and
c) commercial catches in number.

Catch-rate data

The contribution of the catch-rate data for the commercial fishery to the likelihood function is given by:

$$L_{1.a} = \prod_y \prod_i \frac{1}{I_{y,i}^{\mathrm{Comm}} \sqrt{2\pi}\, \sigma_{q,i}^{Comb}} \exp\left(-\frac{(\ell\mathrm{n} I_{y,i}^{\mathrm{Comm}} - \ell\mathrm{n}(q_i^{\mathrm{Comm}} B_{y,i}^{e,\mathrm{Comm}}))^2}{2(\sigma_{q,i}^{Comb})^2} \right) \qquad (8.a)$$

while the contribution of fishery-independent monitoring survey (FIMS) index data to the likelihood function is given by

$$L_{1.b} = \prod_y \prod_i \frac{1}{K_{y,i}^{\mathrm{FIMS}} \sqrt{2\pi}\, \sigma_{q,i}^{Comb}} \exp\left(-\frac{(\ell\mathrm{n} K_{y,i}^{\mathrm{FIMS}} - \ell\mathrm{n}(\tilde{\tilde{q}}^{\mathrm{FIMS}} q_i^{\mathrm{Comm}} B_{y,i}^{e,\mathrm{Comm}}))^2}{2(\sigma_{q,i}^{Comb})^2} \right) \qquad (8.b)$$

where:

q_i^{Comm} is the commercial catchability coefficient;

$I_{y,i}^{\mathrm{Comm}}$ is the catch-rate index for the commercial fleet for year *y* and time-step *i*;

$\sigma_{q,i}^{Comb}$ is the standard deviation of the observation error for the commercial fleet and FIMS surveys combined for time-step *i*;

$\tilde{\tilde{q}}^{\text{FIMS}}$ is the FIMS catchability coefficient; and

$K_{y,i}^{\text{FIMS}}$ is the FIMS catch-rate index for time-step *i* of year *y*.

FIMS catch rates are available (since 2005 for the Southern Zone Rock Lobster Fishery) and are derived from sampling pots spaced evenly across transects which span a larger spatial region than that of the concentrated fishing grounds, where catchability by month is assumed to be the same as that for the commercial fishery. The maximum likelihood estimates for q_i^{Comm} and $\sigma_{q,i}^{Comb}$ were obtained analytically, while the value for $\tilde{\tilde{q}}^{\text{FIMS}}$ was estimated as part of the non-linear search procedure. A separate set of q_i^{Comm} and $\sigma_{q,i}^{Comb}$ were estimated for the years prior to TACC introduction (seasons 1983-1992 for the Southern Zone Rock Lobster Fishery) and the period thereafter.

$B_{y,i}^{e,\text{Comm}}$ is the exploitable biomass available to the commercial fishery (and recreational fishery) during time-step *i* of year *y*:

$$B_{y,i}^{e,Comm} = \sum_s \sum_l V_i^s \; \tilde{S}_{y,i,l}^s \; W_l^s \; e^{-Mt_i/2} N_{y,i,l}^s (1 - \tilde{H}_{y,i,l}^s / 2) \tag{9}$$

Length-frequency data

Length and sex frequency data are available from a sampling program which has been conducted since 1991. This program involves voluntary reporting on the contents of pot lifts by some commercial fishers. The observed fraction, during time-step *i* of year *y* by the commercial fishery, of the catch (in number) of animals of sex *s* in size-class *l* (including undersize) is denoted $\rho_{y,i,l}^{s,\text{Comm}}$. The model-estimate of this quantity, $\hat{\rho}_{y,i,l}^{s,\text{Comm}}$, takes account of the vulnerability of the gear and the numbers in each size-class and sex:

$$\hat{\rho}_{y,i,l}^{s,\text{Comm}} = \tilde{S}_{y,i,l}^s V_i^s (1 - \tilde{p}_{i,l}^s) N_{y,i,l}^s / \sum_{s'} \sum_{l'} \tilde{S}_{y,i,l'}^{s'} V_i^{s'} (1 - \tilde{p}_{i,l'}^{s'}) N_{y,i,l'}^{s'} \tag{10.a}$$

The observed value of $\rho_{y,i,l}^{s,\text{Comm}}$ is assumed to be multinomially distributed, giving the length-sex frequency likelihood function (ignoring multiplicative constants):

$$L_2 = \prod_y \prod_i \prod_l \prod_s \left(\hat{\rho}_{y,i,l}^{s,\text{Comm}} \right)^{n_{y,i,l}^{s,\text{Comm}} \omega} \tag{10.b}$$

where $n_{y,i,l}^{s,\text{Comm}}$ is the observed number of lobsters in the sampling program in time-step *i* of year *y* of sex *s* and size-class *l* , and ω is a down-weighting constant factor to reduce influence of this data relative to the catch-effort data sets (since catch sampling is not random and selectivity is not stationary). Undersize length-sex frequencies are fit as part of the full length-sex frequency data from the sampling program, with the model catch number predictions given by:

$$S_{y,i,l}^s V_i^s (1 - \tilde{p}_{i,l}^s) N_{y,i,l}^s e^{-Mt_i/2} \tag{11.a}$$

The length-sex frequencies for spawners are also assumed to be multinomial samples, except the model catch number predictions are:

$$S_{y,i,l}^s V_i^s \tilde{p}_{i,l}^s N_{y,i,l}^s e^{-Mt_i/2} \tag{11.b}$$

Catch-in-number

The commercial catches in number, $C^N_{y,i}$, are assumed to be lognormally distributed. The contribution of these data to the likelihood function is therefore given by:

$$L_3 = \prod_f \prod_y \prod_i \frac{1}{C^N_{y,i}\sqrt{2\pi}\sigma_N} \exp\left(-\frac{(\ell\text{n}C^N_{y,i} - \ell\text{n}\hat{C}^{N,\text{Comm}}_{y,i})^2}{2\sigma^2_N} \right) \tag{12}$$

where $\hat{C}^N_{y,i} = \sum_s \sum_l V^s_i \,\tilde{S}^s_{y,i,l}\,(1-\tilde{p}^s_{i,l}) N^s_{y,i,l}\, e^{-Mt_i/2} F^{\text{Comm}}_{y,i}$ and σ^{Comm}_N is the standard deviation of the observation error in catch numbers for the commercial fleet, assumed to apply over all time. The spawner discards are also fitted under the assumption that they are lognormally distributed.

Parameter estimation

Table B.1 lists the parameters of the population dynamics model and the objective function, and highlights those parameters assumed to be known exactly and those parameters whose values are estimated by fitting the model to the data. Vulnerability-at-length for each fleet is estimated, separately for each sex, by a logistic function of length, and is the same for commercial and recreational fishers. Female vulnerability by time-step is estimated. Female spawner fractions are based on auxiliary information.

A constraint is placed on the settlement residuals to stabilise the estimation and prevent confounding with mean recruitment. The following term was included in the objective function:

$$P = 0.5\sum_y (\varepsilon_y)^2 / (\sigma^2_{R,y}). \tag{13}$$

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Table B.1.
Parameters of the length-structured model (LenMod) model and their sources for the Southern Zone Rock Lobster Fishery.

Parameter	Description	Value
ε_y	The settlement residuals for year *y*	Estimated
$\ell n(\bar{R})$	Mean settlement	Estimated
$\tilde{\sigma}_R$	The extent of variation in settlement for years after y_{start}	0.5
$\tilde{\tau}$	The extent to which $\sigma_{R,y}$ changes with time	0.8
$X^s_{l',l,i}$	Growth transition matrix	Matrices by sex for months 3 and 8.
M	Natural mortality	0.1 yr^{-1}
V^s_i	Relative vulnerability of males to females by time-step	Estimated
$S^s_{y,i,l}$	Vulnerability of the gear by sex, size-class, time-step, and year.	Estimated as sex-specific logistic functions of length
$\tilde{p}^s_{i,l}$	Proportion of mature spawning animals by sex, size-class and time-step	
Ω^s_i	Fraction of the settlement by time-step and sex	Estimated
Φ^s_l	Proportion of the settlement of animals by sex and size-class	First six length bins: males = 0.35, 0.2, 0.15, 0.15, 0.1, 0.05; females = 0.45, 0.25, 0.15, 0.1, 0.05, 0
Q_l	Egg production as a function of size	
W^s_l	Mass as a function of size and sex	Power function of length
i_{m}	The time-step in which spawning occurs	1
$q^{\text{Comm}}_i, \tilde{\tilde{q}}^{\text{FIMS}}$	Catchability for the commercial fleet and FIMS by time-step *i*	Estimated
$\sigma^{Comb}_{q,i}$	Standard deviation of the observation errors for time-step *i* for the commercial fleet and FIMS surveys combined.	Estimated
σ^{Comm}_N	Standard deviation of the observation error in commercial catch in numbers	Estimated
ω	Down-weighting factor for length-sex data	0.0125

C. Tables:

Supplementary Table S1

Undersize length frequencies per season (January-March) in 4 mm length bins, normalized to 1 across the four bins, from the catch sampling data. Below the length frequencies are provided length selectivity per bin mid-point estimated by LenMod (mean across sex) and the probability of growth from each bin to above legal size derived from growth transition matrices (mean across sex and month) that are inputs into LenMod. Note: Frequencies for November-December differed trivially to those for January-March.

Season (Jan.-Mar.)	4 mm length bins			
	82.5-86.5	86.5-90.5	90.5-94.5	94.5-98.5
1993	0.11	0.21	0.31	0.37
1994	0.13	0.25	0.31	0.31
1995	0.11	0.20	0.30	0.39
1996	0.12	0.21	0.30	0.37
1997	0.12	0.22	0.29	0.37
1998	0.10	0.20	0.32	0.39
1999	0.09	0.19	0.29	0.43
2000	0.06	0.15	0.31	0.48
2001	0.08	0.17	0.30	0.44
2002	0.05	0.15	0.29	0.51
2003	0.09	0.17	0.28	0.46
2004	0.07	0.17	0.30	0.46
2005	0.09	0.19	0.29	0.43
2006	0.07	0.16	0.30	0.47
2007	0.10	0.17	0.27	0.45
2008	0.10	0.18	0.29	0.43
2009	0.15	0.24	0.30	0.31
2010	0.09	0.18	0.30	0.43
2011	0.10	0.19	0.28	0.42
2012	0.12	0.19	0.28	0.41
2013	0.09	0.23	0.31	0.37
Mean relative frequency	0.10	0.19	0.30	0.41
Selectivity (LenMod)	0.36	0.78	0.87	0.88
Growth probability to above legal size	0.57	0.69	0.81	0.92

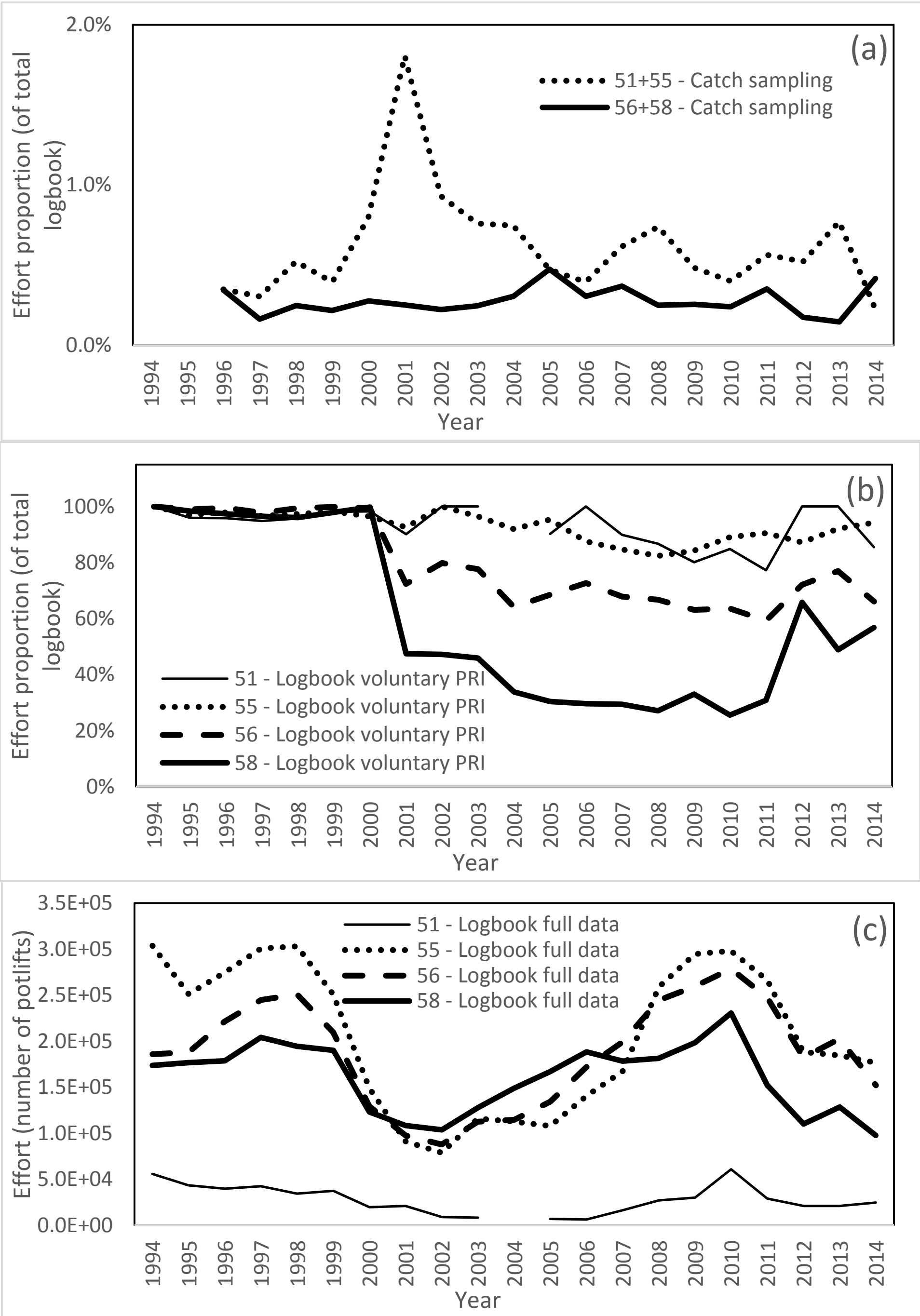
Supplementary Table S2

Coefficient of variation (CV) and 95% confidence intervals (CI) for estimates of yearly recruitment and start-January exploitable population numbers from EDM (base) and free-beta EDM. Cell values consist of CV% with 95% CI in parentheses in units of millions.

	Recruitment		Exploitable population numbers	
Year	EDM (base)	EDM (free-beta)	EDM (base)	EDM (free-beta)
1994	4.5% (2.7-3.3)	4.3% (2.6-3.1)	7.4% (2.7-3.6)	11.0% (1.5-2.3)
1995	5.0% (2.5-3)	5.0% (2.4-2.9)	7.4% (2.9-3.9)	10.3% (1.7-2.6)
1996	6.1% (1.8-2.3)	5.9% (1.7-2.1)	7.3% (3.1-4.1)	9.8% (1.9-2.7)
1997	4.1% (2.7-3.2)	3.5% (2.6-3)	7.1% (2.5-3.3)	11.8% (1.3-2)
1998	4.2% (3.2-3.7)	4.0% (3.1-3.6)	7.1% (2.8-3.7)	10.9% (1.5-2.4)
1999	4.7% (3.5-4.2)	5.4% (3.5-4.3)	7.3% (3.2-4.3)	9.3% (2-2.9)
2000	5.7% (3.2-4)	7.5% (3.1-4.2)	7.7% (3.7-5)	8.2% (2.7-3.7)
2001	6.9% (2.8-3.6)	9.8% (2.7-3.9)	8.0% (4.1-5.6)	8.2% (3.3-4.5)
2002	7.8% (2.5-3.5)	11.9% (2.4-3.9)	8.1% (4.3-6)	8.8% (3.7-5.2)
2003	8.7% (2.2-3)	15.2% (1.6-3)	8.0% (4.7-6.5)	9.5% (4.2-6.1)
2004	7.4% (2.5-3.3)	11.8% (2.1-3.3)	8.0% (4.4-6.1)	8.8% (3.8-5.4)
2005	8.0% (2.1-2.8)	13.2% (1.6-2.7)	7.9% (4.3-5.9)	8.3% (3.6-5)
2006	6.6% (2.4-3.1)	9.4% (2-2.9)	7.7% (4-5.4)	7.8% (3.1-4.2)
2007	8.5% (1.5-2.1)	12.5% (1.2-2)	7.6% (3.7-5)	8.1% (2.7-3.7)
2008	8.6% (1.2-1.6)	7.3% (1.2-1.6)	7.3% (2.9-3.9)	10.6% (1.7-2.5)
2009	4.9% (1.5-1.9)	3.1% (1.6-1.8)	7.2% (2.1-2.7)	13.6% (0.9-1.6)
2010	4.9% (3.2-3.9)	4.7% (3-3.6)	7.1% (1.8-2.4)	13.7% (0.8-1.3)
2011	7.1% (1.6-2.1)	7.5% (1.4-1.9)	7.3% (3.2-4.2)	9.4% (2-2.9)
2012	6.8% (1.3-1.7)	5.2% (1.3-1.6)	7.6% (2.4-3.3)	13.6% (1.1-2)
2013	4.5% (2.3-2.7)	3.8% (2.1-2.5)	7.5% (1.9-2.6)	16.0% (0.7-1.4)
2014			7.7% (2.3-3.1)	14.0% (1.1-1.9)
Mean CV%	6.2%	7.6%	7.5%	10.5%

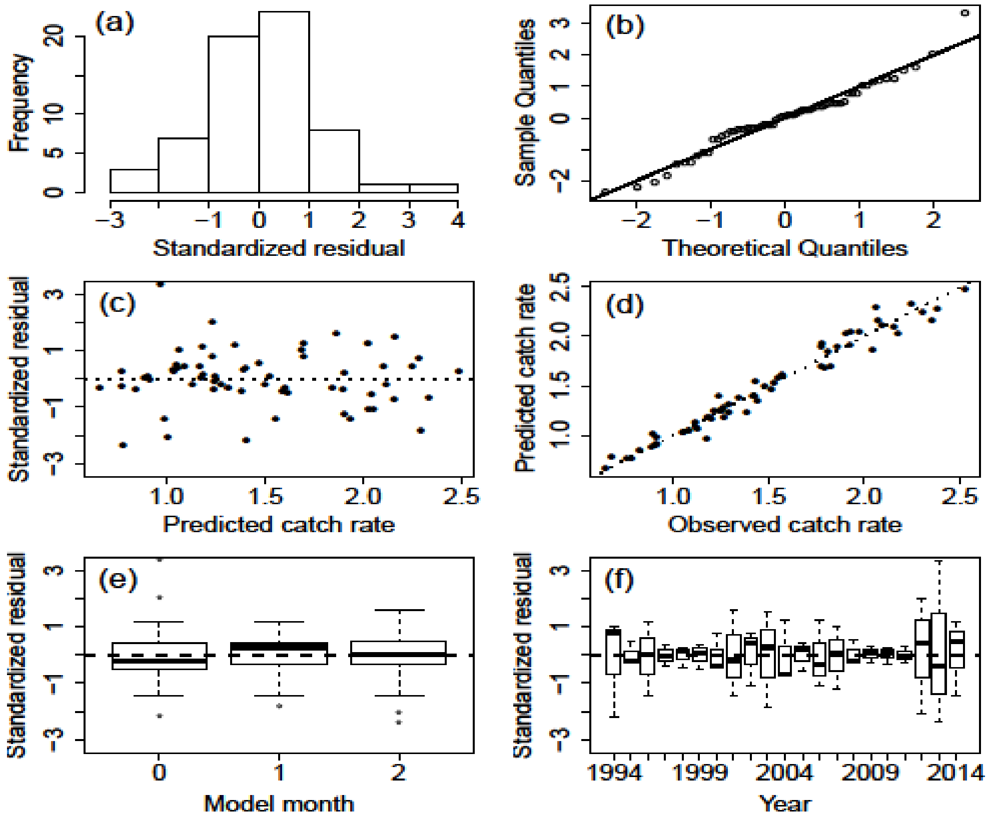
D. Figures:

Supplementary Figure S1



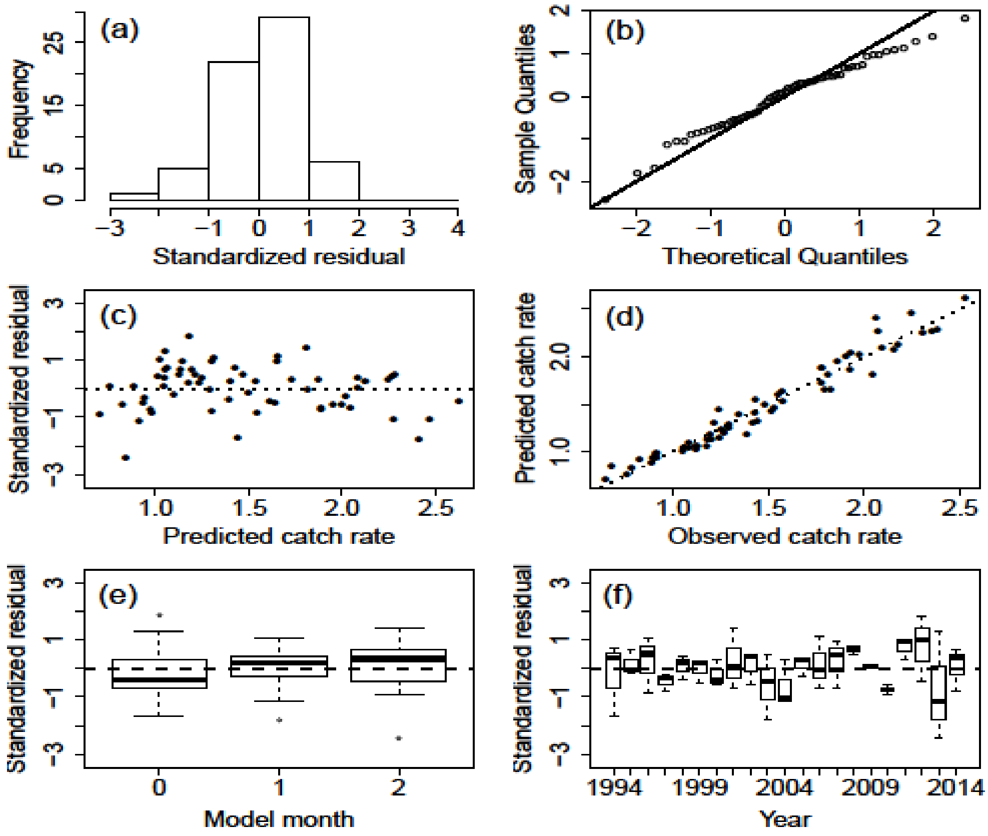
Supplementary Fig. S1. Time series of effort per data source. (a): Reporting rates of effort of the catch sampling data series as a proportion of the corresponding total commercial fishery effort per combined MFA 51+55 and 56+58, and calendar year (January-March). MFAs 51 and 55 are aggregated for data confidentiality reasons, and similarly so for MFAs 56 and 58. (b): Reporting rates of effort with PRI data as a proportion of the corresponding total commercial fishery effort per MFA and calendar year (January-March). (c): Time series of total effort for each of the four major MFA reporting blocks (51, 55, 56, 58) of the South Australian rock lobster Southern Zone commercial fishery, as number of potlifts aggregated over January to March per calendar year.

Supplementary Figure S2



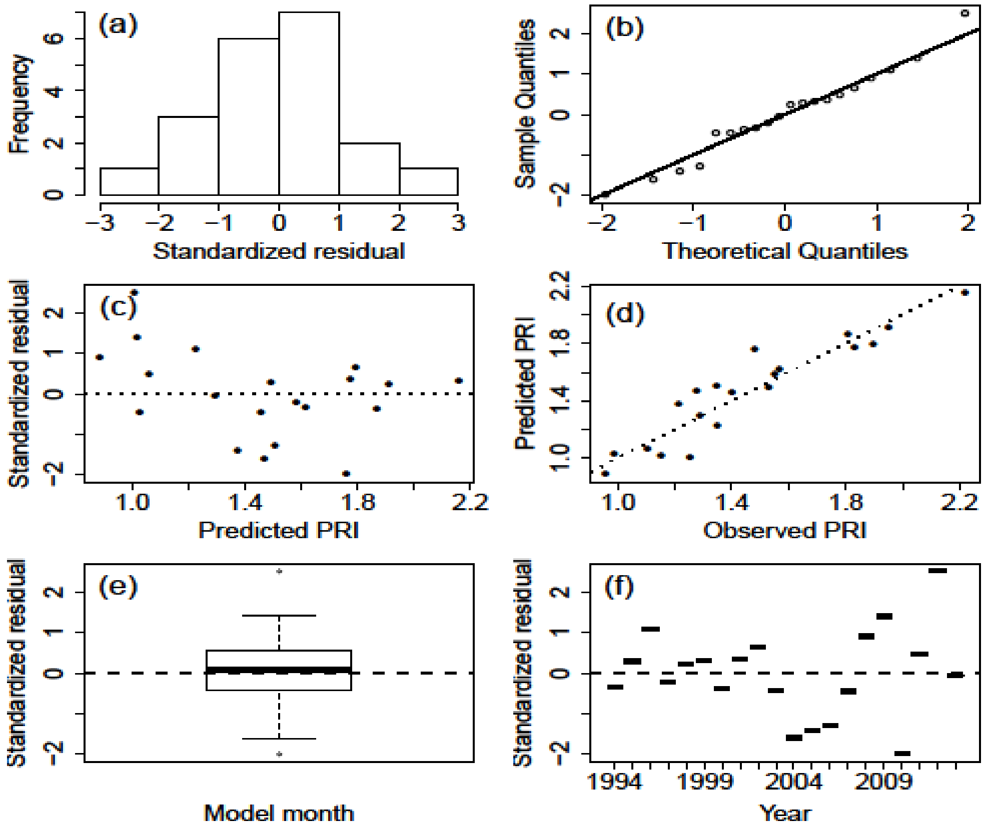
Supplementary Fig. S2. EDM catch rate fit diagnostic plots consisting of (a) histogram of standardized residuals, (b) quantile-quantile plot, (c) trend in standardized residuals versus predicted catch rate, (d) predicted catch rate versus observed catch rate, (e) trend in standardized residuals versus model month (January (0) to March (2)), and (f) trend in standardized residuals versus calendar year (1994-2014). Standardized residuals are defined as log(observed catch rate) minus log(predicted catch rate) divided by the (maximum likelihood) standard deviation.

Supplementary Figure S3



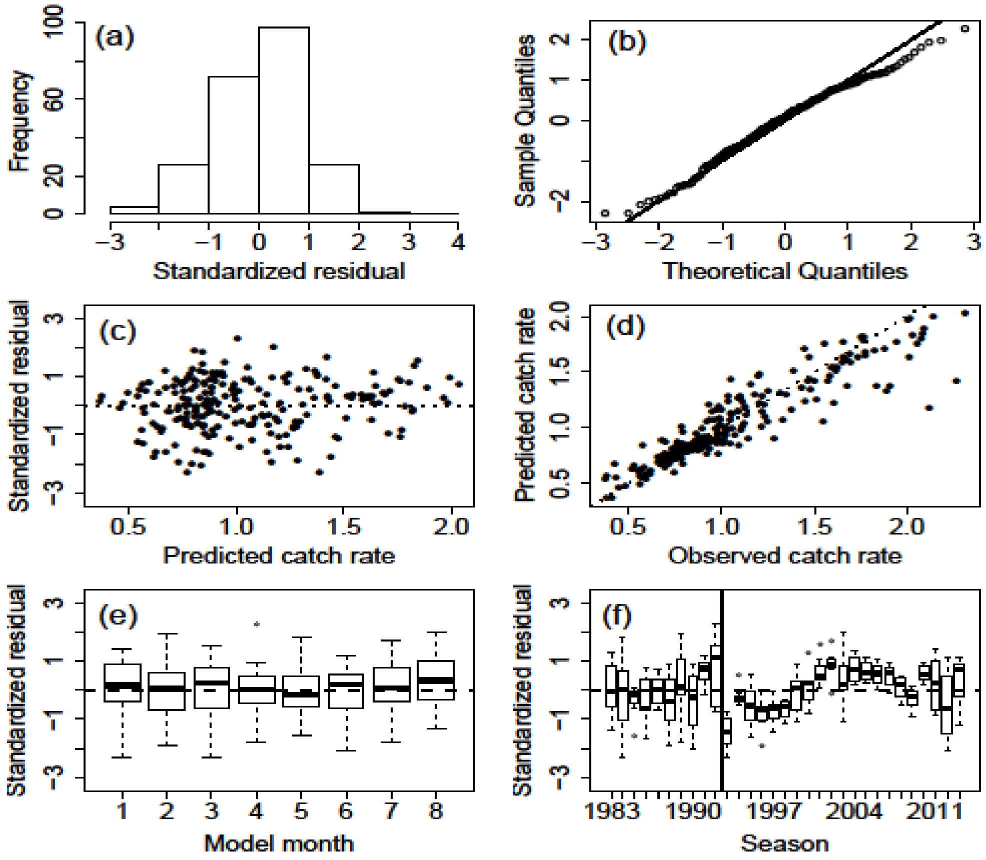
Supplementary Fig. S3. EDM-CSA catch rate fit diagnostic plots consisting of (a) histogram of standardized residuals, (b) quantile-quantile plot, (c) trend in standardized residuals versus predicted catch rate, (d) predicted catch rate versus observed catch rate, (e) trend in standardized residuals versus model month (January (0) to March (2)), and (f) trend in standardized residuals versus calendar year (1994-2014).

Supplementary Figure S4



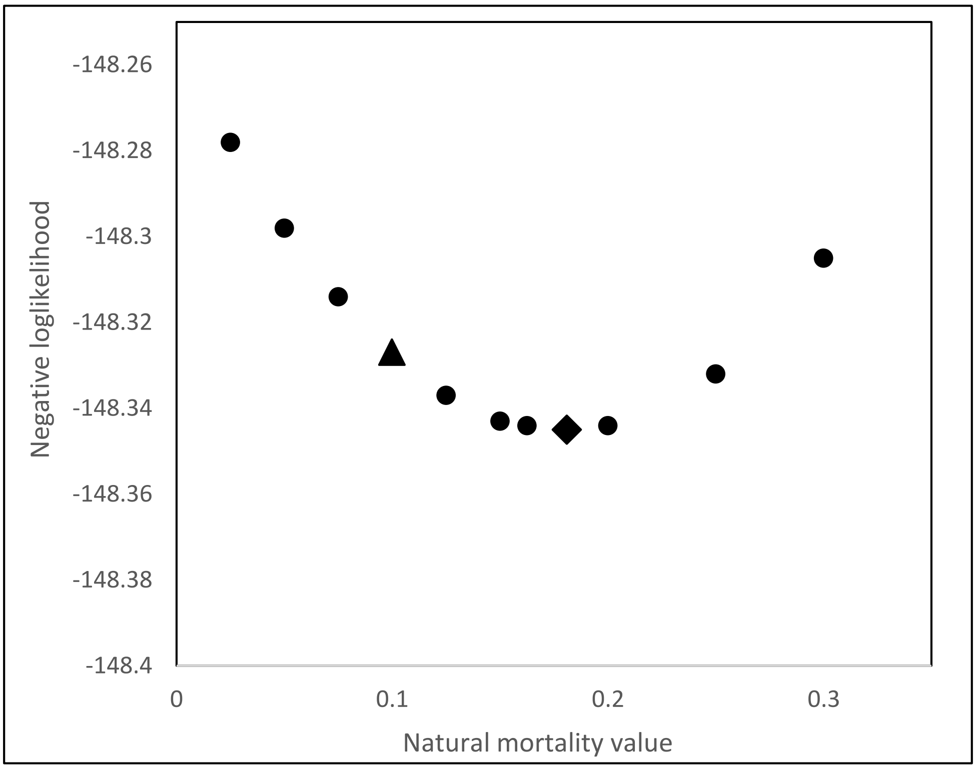
Supplementary Fig. S4. EDM-CSA PRI fit diagnostic plots consisting of (a) histogram of standardized residuals, (b) quantile-quantile plot, (c) trend in standardized residuals versus predicted PRI, (d) predicted PRI versus observed PRI, (e) box plot of standardized residuals, and (f) trend in standardized residuals versus calendar year (1994-2013).

Supplementary Figure S5



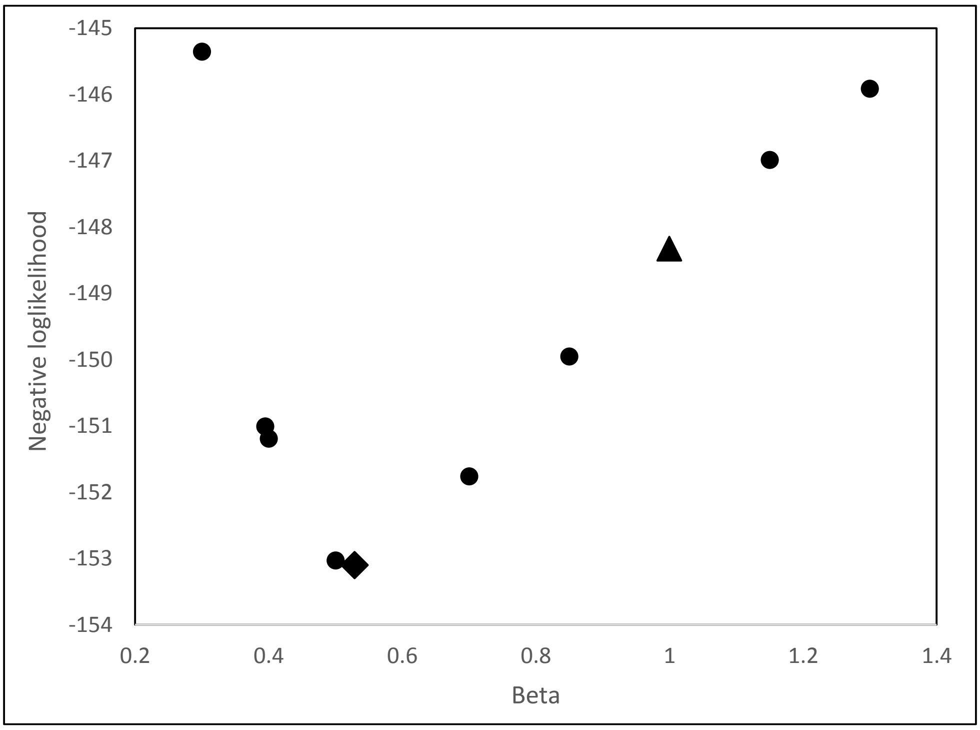
Supplementary Fig. S5. LenMod catch rate fit diagnostic plots consisting of (a) histogram of standardized residuals, (b) quantile-quantile plot, (c) trend in standardized residuals versus predicted catch rate, (d) predicted catch rate versus observed catch rate, (e) trend in standardized residuals versus model month (October (1) to May (8)), and (f) trend in standardized residuals versus fishing season (1983-2013). For reference the vertical line is placed prior to the first season from which EDM and EDM-CSA model time commences, namely season 1993 (calendar year 1994, January).

Supplementary Figure S6



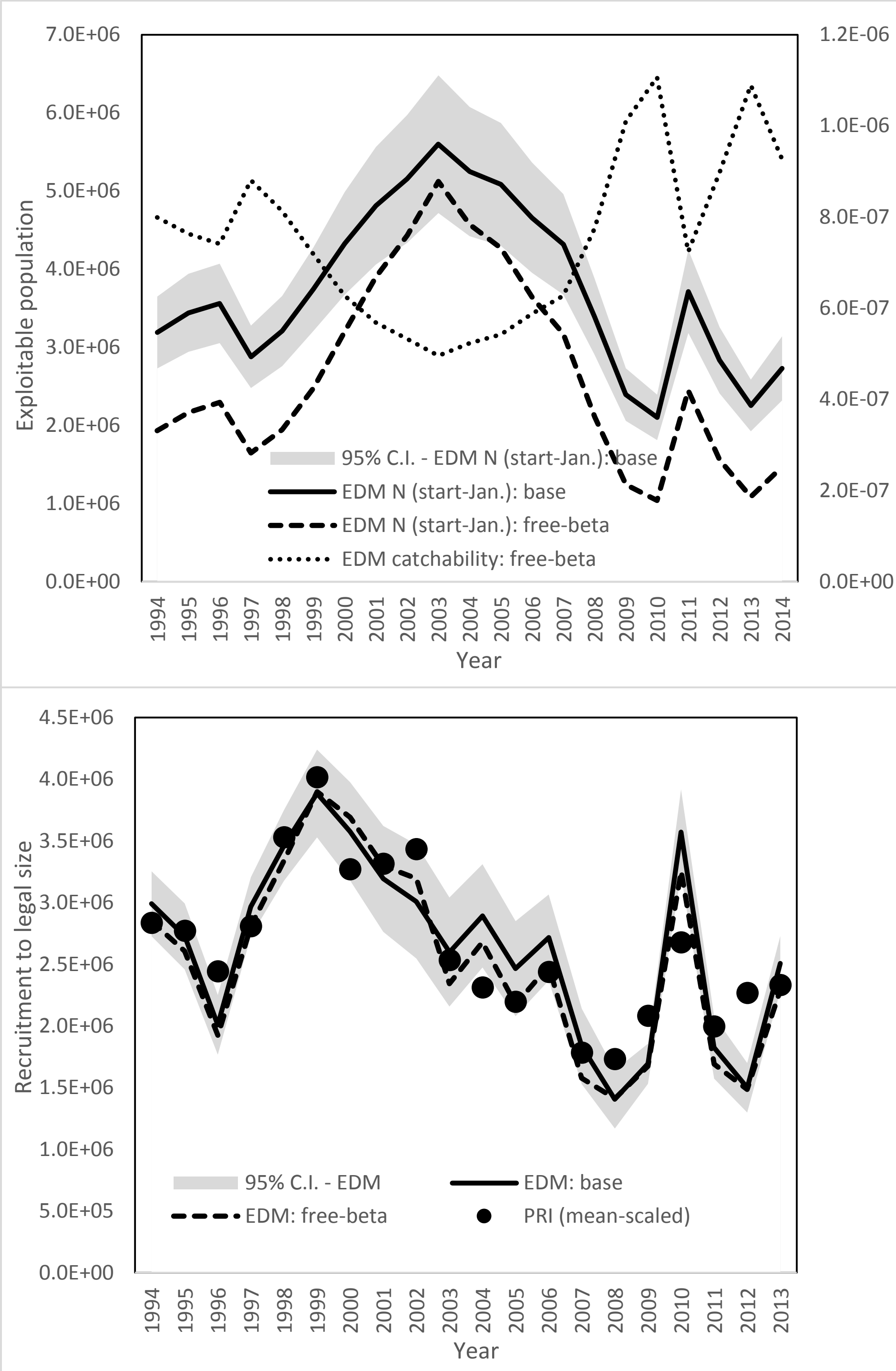
Supplementary Fig. S6. Negative log-likelihood values for EDM runs for different fixed values of natural mortality. The triangle marks the value (0.1) for natural mortality assumed by base EDM, and the diamond is the estimated value for natural mortality when it was freely estimated.

Supplementary Figure S7



Supplementary Fig. S7. Negative log-likelihood values for EDM runs for different fixed values of β. The triangle marks the value for β assumed by base EDM (β = 1), and the diamond is the estimated value for β when it was freely estimated (free-beta EDM).

Supplementary Figure S8



Supplementary Fig. S8. Time series of estimated start-January exploitable population numbers from base EDM and free-beta EDM with corresponding catchability (top), and recruitment to legal size (bottom) series from base EDM and free-beta EDM. The maximum likelihood 95% confidence intervals for base EDM estimates are the shaded areas. Pre-recruit index (PRI) data points (of November-December) are added to the lower panel and are scaled so that the mean equals that of the EDM estimated recruitment series.