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Modelling harvesting strategies for the lobster fishery in northern Europe: the importance of protecting egg-bearing females

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Abstract European lobster populations in Norway and Sweden are severely reduced as a result of intense harvesting over a long time. Various alternative management options have been proposed or endorsed to both facilitate recovery and increase yield. Accordingly, Minimum Landing Size (MLS) regulations are widely used for the European lobster. We developed an individual-based population model which integrates biological knowledge about lobsters' population dynamics to explore how available

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harvesting strategies and management options influence abundance and yield. The model reproduced basic features of a real lobster population in Sweden. Even for a relatively large MLS high fishing effort may still be detrimental to the long term production of the stock, while increasing the MLS further prevents this recruitment overfishing. A moratorium on berried females, in combination with the MLS appears to stabilize population fluctuations and yield, leading to higher yield for all MLS's considered. The female moratorium harvesting strategy also performed better than a maximum size limit. Yield per recruit calculations gave similar quantitative results, and also shows that a larger MLS reduce the risk of growth overfishing. A smaller MLS enables the harvest of many individuals but is very sensitive to increase in effort which easily promotes overfishing.

Keywords European lobster · Female moratorium · Individual-based model · Management · Minimum landing size · Yield per recruit (YPR)

Introduction

Developing sustainable management practices of natural resources typically lags behind exploitation expansion. The dramatic negative effects of a developing fishery on stock dynamics is old news (Beverton and Holt 1957) and is an example of what Garrett Hardin in 1968 called "The tragedy of the commons" (Hardin 1968; ARC Centre of Excellence in Coral Reef Studies 2010). In fisheries, there are many examples of depleted stocks that have or will lead to population collapse (Myers and Worm 2003) unless efficient management regulations can arrest the negative development of exploitation patterns (Worm et al. 2009).



Fig. 1 Map of the study area. The superimposed triangle indicates Kåvra, the sampling site for biological data. Landings in Norway and Sweden reached historically low levels in the 1970s. Several management actions were taken to arrete the development in Sweden. The fishery was at that same time transformed from a mainly commercial activity to an increasingly recreational activity. The recreational fishery is not requested to provide landing or logbook data, hence the low levels of landing since the 1970s despite of management actions. **a** Norwegian commercial landings from the south coast (*dashed line*) and the west coast (*solid line*) since 1935 (Varpe et al. 2005). Norwegian regulations include an MLS of 88–90 mm CL and a ban on berried females since 2009. **b** Swedish commercial landings since 1900. Swedish regulations include MLS of 80 mm CL since 1994 and a ban on berried females since 1985 (Fiskeriverket 2004)

Some notable exceptions exist where management has reacted with policy in time (Fernandes and Cook 2013). Management options are unique to specific fisheries and the gear that are used. They may include for example limitations in effort, seasonal closures, minimum landing sizes, technical regulations of the gear, or combinations of these.

The European lobster (*Homarus gammarus*) stocks in Sweden and Norway have experienced a great decline and subsequent regulations (Sundelöf et al. 2013). From the beginning of the 1960s to the mid 1970s there was a tenfold decline in the (officially reported) landed biomass of lobster in Norway (Fig. 1a) and it has not recovered since despite increasing management efforts. Similarly, the Swedish lobster stock suffered a great decline (Fig. 1b) following high and sustained effort through the late 1930s and 1950s (Sundelöf et al. 2013) with similar management after 1972. Effort has proven difficult to manage and many decapod species are today managed by minimum landing size (MLS) regulations. In combination with an MLS, regulations on maximum landing size may be enforced as well, effectively placing a ban on egg bearing females (female moratorium). In lobster fishery, minimum and maximum size in the catch can be regulated quite efficiently with regulations on the sizes of entrances to and escape gaps from the pots. For many commercial fish species MLS's are prescribed, however, their effectiveness as a management measure is questionable. Within for example demersal mixed trawl fisheries, MLS invokes considerable discard of undersized individuals of several species which are often returned to the sea either dead or dying (Madsen et al. 2013). Discard mortality may be substantial for some decapods (e.g., Spiny lobster, Panulirus interruptus, DiNardo et al. 2002) although not for clawed lobsters who survive discarding at a high rate. In this context an evaluation of MLS regulations and related management principles using European lobster provides a good example of potential effects of discarding in fisheries where size selectivity is close to perfect and discard mortality is minimal.

Already in the mid 18th century a 20 cm total length (TL) MLS was proposed, although an MLS was not implemented as a management measure until 1879 (21 cm TL, Axelsson 1944). The more recent changes to the regulations were induced by the great decline in catches and catches per unit effort (CPUE) during the 1950s and 1960s (Sundelöf et al. 2013). In 1973 the MLS of lobster in Sweden was increased to a TL of 22 cm. A female moratorium was introduced in 1985 to enhance recruitment success and in 1994 the MLS was further increased to 80 mm carapace length (CL; approximately 23 cm TL). Data on total effort in the Swedish lobster fishery are today uncertain, but estimates are that 95,000 pots are currently used (Ulmestrand and Loo 2009). This figure is larger than the 70,000 pots used in the 1950s (Ulmestrand and Loo 2009), and with technological creep including development of pots, boats, engines, line pullers and echo-sounders, each pot can be assumed to be more efficient today. Effort has been regulated, such that recreational and licenced fishermen are allowed to use 14 and 50 pots, respectively. The Norwegian regulations also concern the amount of pots (10 for recreational/100 for licensed fishermen) and prescribe an MLS. The MLS varied geographically in Norway until 2009 when a national MLS (25 cm TL, approximately 88 and 90 mm CL, for females and males, respectively) was

made standard together with a moratorium on berried females (NDF 2011).

Management regulations and their expected effects have been based on yield-per-recruit assessments and estimates of sexual maturity, with little inclusion of recruitment variability, size-based mortality, fecundity or explicit mechanisms of density-dependence. Although the Swedish stock seems to have responded well to management actions (Fiskeriverket 2009), the data are of a population index from limited fisheries data and not substantiated by fisheries independent data, model simulations, or converted by changes in technological development over time. There exists no management plan for the Swedish lobster stock and no thorough quantitative evaluation of alternative management options has been made previously.

A large part of the *H. gammarus* life cycle is unknown, and only when individuals begin entering the fishery at approximately 80 mm CL are they found in any substantial numbers. Very little is known about recruitment (Wahle 2003) and post-recruitment (van der Meeren 2000) mechanisms in this species. However, larvae are pelagic and capable of drifting for a couple of weeks (Annis et al. 2007). Larvae are difficult to catch (Øresland 2008) and sparsely distributed, which makes stock-recruitment patterns and recruitment variability difficult to establish. Adults are fairly stationary showing some homing behaviour, though the spatial behaviour of individuals is poorly documented (but see Moland et al. 2011). Although there are studies on behaviour and interaction outcomes in aquaria (Skog 2009), studies of in situ behaviour are scarce. However, demographic data are available from a European lobster stock on the west coast of Sweden. Here, 2.2 km² of high quality lobster habitat have been protected from harvesting for the past 20 years. Natural mortality, moulting intervals, growth, fecundity, and sexual maturation have been recorded through an extensive markrecapture program (Ulmestrand 2003; Moland et al. 2013a).

Ecological models are increasingly used to support environmental decision making, for example for devising strategies for sustainable management of natural resources (e.g., Schmolke et al. 2010; Grimm et al. 2014). Here, we present an individual-based population model (IBM) of the European lobster to assess alternative harvesting practices. IBMs are a flexible and powerful tool to integrate existing knowledge of demography and behavior of a particular species. They allow exploring the consequences of knowledge gaps by contrasting alternative model assumptions and comparing corresponding model outputs to sets of patterns identified in real populations ("pattern-oriented modelling"; Grimm et al. 2005; Grimm and Railsback 2005, 2012; Railsback and Grimm 2012). Previous lobster IBMs have for example explored larval dispersal of American lobster (*Homarus americanus*, Incze et al. 2010) juvenile behavior and reproducing aggregations of Spiny lobster (*Panulirus argus*, Butler 2003) and climate effects on mortality-based biological reference points for Pronghorn spiny lobster (*Panulirus penicillatus*, Chang et al. 2011). Here, we set up an IBM for management purposes on the previously untested European lobster (*Homarus gammarus*). Our IBM represents the lobsters' entire life cycle.

We first present the IBM, and then use it to assess current management rules and potential effects of alternatives. We explored harvesting strategies based on maximum and MLSs and the role of berried females to the recruitment of lobster populations. We investigated how sensitive the predictions were to alternative recruitment functions, but no economic considerations of, e.g., discount rate or market prices were included in our model. A simpler yield per recruit (YPR) model was used to contrast growth overfishing with the recruitment overfishing explored by the IBM.

Methods

Study species

The European lobster is characterised by a long juvenile phase, slow growth and low fecundity compared to many other commercial fish or decapod species. Most of what is known about European lobsters' ecology comes from observational studies and studies of adolescent or adult individuals, as larvae and early stages of post-settlement have rarely been found in the wild (Linnane et al. 2001; Øresland 2008). The North American relative, H. americanus, grows faster, is larger, produces more eggs and has different habitat preference (Factor 1995). The fishery for American lobster has also been more extensively sampled and is regulated in a different way than its European relative. The life cycle of European lobster is typically defined by a larval stage which settles to a benthic juvenile stage, rarely observed in the field. Some 3-11 years later these begin entering the fishery (Sheehy et al. 1999). Recruitment is assumed to be density-dependent (Wahle 2003). Wahle (2003) proposed an asymptotic stockrecruitment relationship for European lobster. This is a strong assumption about the European lobsters' biology and larval ecology due to the scarce data and large variability associated with any stock recruitment relationship and European lobster in particular. Therefore we model the Swedish lobster population using a flexible formulation previously also applied for other decapod species [Smith and Jensen 2008; Electronic Supplementary Material (ESM) S1]. This allowed for the possibility to evaluate Fig. 2 Scheduling of events in the age-structured and individual-based models. Eggs go through a sequence of yearly mortality events until juveniles are seeded in the IBM. The yearly cycle of events starts on day 213. Adult mortality and foraging are covered by daily routines not shown in this scheme but indicated in Table 1



different compensatory stock-recruitment relationships. The life cycle and how it was implemented into a computer model is illustrated in Fig. 2 (cf. "The model" below and ESM S1 for a complete description of the model and computer code in ESM S2 and S3).

Data

We have used an extensive set of mark-recapture data from a no-take marine protected area (Kåvra) on the West coast of Sweden to parameterize the model. From 1992 to 2007 lobster were caught, marked with numbered T-floy tags and released. Each individual caught was inspected for size, sex, fertile status (old/new eggs under tail), number of claws and signs of disease. The data set consisted of 5000 marked individuals and 7000 recaptures. Egg masses of 54 berried females (75-144 mm CL) have been counted to provide accurate information on fecundity. This large mark-recapture data set of a fishery independent population provided size-at-maturity, natural mortality and growth increments. The data set was described by Ulmestrand (2003) and has since been updated in 2007. We refer to the data as (Ulmestrand 2003) and it was also summarized in Table 1 and Fig. 3 and Figs. S1 and S2 in ESM S1.

The model

A detailed model description following the overview, design concepts, details protocol for describing individualbased models (Grimm et al. 2006, 2010) is in ESM S1. Here we provide an overview of the model's key processes (Fig. 2) and parameters (Tables 1, 2).

The model describes the development of a population of lobsters. The model is age-structured for juveniles and individual-based for adults. We introduce individual traits as the juveniles recruit into the adult phase since we lack detailed information on for example juvenile growth schemes. From a computational perspective it also makes sense to make this simplifying assumption as it substantially reduces runtime. Space is not represented explicitly. The entity egg has only the characteristic age. It reaches the next age class as juvenile after a probability of survival and at 4 years of age juveniles enter the individual-based phase. Each individual is given a number of characters (age, sex, size and maturity status). An additional set of parameters define the individuals' fate in the subroutines: foraging, moulting, adult mortality, harvest, maturation, reproduction, development, recruitment and ageing (see Tables 1, 2; ESM S1). The time-step of the model is one day and simulation time varies between 100 and 400 years depending on type of evaluation.

Simulation experiments

Harvest scenarios

Key parameters to define management strategies were MLS, Maximum Landing Size (MinMaxLS, only used in combination with MLS) and harvest effort (proportion of total habitat fished per year). In one set of simulations we explored the effects on stock size and harvest by

Table 1 Symbol, parameters,values, ranges and units

Symbol	Parameter		Value	Unit
Days			365	days
S	Number of days in one season		67	days
	Age at maturation (years)		4	years
	Maximum age		45	years
z	Adult natural mortality rate		modelled	year ⁻¹
z _{juv} (age)	Juvenile mortality rate	0+	1.11	year ⁻¹
	"	1 +	0.747	year ⁻¹
	"	2+	0.592	year ⁻¹
	"	3+	0.505	year ⁻¹
Α	Total area		1	km ²
D	Detection diameter other lobsters		5	m
v	Lobster movement velocity		20	m/day
C _c	Foraging time lost per interaction		0.5	days
α	Area 'clearance' rate for other lobsters v	D		
Variables				
$\Phi_{\rm p}$	Proportion of fished area (effort)	$A_{\rm f}/A$		
$A_{\rm f}$	Fished area		0.1-1.1	km ²
Von Bertala	nffy parameters, male (Ulmestrand 2003)*			
L_{inf}			173	mm CL
t_0			-0.3	years
Κ			0.139	year ⁻¹
Von Bertala	nffy parameters, female (Ulmestrand 2003)*			
L_{inf}			152	mm CL
t_0			-0.6	years
Κ			0.089	year ⁻¹
Maturity ogi	ve (least squares fit to data, Ulmestrand 200	3)		
k_1			37.6231	
k_2			0.481	
Stock-recruit	tment-relationship			
q	Normal recruitment/recruitment limited		0.06/0.10	
β	Compensatory factor		0.8, 1, 1.8, 2.1	
w	Fair recruitment (for the different β)		3.0, 4.0, 6.7, 7.3 (× 10^5)	
W	Recruitment limited (for the different β)		6.0, 8.0, 13.4, 14.6 (\times 10 ⁵)	

The estimated ΔL_t was fitted to the observed data on ΔL_t , from the lobster tag-recapture experiment in a lobster reserve, by estimating L_{inf} , k and t_0 and minimizing the sum of squared residuals

 $\Delta L_{t} = (L_{inf} - L_{t})(1 - e^{-k(t-t_{0})})$ * The growth parameters (L_{inf} , k and t_{0}) of the von Bertalanffy growth model were estimated by a derivation of the increase in length per time (ΔL_{t})

progressively decreasing MLS with and without a female moratorium. The experiment started with an MLS of 88 mm CL after 50 years of no fishing. After 100 years of fishing the MLS was decreased by 4 mm CL, and so on down to 76 mm CL. This sequence of decreasing MLS efficiently tested the extinction threshold, yield and size of the lobster stock from the management rule. Minimum and maximum landing sizes are management options that can be easily manipulated through limitations on the size of entrance rings and escape-gaps in the traps. Regulations and harvest scenarios in the model have been adopted from operational management strategies in Norway and Sweden that include MLS and a moratorium on berried (egg carrying) females. Effort and MLS were varied to scan parameter space for high and sustainable yields, rendering surfaces of yield for combinations of effort and MLS. The effects of the combination of MLS and MinMaxLS, i.e., more or less selective gear, as well as the ban on berried females, were also explored. The simulations were executed as sensitivity analyses, keeping all but one parameter constant and running the simulation for different values of a key parameter. As outputs, we focussed on the responses of yield and stock biomass.

Sensitivity analyses

A local sensitivity analysis was performed, using long term yield as a summary model output sequentially changing each parameter, one at a time, by ± 5 and 10 %. One simulation run was performed for each level of each parameter (15 parameters with 5 levels). Change in model output was expressed as the relative change in yield divided by the change in parameter (Table S1 in ESM S1).



Fig. 3 Average size-dependence of individual level properties of model lobsters. Size is measured at moulting (a), mortality event (b), hatching of eggs (c), or maturation (d). a Expected yearly growth of males and females. Yearly growth is size- and density-dependent, hence the range of values for males and females (the range is 20-100 % of the growth rate in an unfished population); b Average yearly mortality. c Fecundity (number of eggs). d Probability of a

Several parameters in the model have been introduced with little prior data or information on the range of the value. In particular the shape of the stock recruitment function (β) , and how growth is affected by density (c_c) is not well known. Also the effect of variation in adult natural mortality (z) was central to understand the dynamics of the model. Specific sensitivity analyses on these parameters were performed to see how sensitive the model output was to changes in these parameters (Table 3). Default parameter values are given in Table 1, with the inclusion of a harvesting regime of effort = 0.5 (proportion of area being harvested, a proxy for F), MLS = 80 mm CL and a female moratorium. The three sensitivity parameters were varied separately with the standard values: $\beta = 1, c_c = 0.5$, added mortality = 0. The sensitivity analyses are summarised in Fig. S3 in ESM S1, Table S1 in ESM S1 and simulations are presented in Table 3.

Yield per recruit analysis

The closed model of population dynamic mechanisms portrayed in the IBM assessed the risk of depleting the possibility of future production of recruits, generally termed recruitment overfishing. For comparison, a YPR

female carrying eggs under tail at given sizes. Data are shown in combination with the functions parameterized in Ulmestrand (2003), *triangles in panel* (**c**) are average proportion berried females for mm CL increments in the data, *circles in panel* (**d**) represent data on individuals and *line* was fitted to the data, reproduced in Table 2. The drop in proportion berried females at larger sizes is hypothesized to be an effect of larger females moulting more seldom

analysis was performed on the growth and mortality parameters assumed in the model to assess what is called growth overfishing. YPR estimates the biomass harvested from an average recruit depending on growth, natural and fishing mortality and selectivity in the fishery. Lobster data are typically size-based due to indeterminable age. However, size is correlated with age, making an age-based YPR possible for lobster. For length-at-age conversions the von Bertalanffy growth model was used. Length-at-age and weight-at-age were used to convert numbers-at-age to biomass. The Baranov catch equation (Baranov 1918) was used to simulate fishing by removing individuals from the cohorts. The removals were summed and divided by the initial number of recruits yielding a standardised YPR. The size at which a cohort reaches its maximal biomass has been termed L_{opt} and was calculated by $L_{opt} = L_{inf} \times 3/$ (3 + M/K) (Beverton 1992) where M is natural mortality and K and L_{inf} are the growth exponent and the asymptotic size in the von Bertalanffy growth equation, respectively. Males and females display different vital rates and L_{opt} and YPR were calculated separately for each sex. The reproductive biomass per recruit (R_0) was calculated as the product of biomass-at-age, maturity-at-age and fecundityat-age, per recruit at any given age.

Table 2	The	subroutines	in	the	full	IBM	are	listed	with	their
accompa	nying	parameters								

Subroutine	Parameters					
Foraging	$\varphi_{\rm c}$, density-dependent encounter-rate					
	$c_{\rm c}$, time spent on interference at each encounter event					
	N, density (lobsters km^{-2})					
	$\alpha,$ 'clearance' rate, the area searched for food by each individual per day (km² day ⁻¹)					
	v, average movement speed over a day					
	D, distance at which other lobsters are detected					
	$T_{\rm i}(d)$, accumulated time available for foraging					
Moulting	L_{∞} and K, parameters from the von Bertalanffy growth function					
	ΔL , the length increment at each moult					
	T_i accumulated time available for foraging					
Adult	z, adult mortality					
mortality	p_z , corresponding survival					
Harvest	$\Phi_{\rm p}$, proportion fished area					
	A, modelled area					
	A _f , fished area					
Maturation	$p_{\rm mat}$, probability of maturation at a given size					
	k_1 and k_2 , parameters fitted to data					
Reproduction	F_{i} , fecundity given female size					
Development	Status 1, neuter/unfertilised individuals					
	Status 2, fertilized female					
	Status 3, berried female					
Recruitment	q, larval mortality					
	S, number of eggs					
	w, threshold number of eggs					
	β , rate of overcompensation					
Ageing	Age					
	z_{juv} , juvenile mortality rate, size based (Peterson and Wroblewski 1984)					
	From age structured to individual based					
	Maturing cohort is given individual characters (sex and size, etc.)					

Results

Model-data comparison

First, we ground-truthed our model with data available from the No-Take Marine Protected Area (MPA) Kåvra. Data on the size development of lobster from the sea are based on an extensive mark and recapture program (cf. Methods), but it is not possible to age individual lobsters. In Fig. S4b in ESM S1 the longest surviving individuals recaptured within the MPA are presented with modelled individuals (at low density). This shows that the model gives reasonable size-development at the individual level.

We compared the modelled population structure with the pattern seen in a real population. The modelled sizedistribution reflected the well sampled MPA population reasonably, which has been protected from fishing for 20 years (Fig. S5 in ESM S1). The major difference was the 80–85 mm CL individuals, whose size is not entirely representative due to the selectivity of the sampling gear (pots). In the absence of recruitment variability the simulated stock size-structure still fluctuated slightly (Figs. 4 and S5 in ESM S1) due to random events in the model (adult survival, individual size at seeding in the adult model, the subsequent population structure and reproductive output). Introducing harvesting to such a population gave a phase of transient behaviour when both stock size and structure was affected by size selective harvesting before a new equilibrium was established.

Sensitivity analysis

The sensitivity analysis scanning 15 model parameters (Table S1 in ESM S1) showed a stronger effect of changes to life-history characteristics (both male and female, L_{inf} , K, mortality and size at maturation) than to interaction terms such as clearance rate (α) , loss due to interaction (c_c) , and density dependent encounter rate. At higher effort this picture was slightly altered and density dependent interaction became more important to model behaviour. At high exploitation rates a change in size at maturation heavily influenced yield. The increased number of fertile individuals following a decrease in size at maturation affects reproduction and recruitment positively, and this was reflected in the change in average yield. Overall, the sensitivity analysis showed smaller sensitivity of the model to assumed (clearance rate (α) , loss due to interaction (c_c) , and density dependent encounter rate) than to estimated (mortality, inter-molt time, probability of maturation, von Bertalanffy) parameters. Sensitivity experiments further showed that a change in any of the three tested parameters (β , c_c , z) will induce a systematic change in the absolute number of harvested lobsters (Fig. S3 in ESM S1). Strongly overcompensating recruitment functions (larger β) and reduced adult mortality also returned higher yield. However, the shape of the yield curves remained the same or similar for all parameter values with increasing effort.

MLS, harvesting effort and temporal dynamics

The MLS was reduced stepwise every 100 years from 88 mm CL to 76 mm CL, one scenario without (Fig. 4a, c) and one with (Fig. 4b, d) a female moratorium in addition to the MLS. Small MLS's and large effort pushed the population over the edge into collapse in all scenarios. The MLS must be rather large (88–84 mm CL) to withstand the effects of high effort. Including the female moratorium

 Table 3 Parameter values of scenarios and sensitivity analyses



Simulation experiments were separated into a scenario part, and a sensitivity part to explore effects of management options and parameter values and relate the model to different applied cases

Effort is given as the proportion of fished habitat per year and MLS/MinMaxLS (under control rule 1) is given in mm CL. FM (under control rule 2) is the female moratorium control rule, and AI is the alternative fishing strategy All Individuals above MLS

Sensitivity analyses (presented in Fig. S3 in ESM S1) was set up with the following:

Environmental setting: effort = 0.5, MLS = 80, female moratorium, $\beta = 1$, $c_c = 0.5$, added mortality = 0; the following consecutive changes to parameters were made

 β (in Eq. 10 of model description, Fig. S2 in ESM S1) 0.8, 1.0, 1.8, 2.1

cc (in Eq. 1 of model description) 0.1, 0.3, 0.5, 0.7

 m_{di} , (added to z in Eq. 6 of model description) -0.2, -0.1, 0.0, 0.1, 0.2

protected the harvested populations from overfishing and collapse, even for MLS's below 80 mm CL and for all except the highest effort. However, yield was maximised at a high effort for an MLS of at least 88 mm CL (Fig. 5d) for the female moratorium scenario. In the other case, effort needed to be managed at an intermediate level in order to sustain yield (Fig. 4c).

Harvesting strategies

Harvesting small individuals is detrimental to the stock development, and can lead to population collapse. Iterating the model with the full range of combinations of effort and MLS's revealed the strategies maximizing yield (Fig. 5). Compared to a strategy based only on an MLS, a female moratorium increases yield for small MLS's (Fig. 5b) and the stock is better protected from overfishing and collapse for all but the smallest MLS. The effect of female moratorium in combination with an MLS buffers against population collapse at small MLS's and high effort. The former Norwegian management rule (90 mm CL and no moratorium on berried females) is the bold line in the left panels and the Swedish management rule (80 mm CL and a moratorium on berried females) in the right panels. A female moratorium is particularly beneficial if effort was high and MLS low, but out-competed an MLS strategy over a broad range of strategies, in both recruitment scenarios (Fig. 6).

Introducing a maximum landing size in combination with an MLS of 80 mm CL (MinMaxLS) had only minor effects and did not return higher yield than a female moratorium and an MLS of 80 mm CL (Fig. S7 in ESM S1). Maximum sizes of 108–132 mm CL had only weak effects on yield regardless of the level of effort. A Min-MaxLS will not protect the stock if effort is sufficiently high. In comparison to a female moratorium, an increased MLS made it more difficult to find legal sized individuals, and yield was thus maximised at higher effort (Fig. S7 in ESM S1).

The YPR analysis provided different surfaces for males and females (Fig. 7). The L_{opt} (the size that maximizes cohort biomass, Beverton 1992) for males was 95.3 mm CL and the female equivalent was 70.3 mm CL. Females increase in size slower than males and produce offspring biomass instead. The reproductive value per recruit shows a very similar pattern to the male YPR. Maximum R_0 is produced at 93 mm CL, similar to the L_{opt} for males. At MLS larger than 85 mm CL, F becomes unimportant for the YPR (Fig. 7).

The sex-biased harvest regime of the female moratorium affected the sex ratio in the modelled stock (Fig. S6 in ESM S1). The MLS strategy quickly fished out large females from the system as they grew slower and were not replaced by smaller individuals. Few females were larger than 110 mm CL in the exploited population. The female moratorium strategy did preserve a more unbiased proportion of males in the larger size classes. Compared to harvesting all individuals larger than an MLS, protecting berried females also increased the proportion of males in the smallest of the harvested size classes (80 mm CL) but decreased the proportion of males in the larger size classes.



Fig. 4 Stock size (a, b) and yield (c, d) over time for regulations based on MLS (a, c) and MLS plus a female moratorium (b, d). MLS is decreased over time, and change in regulation is indicated in the figures. Simulations were repeated for five different efforts in the

fishery, simulated as proportions of area being fished (0.1, 0.3, 0.5, 0.7, 0.9, 1.1). Values above 1 means the area was covered more than once annually. Stock size (\mathbf{a}, \mathbf{b}) and yield (\mathbf{c}, \mathbf{d}) for an effort of 1.1 is emphasized via a fat line. Note the logarithmic y axis

Discussion

Our most important result is that a moratorium on berried females can have strong positive effects in terms of both protecting the stock and optimizing yield, particularly if effort and MLS are far from their optimal values. Such a moratorium reduces the fishing mortality of females roughly by half, due to the two-year reproductive cycle of lobster females, as well as securing recruitment particularly at low stock levels. Other management options covered in this study are not as efficient as a moratorium on berried females.

We also showed that small MLS renders high yield at low effort; as effort is increased, yield drops compared to a situation with a larger MLS. A larger MLS secures productivity also under otherwise unsustainable fishing effort. When an MLS was combined with a female moratorium yield was increased for all relevant combinations of MLS and effort. We also found that a maximum landing size in combination with an MLS (MinMaxLS) needs to be small to be efficient and it does not perform better than a female moratorium under our model assumptions.

If heavily fished at an MLS at or below 80 mm CL, little reproductive biomass is retained in the stock. For a female moratorium and an MLS of 80 mm CL, reproductive value is quickly eroded if harvested intensely. Harvesting too much of the 80 mm CL individuals undermines the future reproductive potential, not because the females that are 80 mm CL are very fecund, but because they constitute such a large proportion of the fertile population (Fig. S5 in ESM S1). Moreover, at high effort, very few large individuals remain in the population and the future reproductive potential is almost entirely stored in the females just maturing, at about 75–80 mm CL. The YPR analysis gave similar qualitative results (Fig. 7).



Fig. 5 Yield in kg/km² for the strategy of harvesting all individuals larger than MLS (\mathbf{a}, \mathbf{c}) and larger than MLS with a female moratorium (\mathbf{b}, \mathbf{d}). Harvesting regimes were tested for high recruitment levels (\mathbf{a}, \mathbf{b}) and a recruitment limitation scenario (\mathbf{c}, \mathbf{d})

The YPR analysis and the yield from the IBM both suggest that effort becomes less important for productivity (and thus overfishing) at higher MLS. However, the R_0 analysis of female reproduction suggested that *F* has a substantial negative effect on reproductive potential even with higher MLS. Also, a size selective fishing increase risk of fisheries induced evolution (Jørgensen et al. 2007, 2009) and may reduce CPUE, efficiency and profitability in the fishery (Svedäng et al. 2014).

The YPR and R_0 analyses do not take into account any density dependent effects in the population. The very high maximal R_0 value ($R_0 \gg 2$, Fig. 7c) is probably caused by this lack of density dependence in the R_0 analysis.

The Swedish management regulations may be improved by an increase in MLS. An increase in MLS would return the same yield, better protect the stock from variability in recruitment and make it more resilient to further increases in effort. A smaller MLS enables the harvest of many individuals but as a management option it would need additional regulations on effort to avoid overfishing. Management action to regulate effort would need benchmark data on F that is practically non-existing for the Swedish and Norwegian lobster fisheries. Although our model includes MLS and effort explicitly we are cautious about what are the exact optimal combination on MLS and effort. We have, for example, not included reliable information on size dependent catchability, a significant aspect when assessing harvest regimes.

The Swedish lobster fishery today has only a rudimentary effort regulation and no quota or bag limit regulations. Registered commercial fishermen are allowed 50 pots per license and recreational fishers are allowed 14 pots. Estimates are that 92 % of the approximately 95000 pots used in the Swedish lobster fishery belong to the recreational fishery (Ulmestrand and Loo 2009). MLS, female moratorium and season closure are the two main regulations in this fishery today. Compliance with MLS and female moratorium regulations are both time consuming and expensive to monitor and control. Changes to regulations may not be accepted by fishers immediately and thus cause a lower compliance during some time, a misinterpreted management situation and potential overfishing. In the Fig. 6 Yield of MLS as proportion of yield given a moratorium on berried females $(Y_{MLS}/Y_{moratorium})$. Only for very low effort or very high MLS will the female moratorium not out-compete a simpler MLS management strategy. As seen for both high (**a**) and low (**b**) recruitment, this pattern was not dependent on the level of recruitment



simulations of this study compliance was assumed to be high and in Swedish and Norwegian waters MLS is maintained by the use of escape-gaps in the pots. Deviances from this pattern can be explored in future developments of this model.

Sadykova et al. (2011) found a more beneficial effect of a MinMaxLS strategy in relation to harvesting decapods and stated that "reducing the annual catches by 15 % or more may have been sufficient to avoid the dramatic drop in the population [of Noble crayfish] that was observed in the mid-1980s". A berried-female moratorium protects all sizes of berried females, thus decreasing F efficiently on all sizes giving large effects on yield compared to an MLS. In contrast, a MinMaxLS, will only reduce F on the largest sizes. For high values of F the sieving of legal sized individuals is efficient and large individuals will constitute a very small fraction of the total stock, hence have a very minor effect on total yield (Fig. S7 in ESM S1). The MinMaxLS harvest rule will under such circumstances have only marginal effects on yield compared to a simpler MLS. Under the combined regulation of sizes and effort, as for the Noble crayfish (Sadykova et al. 2011), a MinMaxLS



Fig. 7 Continuous yield per recruit (YPR) model. **a** Output for male YPR given minimum landing size (MLS) and fishing mortality, **b** output for female YPR given minimum landing size and fishing mortality, **c** R_0 given minimum landing size and fishing mortality. Parameters in the YPR was von Bertalanffy parameters, size variable mortality and size to weight conversion parameters (Table 2). The R_0

calculation used the same parameters as the YPR but in combination with the maturation ogive and the fecundity function. Reproductive weight-at-age was calculated as the biomass of females at age times maturity at age times fecundity at age. Reproductive weight-at-age was then aggregated over all sizes and divided by the number of recruits and time steps per year

would be easier to get to work, particularly if the reproductive value of larger individuals is greater. It is possible to design a gear that is restrictive for both a minimum and a maximum legal size (MinMaxLS). Such a strategy is tempting from a management point-of-view due to the diminished cost of control and that the regulation is easily communicated, (one standardized gear, land what you catch!). However, the female moratorium strategy reduces fishing mortality on all sizes of sexually mature females as well as increase egg survival and is by far the more efficient option from a productivity perspective (Fig. S7 in ESM S1).

The female moratorium protects egg-bearing females from being removed by the fishery, increasing the average size of females in the population potentially aggravating the female-to-male mismatch in size distributions. However, the harvesting strategy with a female moratorium did preserve a more unbiased proportion of males in the larger size classes (Fig. S6 in ESM S1) compared to harvesting all individuals larger than MLS. Unless total fishing mortality, F, is very high, a female moratorium may, in fact, increase the fertilization success of larger females and perhaps also the total fertilization success. The counter-intuitive fact that the proportion of males in the 80 mm CL size class was increased rather than decreased in the female moratorium case is an effect of harvesting females that were not yet sexually mature and thus not protected by the female moratorium. The females spend on average longer time in the small size class compared to males of the same size due to the difference in growth rates.

To keep our model simple, we assumed no specific negative effects from sex-selective fishery, although this may exist (e.g., Allendorf and Hard 2009; Zhou et al. 2010). A biased sex ratio may have negative effects on population

resilience and productivity through mechanisms such as females not being mated or reduced genetic quality of fertilized eggs. In the American lobster (*H. americanus*), male limitation is a problem for predominantly small females as they mate with smaller males, with insufficient amount of sperm (Gosselin et al. 2003). In a population with a malebiased fishery, the average size of males will be depressed by the fishery. Consequently the sex ratio will be female biased and size matching in copulating pairs may be off-set such that females copulate with males that may not be able to fertilize entire egg-masses. Either females develop partial egg-masses not fulfilling their reproductive potential or are forced to copulate with several males (Gosselin et al. 2005).

The moratorium on berried females in combination with MLS out-competed the simpler strategy of only an MLS for all relevant parameter combinations. The results on MLS and effort are quite robust and we expect the female moratorium strategy to be further strengthened by maternal effects on the survival of larvae. The dry weight of eggs has been shown to be size dependent, such that larger females produce heavier eggs (Agnalt 2008). Heavier eggs also develop into larger larvae (Moland et al. 2010), a typical case of maternal effect. Larger females may produce more viable offspring and this could have an effect on the efficiency of MinMaxLS harvesting strategy. In such a case our model will underestimate the effect of MinMaxLS on stock and yield, but a female moratorium will also be positively affected by maternal effects on larval survival.

Individual-based models allow the inclusion of more detailed descriptions of individuals and interactions than structured models and this framework is particularly suited for European lobster, with their social interactions and behaviors. To capture heterogeneity in life history characters, IBMs are a reasonable choice of model for decapods. A recently developed tool to overcome the obstacles of no age determination and incremental growth in decapods is the individual-based per-recruit model for the Gulf of Main (GOM) American lobster, H. americanus, fishery (Zhang et al. 2011). In the American lobster case, a tool was developed to estimate biological reference points from biological data on American lobster. This is a good approach for a fishery where fishing mortality and stock status are known. American lobster in the GOM is currently regulated by a legal size window of 83-128 mm CL and V-notching. A maximum size may be reasonable as natural mortality is substantially lower in American lobster (Zhang et al. 2011) compared to European lobster (this study). The Scandinavian lobster fishery is dominated by recreational fishermen with no reporting of catch data. Therefore, our individual-based model evaluates management regimes as scenarios without knowing the exact current fishing mortality or stock status. Conclusions on management options remain similar, apart from the census of fishery mortality, F, made by surveys (of length structure) that connect to adaptive changes in regulations.

Individual variability in growth is documented (Sheehy et al. 1999) but poorly understood. We showed that by seeding individuals in a larger range of sizes a more conservative control rule was needed to optimize a sustainable yield at a high effort (Fig. S8 in ESM S1). A female moratorium again makes this distinction less problematic. For other decapod species, physiological traits are better studied and convincing modelling efforts have been done on incorporating climatic effects on dynamics (Chang et al. 2011).

The amount of landed lobster during the 19th century has been enormous compared to the landings of today. Reports of the export of lobsters from Norway to England in the beginning of the 19th century state some hundreds of thousands of individuals, with a top notion of almost 2 million individuals in 1815 (Solhaug 1983). This equals approximately 1000 metric tonnes, 10 times the landed catch in Norway the last years although landings data are not representative of total catch (Agnalt et al. 2007; Kleiven et al. 2012). In Sweden the landings during the early 1930s were approximately 3 times that of today (Axelsson 1944; Sundelöf et al. 2013). A period of very small landings in the 1960s and 1970s lead to an increased MLS in 1972, 1973 and 1994 and the moratorium on berried females in 1985, but recovery has been slow all the same (Sundelöf et al. 2013).

The access to fishery independent biological data from the no-take area of Kåvra (Ulmestrand 2003) allowed us to parameterize this IBM and explore different management scenarios. Our modelling exercise clearly shows the positive effect on stock size and landings of a stricter management regime. Similar no-take areas have been introduced in southern Norway and will in the coming years provide similar fishery independent statistics as well as information on the efficiency of no-take areas as a management tool (Moland et al. 2013b). These efforts will substantially improve the biological insight into management of lobster in the Skagerrak and in other parts of the lobsters' distribution. However, the lobster stock in Norway has not recovered to historic levels after the depletion in the 1960s and 1970s (Agnalt et al. 2007; Kleiven et al. 2012), although the MLS has been gradually increased beyond 80 mm CL. Today the MLS is set to 25 cm TL (88-90 mm CL) and the Norwegian Directorate of Fisheries invoked a moratorium on berried females in 2009 (NDF 2011) along with a shorter season on the south coast. Through those last regulations the same rules apply throughout Norway. The effects of the moratorium are not yet evaluated and the seasonal fishery of the coming years will reveal the efficiency of the female moratorium.

Although the model captured main aspects of individual growth and population development, it contains a number of simplifying assumptions, which can be relaxed by incorporating additional ecological processes or details within the proposed framework. For example, the model can be further developed by incorporating fertilization limitation, maternal effects, individual-based modeling of juvenile stages, temperature-dependent growth, spatial effects of Norwegian and Swedish regulations, and compliance of fishers to regulations. Such developments would provide a broader scope for testing management alternatives and a more realistic representation of the effects of fisher behaviour.

Differences in the management regimes between Norway and Sweden are not entirely reflected in the modeling results. The Norwegian regulations up to 2008, an MLS of 88-90 mm CL, should according to our model protect sufficient reproductive potential for a good stock to develop. However, the model is parameterized with data from the west coast of Sweden, and the scarce comparable data available (Agnalt et al. 2007) show that growth patterns differ. In that perspective our prediction may not be directly applicable to the Norwegian stock. However, growth of the stock may be slow, and variability in recruitment may further delay the reestablishment of a strong lobster stock. There have been several changes in regulations of Norwegian lobster fishery in the past few years, and if efficiently implemented the female moratorium should facilitate the recovery of the stock. For the Swedish lobster there are no major positive changes in stock size to be expected unless regulations are changed.

Conclusion

Current management of Scandinavian lobster populations is becoming stricter. In our model, an MLS of >80 mm CL

and a moratorium on females are predicted to give high and sustainable yield for Swedish conditions. An MLS >85 mm CL is likely to further increase stock size as well as landed biomass. The new regulation in Norway, adding a moratorium on berried females to the MLS of 25 cm TL (approximately 90 mm CL), should help to recover the Norwegian lobster stock. An MLS of 90 mm CL in combination with a female moratorium provides a large yield but still contributes to a substantial decrease in reproductive value. A smaller MLS would need additional regulations on effort/quota to overcome the risk of overexploitation, which will be difficult to monitor and control.

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