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research paper

Development of an individual-based tag recapture model to benchmark biomass and harvest rates in an iconic lobster fishery

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ABSTRACT.—The West Coast Rock Lobster Managed Fishery (WCRLMF) moved from input to output controls in 2010. This change affected the relativity of fishery-based data sources (e.g., catch rates and landed size composition), making the assessment of the fishery problematic. A novel examination of the stock dynamics was required to ensure the robustness of the stock assessment and associated management arrangements. This study derived estimates of current biomass levels and harvest rates from the release of over 60,000 tagged western rock lobsters (*Panulirus cygnus*). A Brownie tag-recapture (BTR) model was initially implemented to provide an assessment on a fishery-wide basis. Estimates from this were compared to those derived from a novel purpose-built tag-recapture individual-based model (IBM) that accounted for sex, size, month, and location-specific changes in catchability. The two models produced similar estimates on a fishery-wide scale—harvest rate (HR 0.26 vs 0.30, respectively) and legal-sized biomass (about 24,500 vs 20,735 t, respectively)—while the IBM also provided estimates on a far finer spatial and temporal scale. Both models indicate that the WCRLMF is currently in a very sustainable condition and is being fished at a rate below maximum economic yield (HR_{mey} is about 0.39). These findings were in concert with estimates derived for this fishery based on two separate catch-rate based population models, an integrated population model and a biomass-dynamics model. Such strong agreement among all models provides great certainty in the current assessment and management of this important marine resource.

The West Coast Rock Lobster Managed Fishery (WCRLMF) has been managed for over 40 years by ensuring breeding stock levels remain above limit reference points using a range of effort controls such as limited pot numbers, temporal closures, and biological controls (e.g., protection of breeding females and minimum and maximum size limits; de Lestang et al. 2016). The effectiveness of this harvest control system relied heavily on the consistency between fishery-dependent catch rates and lobster abundance. Between 2009 and 2013 the fishery progressively altered its management regime from effort-controls to individual-transferable quotas (Penn et al. 2015). This change in management dramatically altered the behavior of the catching sector, as they moved away from competing with each other for catch under effort controls to maximizing profits through fishing in high beach price periods and reducing their costs (de Lestang et al. 2018). Fishers have now increased pot soak times, are using less bait, and are not moving great distances in search of small increases in catch, all of which have affected their catch rates.

These marked changes in fishing behavior affected the relativity of the long-standing empirical fishery-dependent catch rate indices that were a major component of the assessment of the lobster stocks [e.g., catch rates of legal, undersize, and breeding lobsters (de Lestang et al. 2018)]. A recent study examined the possibility of using alternative data sources unbiased by effort to monitor biomass levels and harvest rates using change-in-ratio techniques (de Lestang et al. 2012). The project concluded that: (1) the current data sources available to the fishery had too many unknowns including size and sex specific timing of growth and movement to enable the assessment of harvest rates using these techniques; and (2) a robust tag-recapture study with multiple releases across different fishing seasons could generate independent assessments of legal biomass and harvest rates. A comprehensive tag-recapture study would also provide increased resolution of the movement dynamics of lobsters, especially the rate of migration between management zones that is likely to have been impacted by altered fishing patterns following a move to output controls (de Lestang and Caputi 2015). Such information is vital to the industry in their discussions of the potential benefits of voluntarily reducing quotas to generate increased localized catch rates (Cooke and Beddington 1984, de Lestang et al. 2012).

In 2008 the Department of Primary Industries and Regional Development (DPIRD) began to develop a stock assessment model that integrated fishery-independent data into the assessment process. With the recent breakdown in the relativity of fishery-dependent catch rates between years, this stock assessment process has been forced to rely heavily on fishery-independent data. Fishery-independent data, however, is currently limited both spatially and temporally and to increase these surveys to collect additional data is both expensive and time consuming (Caputi et al. 2021). Tagging studies have proven to be a good alternative to additional fishery-independent surveys, as they utilize fishing fleets for capture, tagging, release, and recapture which reduces costs dramatically, while their results can remain unaffected by fishers' behavior (Maunder 1998, Pollock et al. 2004, Leroy et al. 2015). The Brownie tag-recapture (BTR) tagging design is especially valuable in this circumstance. This technique utilizes multiple releases of animals separated by relatively short temporal periods (months to years), with the contrast in recaptures between release groups shown to provide accurate and timely estimates of catchability, mortality, and stock size (Hoenig et al. 1998, Ley-Cooper et al. 2013). A limitation of the BTR is its generalized nature, as all tagged animals examined within its structure are treated with common parameters for catchability, tag loss, and tag reporting. For example, to examine the recapture rates of both males and females, they must either be grouped together and examined in one model, with all parameters being an average between the sexes, or must be separated and examined in two separate models, thus reducing the sample size (robustness) of the models. Further reductions in power then occur if animal size or location is to be incorporated into the assessment. An alternative to the BTR is to develop an individual-based tag-recapture model (IBM) that is capable of tracking individual animals throughout the life of the study and treating each animal uniquely yet within a common framework (Pine et al. 2003, Frank and Baret 2013, Senina et al. 2020). The movement of individuals into discrete size-specific spatiotemporal "bins" allows for the catchability of an animal to vary as it grows, moves, matures, and experiences different levels of harvest while maintaining other common parameters across groups (such as reporting rate; Phillips et al. 2018). This ability to allow for individualistic catchability within the integrated model framework, whilst allowing for observations from different groups to collectively inform certain common characteristics, can increase the accuracy and robustness of parameter estimates (Maunder and Punt 2013, Goethel et al. 2019, Senina et al. 2020).

Tag-recapture data is often used in integrated models for the purpose of informing on a subject's movement and growth dynamics (Maunder and Punt 2013), and less often used to inform on survival (Ziegler 2013, Raabe et al. 2014). This is primarily due to the increase in complexity that the addition of such data requires in the structure of many integrated models. This study aims to derive estimates of current biomass levels and harvest rates throughout the WCRLMF based on the multiple release and recapture of tagged lobsters in a spatially and temporally dynamic integrated model framework. A BTR will first be applied, utilizing previous information from tag-loss and tag-reporting experiments, to assess tag-recaptures on a fishery-wide basis. This will produce broad estimates of harvest rate and biomass levels for the fishery, independent of biases associated with fisher behavior. An IBM will then be used to produce similar estimates on the same scale for comparison with the BTR, as well as estimates on a far finer spatial scale, in addition to estimates of migration and growth. The IBM will be developed using the same framework [spatial and temporal scale and on the TMB platform (Kristensen et al. 2016) as the WCRLMF integrated population model (IPM) currently used for assessing this resource]. If the IBM proves reliable in its assessment of the fishery—based only on tag-recaptures—the incorporation of this data into the IPM, in a framework like that of the IBM, will provide additional robustness to the annual fishery assessment.

Methods

Two models were used to estimate harvest rate and legal-sized [≥76 mm carapace length (CL)] biomass: a Brownie Tag-Recapture model (BTR; Brownie et al. 1986) and a novel individual-based population model (IBM). Data inputs differed for the two models (Table 1), with the IBM not requiring previous estimates of tag loss and reporting rate. When estimates were required as inputs (e.g., tag-loss rate in the BTR), estimates and their associated variances reported in de Lestang et al. (2016) were used. The BTR was developed on the R platform, whereas the IBM was developed on the TMB platform due to its greater number of estimatable parameters (13 vs 53 parameters, respectively). Estimated legal biomass and harvest rate levels from these two models were compared to estimates from a biodynamics model (BMD; Online Supplementary Material) and an individual-based population model (de Lestang et al. 2016), neither of which use tag-recapture data for biomass estimation (they are based primarily on catch and effort, with size composition used in the later model).

Table 1. Data or estimate input requirements of the two models Brownie Tag-Recapture model (BTR) and individual-based population model (IBM).

Data/estimate inputs	BTR	IBM
Double tag release and recapture data	- - -	Y
Commercial catch and effort data	Y	Y
Commercial monitoring data	- - -	Y
Independent Survey Data (IBSS)	- - -	Y
Annual level of high-grading	Y	Y
Tag loss rate estimate	Y	- - -
Reporting rate estimate	Y	- - -
Natural mortality	- - -	Y

Tag Release.—Tagging of lobsters was conducted by Department of Primary Industries and Regional Development (DPIRD) staff using standard Hallprint™ T-Bar anchor tags. Tags were inserted ventrally as described by Melville-Smith and Chubb (1997). Only lobsters without obvious damage (e.g., missing appendages) were tagged (Brown and Caputi 1983). Lobsters were released individually, immediately post tagging to the water at the site of their capture, from June 2014 to November 2018 off both commercial and research vessels throughout the fishery (Fig. 1A). Releases from commercial vessels were limited to nonretained lobsters [e.g., those high-graded (legal lobsters released due to their lower value) or protected], whereas those from research vessels consisted of all captured lobsters. This limitation on lobsters available for tagging on commercial vessels was not considered too restrictive as, due to rapid changes in the relationship between lobster size and value (beach price), those lobsters high graded one week became the targeted lobsters the following, thus generally allowing a full-size range of lobsters to be tagged from commercial vessels (35–152 mm CL). For estimating fishing mortality, the data have been limited to only those lobsters released with CL ≥ 76 mm (lobsters below this have a substantially reduced catchability due to the use of escape gaps in lobster pots). All lobsters tagged (irrespective of release size) were used in the determination of growth and movement in the IBM.

Additional tagging was conducted to aid in the assessment of tag loss rates (Hearn et al. 2003), in the form of two separate trials, double tagging with the two T-bar tags (TT) or tagging with one T-bar tag and the application of a permanent month-specific mark (TP). The TT data consisted of releasing lobsters tagged with two standard T-Bar anchor tags inserted ventrally on either side of the lateral line into the abdomen. A total of 1032 TT lobsters were released across the fishery from 2014 to 2016. All releases occurred in water depths >40 m with most lobsters being mature and larger than 76 mm CL. The tag-mark trial (TP) consisted of the release of lobsters tagged with a single T-Bar tag and the marking of a month-specific pleopod via snipping with scissors. Each month a different pleopod was marked allowing its release month to be determined upon recapture. For the TP trials a total of 7946 lobsters were released between 2014 and 2016 and all recaptures were conducted via research surveys since the marked pleopod had to be examined. All pleopods which had been previously marked were recorded and re-snipped to ensure they remained obvious. Since the pleopod would be fully regrown after two molts and therefore the mark undistinguishable, the data was limited to liberties of 13 mo.

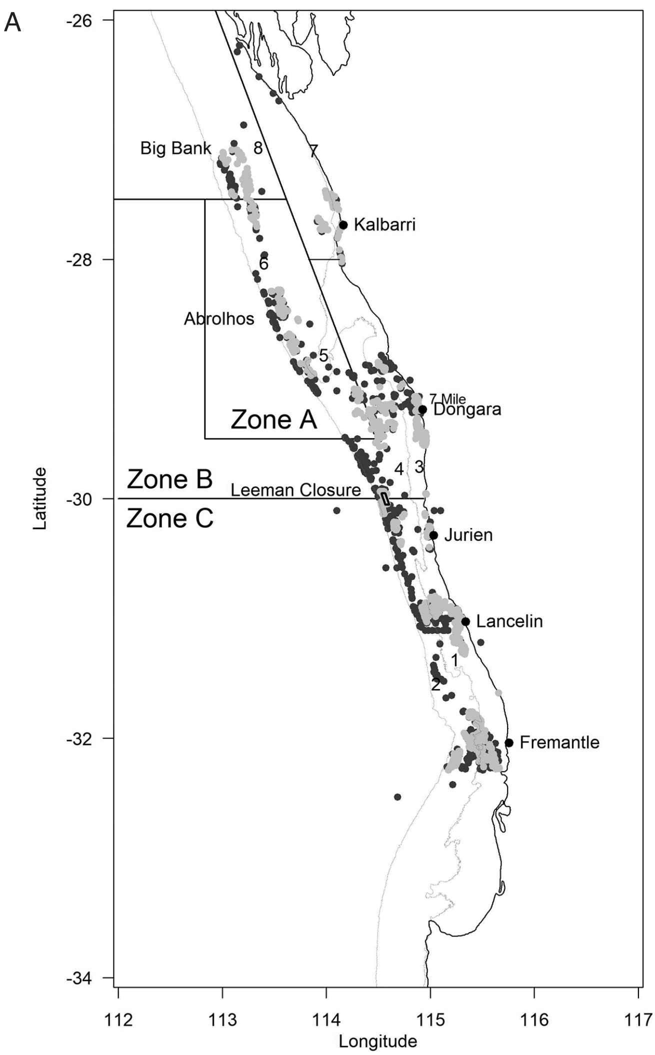

Figure 1A. Release (light grey points) and recapture (dark grey points) locations of lobsters tagged in the three management zones of the fishery (A, B, or C), separated by solid black lines, which in combination with the 40 m and 200 m isobaths (light grey dotted lines) delineate the various areas used in the individual-based model (areas identified by values 1–8).

Tag Recaptures.—Information from recaptured lobsters was provided by commercial and recreational fishers as well as research staff during research trips. Information requested included recapture location (GPS), recapture date, sex, size, and condition (color, maturity state, and appendage damage). All tag-release and recapture data were stored on a DPIRD-owned SQL database. Prior to analysis, the tagging database was examined for obvious erroneous information. Records were excluded from analysis if the tagged lobster was reported to have changed sex between release and recapture or was reported to have been released or recaptured on land (<1% observations).

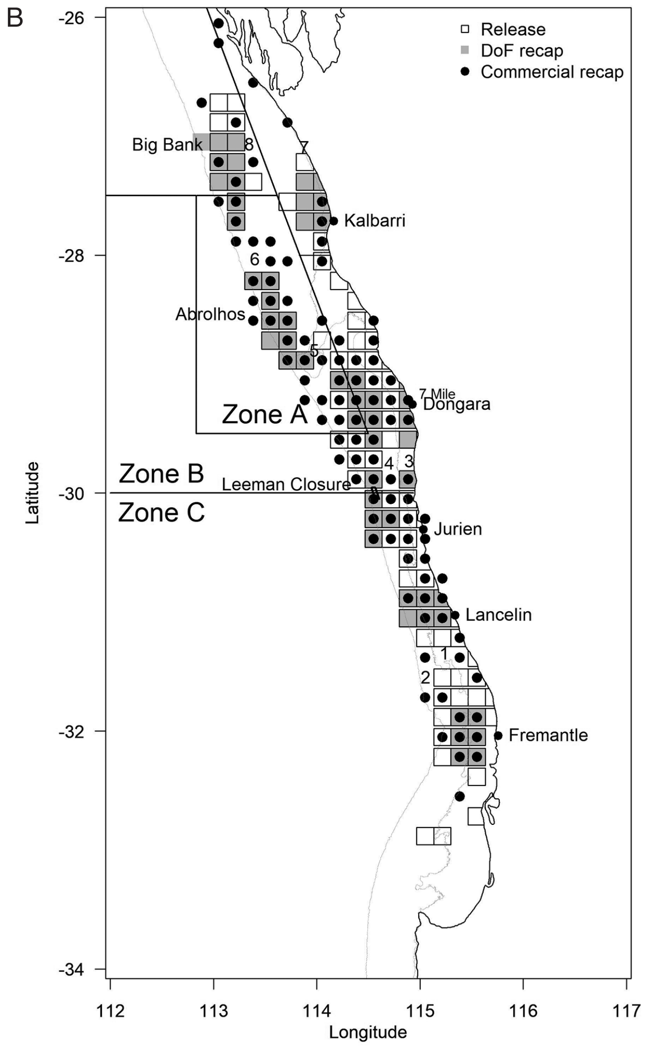

Figure 1B. Map has been delineated into 10 × 10 nm blocks, showing areas for research monitoring (black border square), research tag returns (black dot), and commercial tag returns (grey shaded) within the West Coast Rock Lobster Managed Fishery. Ports from where monitoring are conducted are denoted by small black dots and associated location over the land.

Commercial Catch and Effort Data.—It is a mandatory requirement for catch and effort data to be completed by all fishers at the conclusion of each fishing trip via a Catch Disposal Record (CDR) recording the weight (kg) of retained lobster and the number of pot lifts within a 10 × 10 nm block. The number of legal lobsters caught and returned (high-graded) was also recorded. For further information, *see* de Lestang et al. (2016).

Commercial Monitoring Data.—Research staff undertake monthly fishery-dependent monitoring of size, sex, reproductive state, and color (indicative of migratory phase) of lobsters at six locations (Fremantle, Lancelin, Jurien, Dongara, Kalbarri, and Abrolhos Islands) throughout the fishery (Fig. 1B) in four depth categories (<10, 10–20, 20–30, and >30 fathoms). For more details on the catch monitoring program, *see* de Lestang et al. (2016).

Independent Survey Data.—DPIRD conducts annual independent breeding stock surveys (IBSS) at six deepwater locations throughout the fishery in September–November each year. These surveys are standardized for changes in fishing behavior and are staffed by DPIRD staff on commercial vessels. Every lobster captured during these trips is examined closely, therefore all those with a tag would be expected to be discovered (would have a reporting rate of 100%). For more details on the IBSS, *see* de Lestang et al. (2016).

Brownie Tag-Recapture Model.—A fishery-wide harvest rate and legal biomass estimate was determined using a BTR model (Brownie et al. 1986, Lauretta and Goethel 2017), which required lobster tag and recapture data, commercial catch and effort data, and prior estimates of tag loss and tag reporting (Table 1).

The BTR estimates the month-specific catchability of an average lobster (q_m), i.e., the probability of capturing a lobster with one unit of effort. The BTR was built on a monthly time scale spanning August 2014 to December 2018 (53 mo) and treated the entire WCRLMF (Fremantle to Kalbarri; Fig. 1) as a single stock unit. The BTR was fitted to all tagged lobster (CL ≥ 76 mm) released during this period (35,661), of which a total of 1972 tagged lobsters were reported to the Department that fitted the requirements of use in this model. For example, a recaptured lobster could still be used in the model if it had an unknown recapture CL, or unknown recapture location. The size composition of tagged lobsters was assumed to be proportional to lobster sizes within the commercially caught population (as tagged lobsters were randomly sampled from commercial catches). Released lobsters were also assumed to have mixed within the population within the first month at liberty (i.e., there was not a period of concentrated tags in any area). The model equation was:

$$\lambda_1 = O_{l,r} \ln\left(T_{r-l} \varsigma_r \left(\frac{F_r}{(F_r + M)} \right) (1 - \exp(-F_r - M)) \exp\left(-\sum_{t=l}^{r-1} F_t - (r-l)\, M \right) \right),$$

where λ_1 is the log-likelihood associated with the number of observed reported lobsters ($O_{l,r}$) that were released in month/year (l), recaptured in month/year (r) and t is a specific month/year. T_{r-l} is the observed proportion of lobsters still retaining their tag after a specific time at liberty (recapture month – release month), ς_r is the reporting rate in a month/year combination (both predetermined; *see* IBM) and M is the monthly instantaneous rate of natural mortality (estimated parameter). F_r is the fishing mortality in a specific month of a year based on the equation:

$$F_r = E_r q_m,$$

where E_r is the observed effort in pot lifts in the recapture month/year combination and q_m is the estimated catchability of lobsters in that recapture month (m; q_m does not differ between years, only months).

A second log-likelihood component (λ_2) was derived using the lobsters that were not recaught/reported ($Q_{l,r}$):

$$\lambda_2 = Q_{l,r} \ln \left(1 - \left(T_{r-l}\varsigma_r \left(\frac{F_r}{(F_r + M)}\right)(1 - \exp(-F_r - M)) \exp\left(-\sum_{t=l}^{r-1} F_t - (r-l)M\right)\right)\right).$$

The sum of the two log-likelihood components was then maximized in R using the "nlminb" routine to estimate the 13 parameters (R Core Team 2019).

Estimates produced by the model included the annual harvest rate (*HR*), which is derived from annual estimates of F_a, and legal biomass (derived from the estimated *HR* and the known commercial catch). The equation used to derive these estimates was:

$$HR = \frac{F_a}{(F_a + 12M)}\left(1 - e^{(-F_a - 12M)}\right)\kappa,$$

where the estimates of monthly fishing mortality (F_m) are averaged for each month and then summed across a fishing season to derive annual estimates of F [$Fa = \sum_{m=1}^{12} F_m$] (Huusko and Hyvärinen 2005, Wiedenmann and Jensen 2018). κ is the proportion of the legal catch retained [not high graded, currently set to 0.75; based on the average level of high grading recorded over the study period (*see* de Lestang et al. 2016 for further details on high grading)]. The legal biomass estimate is based on the average landed commercial catch from the 2015 to 2018 fishing seasons (6400 t) divided by the *HR*.

The model was initialized with the 12 (unique for each month) catchability parameters set to 1.0e^{-7} and natural monthly mortality set to 0.0125 (Online Table S1). Estimates of uncertainty were derived from 20,000 bootstrap runs of the model whereby the observations used in the log-likelihood functions were randomly sampled.

Individual-Based Model.—Fishery-wide harvest rates and legal biomass estimates for each fishing season 2014 to 2018 were determined using an IBM. Inputs to the model were lobster release and recapture data, double-tagging data, commercial catch and effort data, fishery-dependent monitoring data, high-grading and discard (return of nonlegal lobster) data, and fishery-independent survey data (Table 1). The model did not require the input of any previously determined parameter estimates except for an estimate of natural mortality and was assumed to be 0.15 yr^{-1} (de Lestang et al. 2016). The model dealt with each tag-released lobster individually, adding it to the model framework when tagged and then using its time at liberty, release size, sex, and the level of fishing exploitation in each cell as well as average sex-specific migration behavior to adjust the likelihood of it being in a specific area on the date when it was recaptured (as well as being in all other areas). As such the model tracks each individual lobster through its biological processes (growth, natural mortality, and movement) and exposes it to spatiotemporal-specific commercial and survey harvest for its period at liberty if it was reported to have been caught, or for the timespan of the model if it had not been recaptured (until the end of the 2018 fishing season). The IBM is built on the same temporal and spatial scale as that used by a stock assessment model currently used in the fishery (Table 2, Fig. 1). The IBM was fitted to all tags released during the 2014–2018 fishing seasons (51,563) that had a known sex, a CL > 40 mm, and were at liberty for at least 2 mo. Of the released lobsters 33,661 were used in the model to determine catchability of the commercial sector as they had a CL ≥ 76 mm and were not recaptured during a survey or the recreational sector. Of the 1972 recaptured lobsters only a subset could be used for estimating growth (1612)

Table 2. Temporal scale of the individual-based population model (IBM) and associated processes.

Time Step	Time Step (Months of Growth)	Model Activity
1	15 Jan–Feb (1 mo)	½ migration north Growth Mature females protected M and F mortality and tag loss ½ migration north
2	Mar–Apr (2 mo)	Growth M and F mortality and tag loss
3	May–June (2 mo)	Growth M and F mortality and tag loss
4	July–14 Sep (3 mo)	Growth M and F mortality and tag loss
5	15 Sep–14 Nov (2 mo)	Growth Mature females protected M and F mortality and tag loss
6	15 Nov– 4 Dec (1 mo)	Growth Mature females protected M and F mortality and tag loss
7	15 Dec–14 Jan (1 mo)	½ migration offshore Growth Mature females protected M and F mortality and tag loss ½ migration offshore

and movement patterns (1947), as these lobsters had records of their release and recapture size or location, respectively. The model contained two main components, a tag loss (produced one likelihood value) and a population component (produced two likelihood values: growth and migration/survival). The three likelihood values were summed to allow the model to fit each aspect of the observed data simultaneously.

Tag Loss Component.—The methodology of Myers and Barrowman (1996) was used to estimate the rate of tag loss. This technique breaks tag loss down into two separate components, initial tag shedding (ρ; instant loss due to poor technique or mortality) and chronic tag loss (ϕ), which is a constant rate of loss over time (t). The negative log-likelihood produced by the TT and TP trials were combined (e.g., $\lambda_L = \lambda_{TT} + \lambda_{TP}$) to produce a single tag-loss likelihood component (λ_L). For more details on this method, *see* Online Supplementary Material.

Population Component.—The population component of the model tracked the probability of each tagged lobster over the time-steps corresponding to that lobster's liberty, or until the end of the 2018 fishing season if the lobster was not recaptured. Within each time-step the survival probability of a lobster was subjected to the processes outlined for that time-step (Table 2), which included migration (½ probability), growth, mortality (natural and fishing), and migration (½ probability), in that order. The timing of the various processes was based on previously reported *Panulirus cygnus* biology (de Lestang et al. 2016).

Migration.—For the western rock lobster, migration begins in shallow water areas in late November/early December each year, with a movement directly offshore, which then changes to a northward deepwater migration in January/February (de Lestang 2014). Since the first IBM time-step spans 15 January–28 February (Table 2),

Table 3. Predetermined movement matrix identifying which model areas lobsters can move between (based on de Lestang 2014). O denotes offshore movement (in time-step 7) and N denotes north-wards movement (in time-step 1).

To	From						
	1	2	3	4	5	6	7
1	---	---	---	---	---	---	---
2	O	---	---	---	---	---	---
3	---	---	---	---	---	---	---
4	---	N	O	---	---	---	---
5	---	---	---	---	---	---	---
6	---	N	---	N	O	---	---
7	---	---	---	---	---	---	---
8	---	N	---	N	---	N	O

migration occurs northwards during this time-step, with the subsequent year's migration starting in shallow water and moving offshore in the last model time-step of each fishing season (15 December–14 January). The probability (G_d) of a lobster migrating into an area from another is determined by four factors: (1) the lobster's estimated CL for that time-step (L_i); (2) a normal distribution, scaled to a maximum of 1.0 (when $L_i = \alpha_f$) where α_f is an area-specific mean CL of migration from area f (seven parameters for areas 1–7) and one of two standard deviation parameters common for all shallow- or deepwater areas, respectively (σ_g^m, where g represents depth); (3) a second area-specific parameter [β_f, (seven parameters for areas 1–7)] representing the proportion of the scaled normal distribution that migrates; and (4) a predefined movement matrix (K_{dft}; Table 3) that identifies during each time-step (t) which source area (f) lobsters move to which sink area (d). The movement equation was:

$$G_d = K_{tfd}\beta_f \left(\frac{N\left(L_i, \sigma_d^m\right)}{N\left(\alpha_f, \sigma_d^m\right)} \right).$$

Growth.—In western rock lobster, growth declines with increasing size/age, and although it is almost continuous in small/younger lobsters, it becomes intermittent and synchronous throughout that sex of the population in later life (Chittleborough 1976, de Lestang 2018). Although growth is not constant in invertebrates (occurs stepwise due to molting), previous work has shown that growth can be well replicated by growing individuals intermittently either on a short time scale (monthly) or longer time scale (biannually; Punt et al. 2013, de Lestang 2018). The IBM applied growth on a time-step scale, i.e., increasing the length of a lobster during every time-step based on the temporal length of that time step (Table 3). If a time step contained part months (e.g., 1.5 mo) only whole months of growth were applied. This resulted in some time-steps being applied slightly too much growth (e.g., time-step 4) and others too little (time-step 1), as described in Table 2. This was not considered to have an impact on the modelling as the growth of lobsters was only used for those at liberty for over 6 mo and the expected change in CL over ½ month is less than much of the error produced when measuring a lobster. The IBM used a four parameter inverse logistic equation to describe the relationship between body size and increase in body size over a period of 1 mo. If 2 mo of growth was needed to be applied to a lobster, the equation was applied twice. The equation used was:

$$L_{a,s,n+1} = L_{a,s,n} + (\delta_{a,s} + \eta_{a,s})/(1 + e^{((L_{a,s,n} - \gamma_{a,s})/\kappa_{a,s})}) + \eta_{a,s},$$

where the CL ($L_{a,s,n+1}$) of a lobster after 1 mo (*n*) is based on the area (*a*) and sex (*s*) specific parameters for maximum growth rate ($\delta_{a,s}$), minimum growth rate ($\eta_{a,s}$), an inflection point ($\gamma_{a,s}$) and a rate of change in growth ($\kappa_{a,s}$). The log-likelihood (λ_g) of a lobster having been grown to the length of when it was recaptured was determined using the equation:

$$\lambda_g = \sum_{i=1}^{n} -\ln\left(\frac{1}{\sigma_g\sqrt{2\pi}} e^{\frac{(K_i - L_i)^2}{2\sigma_g^2}}\right),$$

where K_i and L_i are the observed and model estimated lengths of the i^{th} lobster, and σ_g is a standard deviation growth parameter, common for all areas and sexes.

Tag Reporting Component.—Commercial fishing effort data was divided into two groups based on the presence of government staff on the fishing trip as part of the commercial monitoring program (*see* de Lestang et al. 2016), to account for differential tag reporting rate. During commercial monitoring, government staff examine every lobster carefully and are assumed to detect and report all tag-recaptured lobsters. Commercial operators have a different focus and have been found to miss tagged lobsters as they do not always examine the underside of every animal landed. The IBM uses the contrast between tag recaptures from these two groups in each model region and time-step to estimate commercial tag reporting rate (*see below*).

Model Structure.—After applying ½ migration and the time-steps' growth, the probability of a lobster being in that area in that timestep ($P_{a,t}$) was used to calculate the probability of it being caught ($\tilde{\Gamma}^g$) by each commercial group (monitoring or not: *g*) based on their level of fishing mortality (F^g) in that model area (*a*) and time-step (*t*) using the equations:

$$F_{a,t}^{g} = q_t E_{a,t}^{g},$$

$$Z_{a,t} = \tau_t T + \tau_t M + \sum_{i=1}^{g} F_{a,t}^{i},$$

$$\tilde{\Gamma}_{a,t}^{g} = P_{a,t}\frac{F_{a,t}^{g}}{Z_{a,t}}\left(1 - e^{(-Z_{a,t})}\right),$$

with catchability (q_t) being unique for each time-step (common across years), *T* is the natural log monthly rate of tag loss, *M* represents monthly natural mortality (set at 0.0125 mo^{-1}), τ is the temporal length of the time-step in months, and $E^{g}_{a,t}$ being the effort in pot lifts for each commercial group. If a lobster was recaptured by a vessel without a government observer, its probability of being caught was further adjusted by the model estimated reporting rate (ς, common across all areas and time-steps).

If a lobster remained at liberty in a time-step its probability of being in that model area was reduced by the product of the probability of being caught and not reported, natural mortality, and tag loss using the equation:

$$P_{a,t+1} = P_{a,t}e^{(-Z_{a,t})}.$$

The log-likelihood (λ_c) of a lobster having been caught in a model area and time-step and not caught in other model areas and time-steps was determined using the equation:

$$\lambda_c = \sum_{j=1}^{g}\sum_{i=1}^{h} -\ln(\varsigma\widetilde{\Gamma}_i^j) + \sum_{j=1}^{g}\sum_{i=1}^{l} -\ln(1-\widetilde{\Gamma}_i^j),$$

where h and l represent all captured and nonrecaptured lobsters, respectively, in each area and time-step and ς is set to 1 if government staff are on-board (otherwise it is estimated and constrained to be between 0 and 1). The parameters used to initialize the model are listed in Online Table S1. The total log-likelihood of the observations given the model parameters was:

$$\lambda_T = \lambda_L + \lambda_g + \lambda_c.$$

The primary objective of the model was to produce estimates of commercial harvest rates [HR^l: proportion of available (legal) lobsters extracted from the fishery, i.e., retained after discards/high-grading has occurred], and legal biomass (LB^l: all lobster ≥76 mm CL) in the fishery. These were estimated on a fishery-wide fishing-season basis (2014–2018) using the following equations:

$$F_{y,a,t}^{o} = \sum_{i=1}^{g} F_{y,a,t}^{i},$$

where the total fishing mortality (F^0) is derived from the fishing mortality estimates of the two commercial fishing groups (g), i.e., with and without departmental monitoring staff. The harvest rate was then determined by the equation:

$$HR_y^I = \sum_{j=1}^{t}\sum_{i=1}^{a}(1-H_{y,i,j})\frac{\sum_{j=1}^{t}\sum_{i=1}^{a}F_{y,i,j}^{t}}{\sum_{j=1}^{t}\sum_{i=1}^{a}Z_{y,i,j}}\left(1-e^{\left(-\sum_{j=1}^{t}\sum_{i=1}^{a}F_{y,i,j}^{t}-12M\right)}\right),$$

which is adjusted for average discards/high-grading (H) in that model time-step and year and legal biomass is calculated by the equation:

$$LB_y^I = \frac{C_y}{HR_y^I},$$

where C represents the commercial catch in year y.

Results

A total of 64,623 lobsters ranging in size from 29 to 158 mm CL were released between 2014 and 2018, and when limited to those lobsters of an exploitable size (≥76 mm CL) for estimating harvest rates and legal biomass, this reduced the total number of lobsters for this analysis to 35,661.

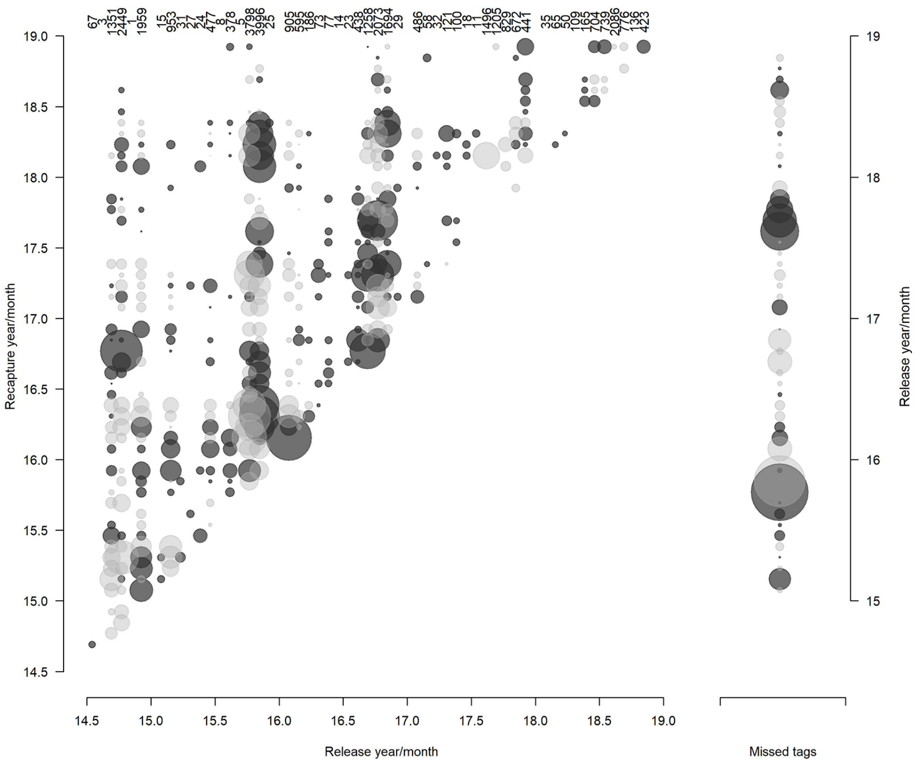

Figure 2. Residual plot from Brownie tag-recapture model (BTR) of observed and estimated tag-returns from each release pulse in each recapture year/month in decimal form (e.g., 15.0 = January 2015 and 15.5 = July 2015). Positive and negative residuals are identified by light and dark grey shading, respectively, with the symbol's size indicating the relative magnitude of the residual. Numbers at the top show the number of tags released during that month. Missed tags represent the tags that were not reported and are presented on a different scale to the reported tags [symbol size is not comparable between groups (recaptured vs missed), only within groups].

Brownie Tag-Recapture Model.—

Diagnostics.—Two diagnostics were produced to assess the fit of the BTR model to the observed data: the residuals associated with reported lobsters and those with un-reported lobsters (Fig. 2). Although the model failed to replicate some of the high recapture rates, there were no obvious patterns across the residual plot that would have indicated a missing component in the model (Fig. 2). There were four areas of increased residual size (late 2014/early 2015, late 2015/early 2016, late 2016/early 2017, and late 2017/early 2018), and these were relatively well split between positive and negative residuals. The increased size of the residuals in these four time periods are likely related to the increased number of tags released during these periods. The annual Independent Breeding Stock Surveys (IBSS) occurs at the end of each year (surveys are conducted annually in September–November) and was an opportunity for releasing and recapturing large numbers of tags.

Outputs (Harvest Rate and Biomass).—Monthly catchability was estimated to increase from $1.5e^{-5}$ in January to peak of $4.1e^{-5}$ in April before declining to low levels in

June and July ($1.2e^{-5}$ and $1.3e^{-5}$, respectively). Estimated catchability then increased again slightly to reach a smaller peak in September ($1.8e^{-5}$) before declining through until a low of $1.1e^{-5}$ in December. Monthly natural mortality (95% CI) was estimated to be 0.010 ($2.8e^{-3}$) per month which equates to an annual rate of 0.129 (0.034).

The BTR model estimated the average (95% CI) harvest rate (HR^B) for tagged lobsters during the period 2014 to 2018 (the time span of the model) to have been 35% (14%). This estimate is based on all captured lobsters over legal size and hence includes those which are protected from capture (e.g., reproductively active females) as well as those high-graded (about 25% of the legal catch was high graded over this period). As a result, it does not represent the true harvest rate, i.e., the proportion of the legal catch landed. The true exploitation rate was estimated by adjusting the harvest rate by the high grading rate (25%), resulting in a harvest rate estimate of 26% (11%). Based on this harvest rate estimate and the average landings of about 6400 t over the past four fishing seasons, the estimated average biomass of legal lobsters over these three seasons is 24,500 t (6300 t).

Individual-Based Model.—Of the 1032 lobsters released with two T-Bar tags (TT), 134 were recaptured with either both tags present (96) or only one tag present (38). Of the 7946 TP lobsters released, 841 were recaptured with one T-bar tag and one marked pleopod, while only 66 were caught with a missing T-Bar tag (as identified by the marking of their month-specific pleopod).

Diagnostics.—Residuals between the observed and estimated tag loss component of the IBM showed no progressive patterns across liberties or between the two tag loss trials (TT or TP) which indicated there was no major missing components in the model (Fig. 3A). Observations with large sample sizes generally displayed smaller residuals (better fit) than those with much smaller sample sizes. As such overall the model fits better to the TP (Fig. 3C) data than TT data (Fig. 3B), as the TT data has a greater variability between successive temporal observations.

Residuals between observed and estimated CL of recaptured lobsters showed no progressive trends or patterns when plotted against different characteristics that existed in the data, namely release CL, recapture source (who reported the lobster), sex of lobster, release location, or the time at liberty (Fig. 4). This indicates that the model was sufficiently capable of replicating the tag-recapture growth of lobsters. The residual plots also highlighted low samples for lobsters released with a CL > 120 mm, returned by commercial monitoring, females and males in area 7 and at liberty for more than 24 mo (although a good sample size does exist for lobsters at liberty for 36 mo).

Migration was well replicated by the model as indicated by the high concordance correlation coefficient (ρc) in each release location (Fig 5A–H). These plots also highlight a lack of recaptures that occurred for tagged lobsters released in locations 5 and 7 in their directly offshore model location (6 and 8, respectively). This is partly explained by the small release sample sizes within these two areas, but also indicates a relatively lower rate of migration from these areas.

Outputs (Harvest Rate and Biomass).—The IBM estimated the proportion (95% CI) of lobsters retaining a tag following release (i.e., 1- instantaneous tag loss) was 0.94 ($6.7e^{-3}$) and a constant monthly tag loss (i.e., chronic tag loss) of $7.6e^{-3}$ ($1.3e^{-3}$). Based

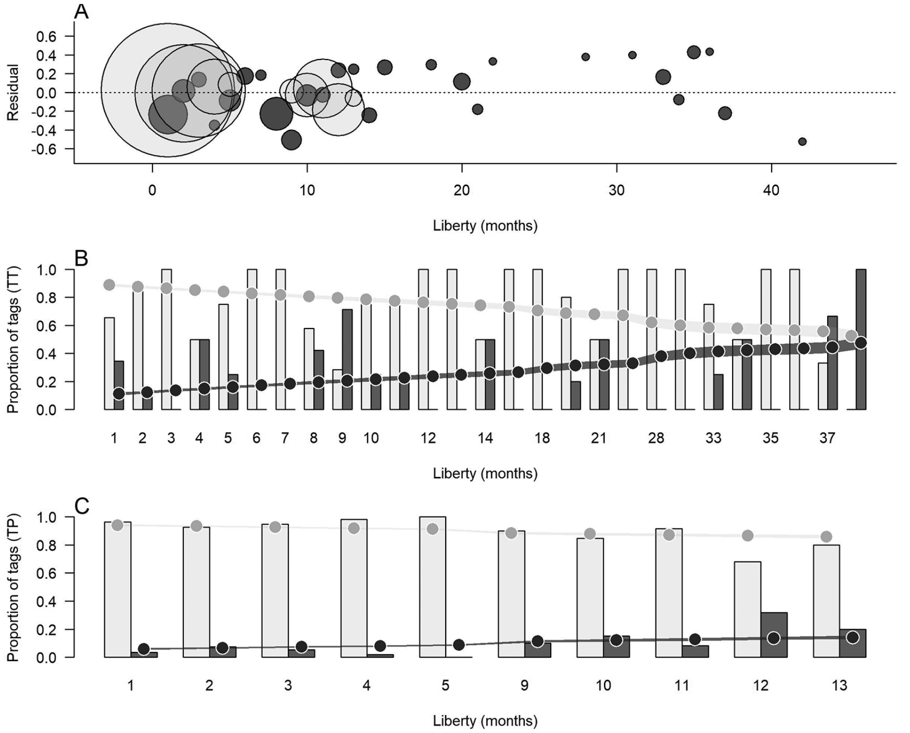

Figure 3. (A) Residual plot from the individual-based model (IBM) combined TT/TP component with the diameter of the light and dark grey circles representing the relative square root number of lobsters for that observation from the TT and TP datasets, respectively. The largest diameter represents 308 lobsters, and the smallest represents 1 lobster. (B) Observed (bars) proportion of lobsters caught with two T-Bar tags (light grey) or only one T-Bar tag (dark grey) across the range and liberties with model estimated proportions shown as solid points with associated 95% CI (translucent zones). (C) Observed (bars) proportion of lobsters caught with one T-Bar tag and one snipped pleopod (light grey) or only a snipped pleopod (dark grey) across the range and liberties with model estimated proportions shown as solid points with associated 95% CI (translucent zones).

on the contrast in returns of tagged lobsters between commercial vessels with and without observers onboard, the model estimated the average tag reporting rate of commercial fishers across the study period (e.g., throughout the fishery and across the four years) to be 47.9% (11.2%).

Tagged lobster catchability was estimated to have increased slightly from late January/February period ($3.1e^{-7}$) to peak in March/April ($4.3e^{-7}$) before progressively declining to the lowest catchability ($1.3e^{-7}$) in late November/early December (Fig. 6A). Catchability then started to increase again in late December/early January ($2.4e^{-7}$). This temporal pattern of estimated catchability was very similar (albeit on a slightly different temporal scale) to that produced by the BTR model with catchability cycling from a peak in March/April to a minimum in November.

The harvest rate (95% CI) of tagged lobsters estimated by the model declined marginally from 0.34 (0.06) in 2015 to 0.29 (0.06) in 2017 and then increased slightly in 2018 [0.31 (0.05); Fig. 6B]. Lobster biomass, as represented by the tagged lobsters (which were considered representative of all lobsters with a CL ≥ 76 mm), was

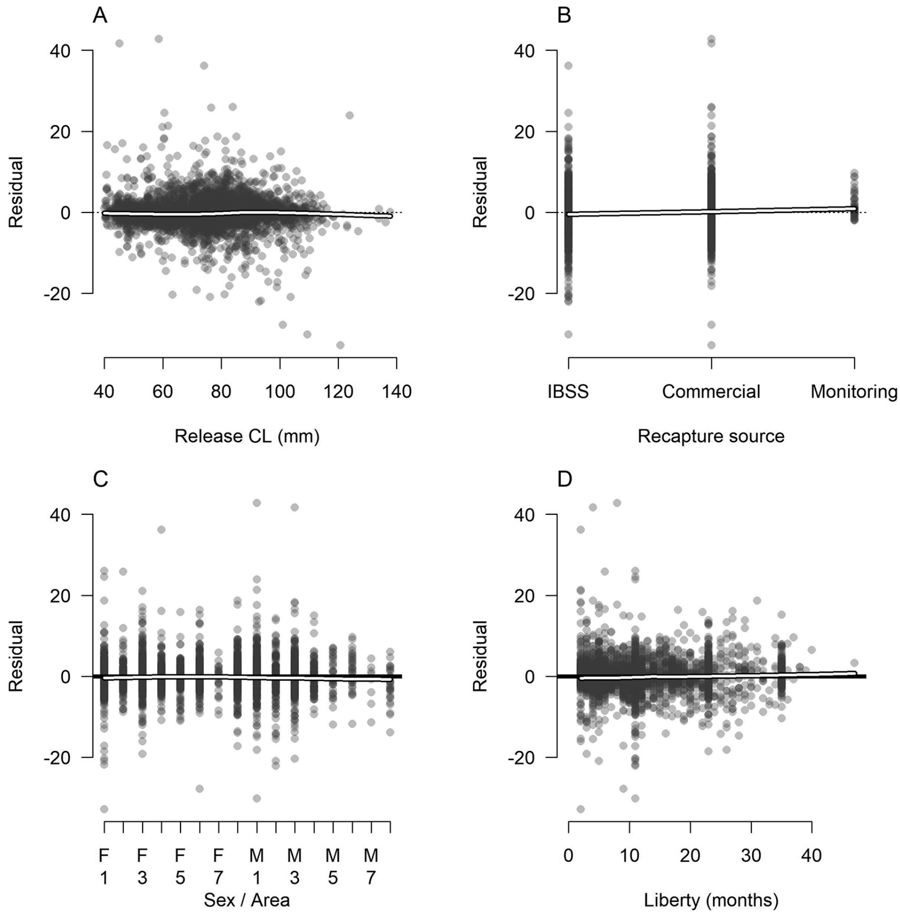

Figure 4. Standardized residuals plots between observed and estimated CL of recaptured lobsters against (A) release CL, (B) recapture source, (C) lobster sex and release area, and (D) time at liberty. The horizontal solid black line represents zero and the white line represents a lowess smoothed line of the residuals.

estimated to have increased over the study period from about 18,428 t in 2015 to about 22,361 t in 2017 before declining slightly in 2018 to about 21,552 t (Fig. 6C).

On a finer spatial scale, the model estimated markedly different biomass levels in the various model areas (Fig. 7). The southern model areas (1 and 2), representing the entire management of Zone C, were estimated to have the largest legal (≥76 mm) biomass levels (4000–8000 t, depending on the fishing season). In contrast, the most northern model areas (7 and 8), which represent part of management Zone B, had the lowest legal biomass levels (250–600 t, depending on fishing season). All deepwater areas (2, 4, 6, and 8) generally showed a progressive increase in biomass levels over the study period, whereas shallow-water locations generally remained constant (Fig. 7).

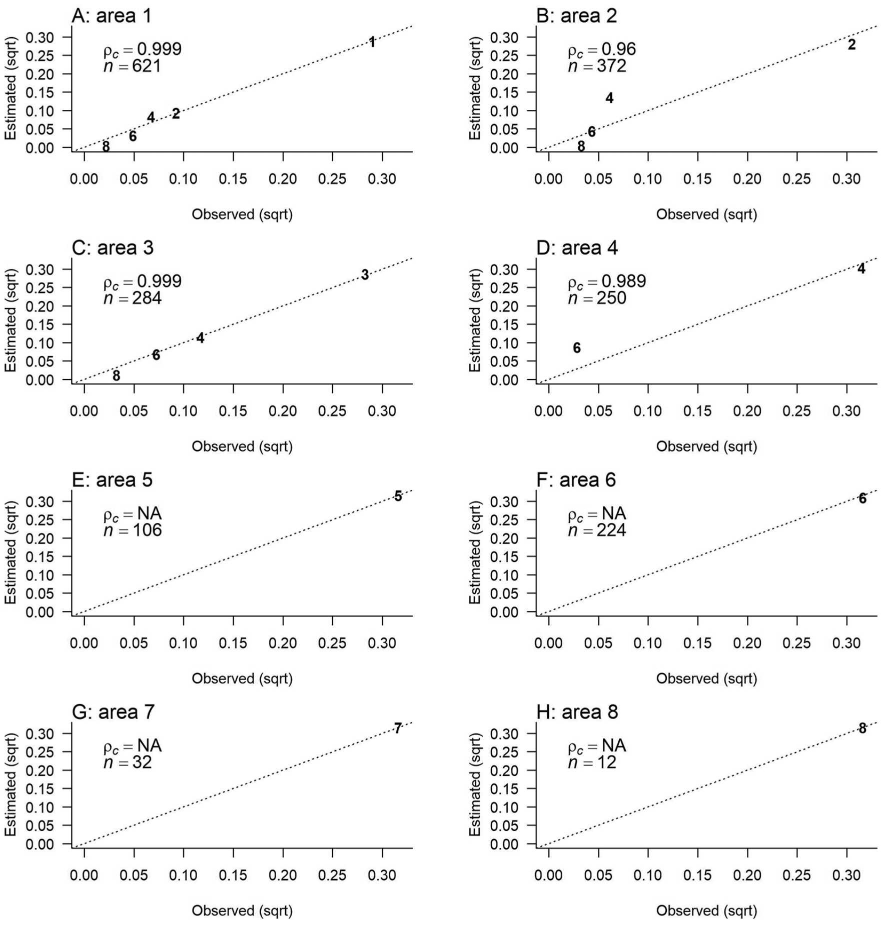

Figure 5. Proportion of lobsters released in each model area showing the square root of the observed and estimated proportions recaptured in each model location (identified by the numeric). The dotted line shows the line of concordance, ρ_c the concordance correlation coefficient, and *n* the sample size of lobsters released in the model region and recaptured in any region.

Discussion

This study produced contemporary tagging estimates of harvest rates and legal biomass for the West Coast Rock Lobster Managed Fishery using two different modelling approaches, the well-tested BTR and a novel model development (IBM), capable of replicating the finer temporal and spatial scale attributes of this resource. Both models produced very similar estimates for fishery-wide exploitation rate (0.26 vs 0.29–0.33) and legal (≥76 mm) biomass (about 24,500 vs 18,428–22,361 t). These estimates indicate that the western rock lobster resource is currently in a sustainable condition and is being fished at a harvest rate below that considered to represent maximum economic yield (HR_{MEY} about 0.39; Caputi et al. 2018) and well below that representing maximum sustainable yield (HR_{MSY} about 0.7; Caputi et al. 2018). These findings are in concert with estimates derived for this fishery during recent annual stock assessments, based on two separate population models, Integrated Population

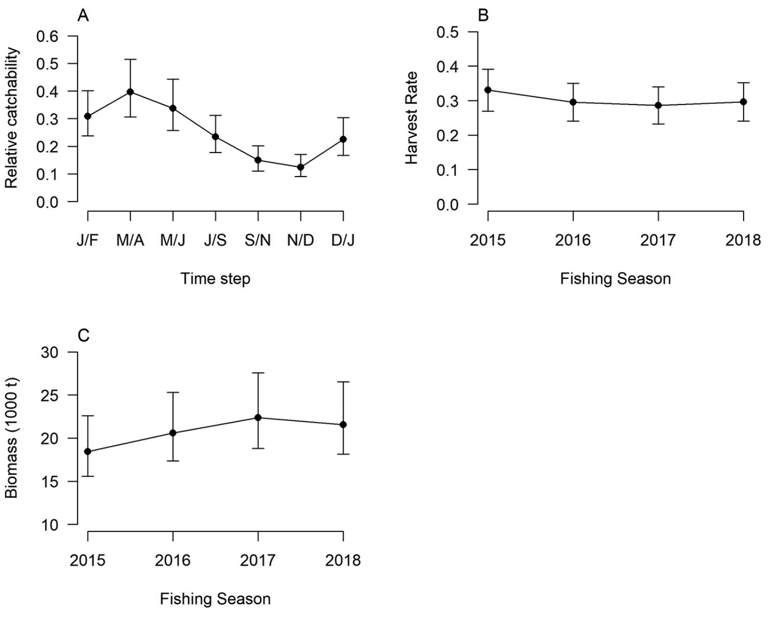

Figure 6. Model estimated (95% CI) (A) relative catchability of tagged lobsters, (B) commercial harvest rate, and (C) biomass of all legal-sized lobsters (carapace length ≥ 76 mm).

Model (IPM) and Biomass-Dynamics model (BDM; Online Supplementary Material). For example, over the years 2014–2018, the BDM estimated the fishery-wide harvest rate to have a mean of about 0.26 and a legal biomass of about 26,000 t (Online Fig. S2A), values very close to those estimated by the two tagging models. Such strong agreement between all four models provides a greater certainty in the current assessment and management of this important fish resource.

The BTR model used in this study has a proven formulation and is considered robust and appropriate for estimating exploitation rates and biomass levels from tag-recapture animals (Hoenig et al. 1998, Ley-Cooper et al. 2013). This is in direct contrast to the IBM, a newly formulated model that was untested. The BTR model produced a robust global estimate and served as a good cross check of the untested finer-scale estimates derived by the IBM. The IBM has several advantages over the BTR which was not easily adaptable to a highly dynamic system, wherein animals move and experience different levels of catchability and retention depending on their size, sex, and spatial location.

Both models highlight the value of tag-recapture data for examining exploitation levels and biomass in a wild capture fishery, essential information required for their sustainable management. However, due to the complex nature of tag-recapture data and the requirement to have a good understanding of tag loss and reporting rate, it is rarely incorporated into integrated population models for any purpose other than estimating movement or growth (Punt et al. 2013, 2016, de Lestang et al. 2019). The IBM developed in this study was based on the same spatial and temporal scales used in DPIRD's new IPM being developed for western rock lobster. This was intentional, with a view that tag-recapture data can be utilized in this new model for the

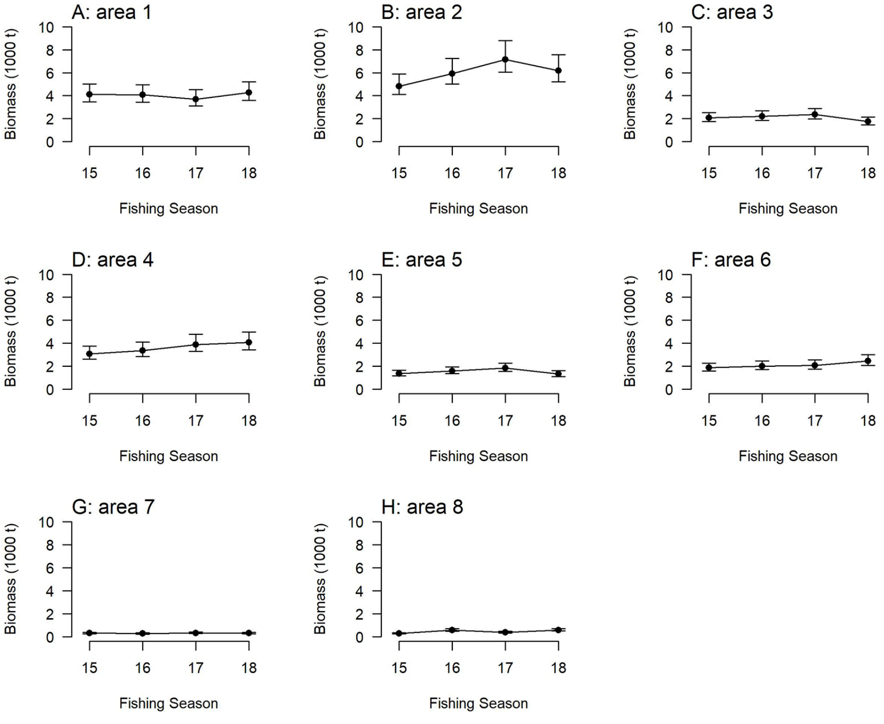

Figure 7. Model estimated (95% CI) spatial-specific biomasses of all legal-sized lobsters (carapace length ≥ 76 mm) in each area of the individual-based model (IBM).

estimation of fishing mortality, increasing the new model's comprehensiveness and robustness for producing appropriate management advice.

Legal (≥76 mm CL) biomass levels estimated in this study showed a gradual increase over the course of the study. With the advantage of its spatially explicit estimates, the IBM was capable of showing that this increase was driven by the offshore deepwater locations (Fig. 7). Juvenile western rock lobster settle in the nearshore environment, but move offshore to deeper areas at the age of about 4 yrs postsettlement (de Lestang 2014). With relatively low fishing levels (i.e., *HR* below those at HR_{MEY}) and a stock that has an ontogenetic offshore migration, any stock build-up would be expected to occur in the offshore areas (Jennings 2000). Of the model locations, the two southern locations were estimated to have the largest biomass levels, while those in the very north of the fishery have the lowest. These estimates need to be considered in the context of their relative spatial size, with the two southern locations being far bigger spatially than any other locations within the model and as such they would have the greatest habitat for lobsters (Fig. 1). Furthermore, this study commenced three years following the 2011 extreme marine heat wave, an event that significantly affected the habitat and stock levels of some fisheries in the northern half of the WCRLMF (Pearce and Feng 2013). Specifically, this heat wave event was shown to have impacted the survival of juvenile lobster in northern model locations (area 7 and possibly area 3), with this impact only starting to dissipate almost 10 years later (Caputi et al. 2019). As such, it is possible that biomass levels within this part of the fishery would have been negatively affected to a much greater extent than those in more southern areas of the fishery leading to the lower estimates of biomass in these regions.

This study examined tag loss and reporting rate within the IBM, which has the advantage that variances associated their estimation were incorporated into the estimates of harvest rate and biomass levels. Tag loss was found to be relatively low in western rock lobster [6% and 0.7%, for instantaneous and chronic (monthly) tag loss, respectively], which results in many marked animals remaining within the system for many years. This permits a robust estimate of population dynamics parameters such as survival, movement, and growth. This extended tag retention is supported by the fact that some tagged western rock lobsters have been returned after being at liberty for over 15 yrs. This level of tag loss was lower than that reported for a similar lobster (*Panulirus argus*) with a similar tag type (T-bar), although only combinations of instantaneous and chronic tag loss have been reported and were between 4% and 14% mo^{-1} (Davis 1978, Ley-Cooper et al. 2013, Olsen et al. 2017). A much closer estimate was produced by González-Vicente et al. (2012), who showed an instantaneous tag loss almost identical to this study for the spiny lobster *Palinurus elephas* based on a double tagging trial (7% for males and 5% for females). It should be noted however that tag loss, especially instantaneous tag loss, has been shown to be strongly influenced by the molt stage of the tagged animal, with pre-molt lobsters having much higher rates than those in intermolt (Comeau and Mallet 2003). As the estimate produced in this study was based on double tagging in multiple months and across a range of lobster sizes and both sexes, it can be considered an average of the two sexes and would have been based on intermolt lobsters.

The release of double tags proved to be a very efficient method for examining tag loss, as it was not affected by the recapturing party, e.g., commercial or independent survey. In most cases when a fisher noticed a tag they also saw and reported the second tag if it was present. The ability to have double and single tags reported by all fishers allowed for a greater range of lobsters in more areas to be examined for tag loss. By contrast the TP trials required trained survey staff to examine all captured lobsters for a marked pleopod. The TP trials also had a finite duration due to pleopods regrowing over successive molts. It is therefore not surprising that the TT method has been used in other fisheries previously (e.g., Frusher and Hoenig 2001, González-Vicente et al. 2012), whereas the TP trial was unique to this study. However, combining the data from the two techniques (TT and TP) allowed the advantages from each method to be incorporated into the overall estimate of tag loss, producing more robust estimates of both instantaneous and chronic tag loss. The TP trial was staff intensive but provided numerous samples over a relatively short liberty of releases, enabling the combined model to produce a good estimate of instantaneous tag loss. The TT trial, by contrast, produced a smaller sample size in the short term but provided data on tag loss up to 44 mo after release, which was considerably longer than the TP trial (about 12 mo). This long time series was invaluable for examining the rate of chronic tag loss. Therefore, future studies of tag loss should examine the utilization of both techniques to get a robust estimate of all components of tag loss.

The IBM estimated an overall tag reporting rate of the commercial fleet to be about 50%, thus only half of the available data was collected during this study. It is important to highlight that this estimate does not represent a proportion of fishers who return tags, rather it is a proportion of pots pulled and is therefore more equivalent to the proportion of fishers reporting tags, weighted by the relative number of pots fished by each fisher over the fishing season. This estimate shows that the reporting of tags in the WCRLMF was well below optimal and that there are many fishers within the fishery that simply do not return tags. A preliminary examination of fishers that do and do not return tags shows a very skewed distribution, with some fishers having never returned any tags and others that consistently report tagged animals. DPIRD provided five options for fishers to report tags, many of which require very little effort. In addition, the importance of the study and benefits associated with a high reporting rate were publicized *ad nauseam* in flyers to fishers and at industry meetings throughout the life of the project. Even the use of a high value annual lottery of $3000 USD did not alter some fisher's behavior, an incentive that has been beneficial in other fisheries (Green et al. 1983). There may be advantages for future studies to first conduct a survey of fishers to ascertain what drives participation in such a trial (e.g., reporting tags) and what activities may be undertaken to increase future participation.

A potential driver which may have historically reduced reporting rate was the introduction of a particular fishery management arrangement in 1993. This arrangement prohibited the retention of lobsters <77 mm CL from 15 November to 1 February each season. The intent of the arrangement was to reduce effort on migrating lobsters (migration starts in November). This led to a view amongst fishers that increased numbers of lobsters would be able to move from one inshore management zone (Zone B) into another zone further offshore (Zone A) without being available for capture and thus those fishing in Zone B would miss their opportunity to capture this stock. As such, many fishers within Zone A were concerned that reporting tagged lobsters would add credence to this perception of in-equitability and force authorities into altering this management arrangement. This resulted in a marked bias in tag reporting between fishers in different fishing zones and to some "interesting" movement patterns being displayed by tagged lobsters, as they appeared to stop at the boundary between Zone A and B (de Lestang 2014). In 2014, one year before this study was to commence, the management arrangements surrounding 76 mm lobster were reversed, and the perceived in-equitability between zones was no longer an issue. There is the potential that legacies of this management measure and the resultant differential reporting of tagged lobsters may have persisted. Preliminary examination of tag returns by area during this study did not find a significant difference in return rates between any of the fishing zones.

This study successfully developed an IBM that produced fine spatial and temporal scale estimates of harvest rate and biomass within a large commercial lobster fishery. Estimates from this model agreed with those derived from another well tested tag-recapture model (BTR) as well as two other models which are based on different data (e.g., legal catch rate, undersize catch rate, and size composition). A major benefit of the IBM was its independence from fishing behavior and the changes that have occurred in fishing efficiency, catch composition, and catch rates of the commercial fleet since the fisheries moved to quotas in 2010. As such, the inclusion of this model form into the already developed IPM for this fishery will increase the subsequent model's ability to robustly estimate key stock dynamics and inform the management of this marine resource.

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