



Small marine protected areas cannot sustain spill-over of the seasonally moving spiny lobster *Jasus edwardsii*

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ABSTRACT: Fishing is often concentrated near marine protected area (MPA) boundaries due to expectations of greater catches associated with the 'spill-over' of adult individuals. This is known to reduce populations near MPA boundaries, but our understanding of the long-term sustainability of this harvest remains limited. Over the last 25 yr, the spiny lobster *Jasus edwardsii* has experienced serious declines within north-eastern New Zealand MPAs. Prior to reductions, commercial fishers concentrated effort on offshore boundaries, targeting lobsters undertaking seasonal offshore movements. While this spill-over highlighted the success of these MPAs, it also indicated they were too small to encapsulate seasonal movements. In recent years fishers rarely target this area, and the extent to which lobsters move offshore is unknown. To address this knowledge gap, potting surveys were conducted in 2018–2019 to examine seasonal shifts in population distribution. Seasonal changes in habitat use were evident but mostly constrained to coastal reef habitat, with ~5% caught offshore of reef and only one individual caught beyond offshore boundaries. Comparison with commercial catch data from reserve boundaries during 1994–1997 revealed reduced abundances and changes in the size and sex of lobsters caught offshore. In contrast to 1994–1997, only large males were caught offshore of reef habitat. At low densities, females and small males may maintain greater association with the protective reef structure. The historic offshore boundary spill-over harvest reflected offshore movements at high population densities but likely contributed to population declines, altering the extent to which lobsters move offshore and eventually closing this spill-over pathway.

KEY WORDS: Marine protected areas · Marine reserves · Spill-over · Fishing impacts · Spiny lobster · *Jasus edwardsii*

1. INTRODUCTION

Heavily fished species are known to maintain higher population biomasses, densities and body sizes within Marine Protected Areas (MPAs) compared to adjacent fished areas (Halpern & Warner 2002, Edgar et al. 2014, Giakoumi et al. 2017, Spanier 2024). In some mobile species, these positive MPA effects can transcend MPA boundaries through movements of individuals out of the MPA and into adjacent fished areas (Hilborn et al. 2004). The cumu-

lative effect of these movements is commonly referred to as spill-over (Roberts et al. 2001). Driven by perceptions that this spill-over will increase catch success, fishing effort is often heavily concentrated on or near MPA boundaries, a behaviour known as fishing the line (i.e. McClanahan & Kaunda-Arara 1996, Kellner et al. 2007, Lenihan et al. 2024). While this fishing behaviour can increase yields (Murawski et al. 2004), the removal of spill-over biomass can also limit the ability of the MPA to effectively achieve conservation objectives (Ohayon et al. 2021). When

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fished populations are heavily depleted, the harvesting of mobile species around the boundaries of MPAs can deplete abundances within reserves in areas adjacent to boundaries. Such 'edge effects' conceptually represent a reduction in the effective size of the MPA (Krueck 2021). Numerous studies have shown how fishing the line can alter the spatial distributions of protected populations within MPA boundaries (Nillos Kleiven et al. 2019, Goñi et al. 2006, Halpern et al. 2009, Hanns & Shears 2023), yet examples showing the broader impacts of this harvesting strategy on protected populations are limited. Understanding these impacts will provide important information on MPA effectiveness and overall performance and better guide the establishment of future MPAs.

Spill-over has been documented across a range of mobile taxa, including large mobile invertebrates such as lobster, and it has been shown to provide tangible benefits to adjacent fisheries (Abesamis & Russ 2005, Lenihan et al. 2021). Goñi et al. (2010) estimated that spill-over of the Mediterranean spiny lobster *Palinurus elephas* facilitated a 10% net increase in catch weight following 8–17 yr of MPA implementation. In California, the total catch of the spiny lobster *Panulirus interruptus* was found to have increased by 225% following 6 yr of MPA protection (Lenihan et al. 2021). In Norway, Moland et al. (2013) reported an 87% increase in European lobster *Homarus gammarus* in adjacent control areas 4 yr after MPA establishment. In the Mexican Caribbean, Ley-Cooper et al. (2014) estimated that 15–20% of all adult *Panulirus argus* dwelling in an offshore MPA moved into the inshore fishery and were exploited. Spill-over has been attributed to a range of different processes, including density-independent activities such as nomadism and home range movements, seasonal migrations and migrations forced by extraordinary environmental events, and density-dependent movements such as competitive displacements towards low-density areas (Goñi et al. 2011, Grüss et al. 2011). Spill-over is also known to be heavily influenced by species mobility (Claudet et al. 2010), marine reserve size (Kramer & Chapman 1999) and habitat continuity across reserve boundaries (Freeman et al. 2009, Kay et al. 2012). Due to this underlying complexity, the impact of harvesting spill-over on protected populations is context-dependent and variable.

The spiny lobster *Jasus edwardsii* supports a highly valued fishery (Booth 2008) and has responded positively to marine reserve protection throughout New Zealand (Kelly 1999, Shears et al. 2006, Freeman 2008, Jack & Wing 2010). In north-eastern New Zealand (NENZ), Kelly et al. (2002) documented commercial fishers targeting *J. edwardsii* (hereafter referred to as

lobster) seasonally spilling over the offshore boundary of the Cape Rodney to Okakari Point (CROP) Marine Reserve. Similar fishing behaviour was also observed offshore of the Tāwharanui Marine Reserve (TAWH) and the Te Whanganui-o-Hei/Cathedral Cove Marine Reserve (S. Kelly pers. obs.). These fishers were found to be catching lobsters on deep, soft-sediment habitat far from any reef habitat, but obtaining catches that, on average, are similar in size to coastal rocky reef areas. Catches comprised male and female lobsters but were seasonally variable in composition and size. This spill-over was attributed to seasonal offshore movements following ecdysis and mating (Kelly 2001, Kelly & MacDiarmid 2003). The synchronicity of these offshore movements with peaks in feeding activity by captive lobsters suggested that these movements were likely density-independent foraging excursions driven by energetic deficits accrued during ecdysis and mating (Kelly et al. 1999, Kelly 2001).

Although this spill-over harvest highlighted the value of MPA-facilitated population recovery to the local fishery (Kelly et al. 2002), it also suggested that these MPAs were too small to effectively encapsulate seasonal offshore movements. Kelly & MacDiarmid (2003) warned the sustained and targeted harvest of lobsters that were seasonally moving offshore could alter the population's structure through reductions in protected population size and rates of growth. In the time since that statement was published, these populations have undergone severe declines (LaScala-Gruenewald et al. 2021, Hanns et al. 2022, Nessia et al. 2024) and the extent to which these offshore movements still occur is unknown. In recent years, lobster fishing on the offshore boundary appears to be less common (B. J. Hanns pers. obs.), suggesting that offshore movements may no longer be supporting a spill-over fishery. Reductions within NENZ MPA populations mirrored reductions in the fishery catch per unit effort (CPUE) and were attributed to prolonged fishing stress at the offshore boundary combined with an extended period of low recruitment (Webber et al. 2018, LaScala-Gruenewald et al. 2021).

In this study, we investigated the connection between the historic offshore spill-over harvest, population declines and changes in seasonal offshore movements and explored whether these movements still facilitate spill-over out of 2 NENZ MPAs. Seasonal shifts in population distributions on coastal reef and offshore sand habitats were inferred from potting-survey catch data. These data were used to determine whether seasonal offshore movements still occur, how they differ with sex and size, and how contemporary populations of lobster are distributed across broad

habitat types (i.e. rocky reef and sand) and depth strata within each reserve. To determine how seasonal offshore movements, catch rates and catch composition (size and sex of individuals caught) may have changed following large-scale declines, these data were also compared with historic (1994–1997) commercial catch data from the offshore boundary area over deep sand habitat (i.e. Kelly et al. 2002). With this study, we aim to provide a greater understanding of the broader impacts of harvesting spill-over biomass to better inform the management, design and future implementation of MPAs.

2. MATERIALS AND METHODS

2.1. Study system

This study was carried out within and adjacent to 2 of New Zealand's oldest no-take (fully protected) marine reserves: the CROP, established in 1977, and the TAWH, which has been completely no-take since 1981 (initially as the 'Tāwharanui Marine Park' but redesignated as the 'Tāwharanui Marine Reserve' in 2011). Both reserves are situated in the outer Hauraki Gulf in NENZ (Fig. 1). This area is characterised by a temperate rocky reef ecosystem dominated by a mix of kelp forest and urchin barrens, with kelp forest habitat more expansive within the boundaries of the marine reserves (Shears & Babcock 2002, 2004). The CROP marine reserve covers approximately 5.4 km of

longshore rocky coastline and extends 800 m offshore, encompassing an area of 5.2 km². The subtidal rocky reef extends mostly unbroken across the longshore boundaries of the reserve to a depth of 20–25 m. The TAWH marine reserve spans approximately 4.2 km of rocky and sandy beach coastline. Its boundary sits between 430 and 900 m offshore and covers an area of 3.9 km². Both CROP and TAWH are coastal marine reserves: those that protect a section of coastline and are geometrically characterized by longshore boundaries that determine the longshore extent and an offshore boundary that determines the offshore extent of protection. The offshore boundaries of both reserves are set roughly parallel to the coastline along continuous deep sandy benthic habitat, thus containing the coastal rocky reef with an area of sandy habitat between the offshore boundary and the reef edge (Fig. 1).

2.2. Potting survey

Commercial potting methods were used to capture lobsters and provide spatially explicit CPUE (hereafter referred to as catch rate) data from within both marine reserves and fished areas. Potting surveys were carried out in 2018 and 2019 during autumn (March–April) and spring (November–December). Autumn surveys aimed to target individuals on the reef prior to female ecdysis and mating occurring late April–June, while spring surveys targeted individuals post male ecdysis and female egg release occurring between September and early November (MacDiarmid 1989). These 2 periods were surveyed because they represent times when lobsters would most likely be on reef habitat (i.e. autumn) and when they would be most likely to be moving offshore of reef habitat (i.e. spring). An additional winter (August) survey was included in 2019, only within CROP, to investigate distribution shifts after mating and those preceding egg release. Pots were deployed overnight for no longer than 24 h. Potting station positioning in reserve and fished areas was stratified by depth, with representation of shallow (<10 m) and deep (>15 m in CROP, >10 m in TAWH) reef habitat, on offshore sand habitats (>10 m) and shallow sand habitat (<10 m) in between areas of reef. Within each reserve, potting stations were positioned to be representative of the reserve's

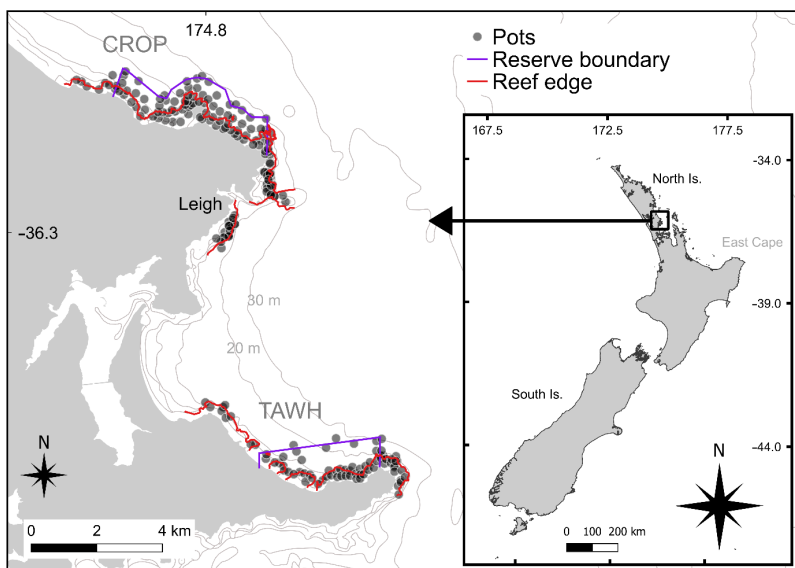


Fig. 1. Potting surveys carried out in 2018 and 2019 within and adjacent to the Cape Rodney to Okakari Point (CROP) and Tāwharanui (TAWH) marine reserves on the north-eastern New Zealand coast

longshore extent within each depth strata and broad-scale habitat types (i.e. shallow and deep reef, shallow and deep sand habitats). On each day of sampling, 20–25 pots were dropped and lifted; daily pot positions were randomly selected from a list of pre-determined positions. Each seasonal survey was undertaken over as short of a period as possible to minimize time lags between the first and last potting station sampled, and therefore limit within-survey temporal variability confounding between-survey (i.e. seasonal) analyses (for survey design structure, including dates and number of pot-lifts within and outside each marine reserve for each season and year, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m753p105_supp.pdf).

All surveys were carried out using the same commercial fishing vessel, fisher and potting equipment. Pots were the standard reinforced steel pot used within the local lobster fishery. Filleted fish frames were used as bait, with the species varying according to availability. The bait species included snapper *Chrysophrys auratus*, gurnard *Chelidonichthys kumu* and tarakihi *Nemadactylus macropterus*. The survey work was approved by the University of Auckland Animal Ethics Committee (reference number 001963).

2.3. Lobster sampling procedures

All captured lobsters were measured and sexed. Carapace length (CL, in mm) was measured between the antennal platform and the dorsal posterior margin of the carapace along the midline. Tail width (TW, in mm) was measured in a straight line between the tips of the primary spines on the second segment of the tail. TW and CL measurements were taken with vernier callipers to the nearest 0.1 mm. The sex and reproductive status of each lobster was determined using sexually dimorphic features such as the 5th peripod and pleopod anatomy (Paterson 1968, MacDiarmid 1991). Females were classed as either mature or juvenile based on reproductive stage, as determined by the length of the setae on the pleopods (mature: 6 mm or longer) (MacDiarmid 1989). Individual weights of each lobster were measured to the nearest 0.01 g using digital fish scales.

2.4. Data analysis

All data analysis was undertaken in R (v.4.0.3, R Core Team 2023). The 'brms' package (Bürkner 2017) was used to fit Bayesian models using the Hamiltonian

Monte Carlo algorithm implemented in the programming language Stan (Carpenter et al. 2017). All models were run using generalized priors, and chain convergences were assessed using the \hat{R} statistic (Gelman & Rubin 1992).

2.4.1. Seasonal catch rate

To determine how catch rates (number of lobsters per pot lift) differed between areas (CROP, TAWH), status (reserve, fished), season (autumn, spring) and year (2018, 2019), catch data were modelled using a zero-inflated model design with a negative binomial distribution (see Bürkner 2017). The zero-inflated model was used due to excess zeros (i.e. empty pot lifts). This model (Model 1) aimed to test the generality of the reserve effects (difference between reserve and fished areas during each surveying period) between areas, survey years and seasons as well as interactions among any combination of these effects. Conditional mean catch-rate estimates across all location–status–season–year combinations were plotted to provide an overall indication of catch variation and seasonal patterns across all surveys. Posterior pairwise differences between these combinations were then assessed by testing the 95% highest posterior density intervals (HDI) of group means. Differences were considered significant if the 95% HDI of group differences did not cross zero. To accommodate differences in the likelihood of empty pots between fished and marine reserve areas, the zero-inflation probability (z_i ; likelihood of a pot being empty) was predicted by status in Model 1. Date was included as a random factor in the non-zero part of the model to account for potential temporal mismatches associated with time-lags between the first and last day of surveying within each seasonal survey. Model 1 was fitted separately for male and female catch data:

Model 1: Catch rate \sim Location \times Status \times Season \times Year + (1|Date), $z_i \sim$ Status

2.4.2. Comparison of contemporary survey data with 1990s commercial catch

Seasonal potting survey data from 2018–2019 were compared with historic commercial catch data from 1994–1997. The historic data set included data presented in Kelly et al. (2002) as well as unpublished data collected by S. Kelly at the same time. Kelly et al. (2002) described the commercial pots as being set in

the offshore areas around the marine reserve on sand or remote patch reef in about 25–35 m water depth. For comparison with the contemporary potting survey data, historic data were grouped by season: autumn (May–June), winter (July–August) and spring (September–October).

This analysis aimed to determine how historic catch rates (kg pot^{-1}) and composition (size and sex of lobsters) from the offshore boundary of CROP compared with the 2018–2019 catch from the following areas: on reef within marine reserve boundaries, on sand within marine reserve boundaries (shallow and deep sand habitats) and on sand within 100 m of the offshore boundary within and outside of the marine reserve. The latter area was formed to maximise potting effort from the offshore boundary area. Data from the 2018 and 2019 potting surveys were pooled due to comparatively low numbers of lobsters caught on sand habitat and within 100 m of the offshore boundary. Pooling ensured that the 2018–2019 effort was similar to the commercial potting effort from 1994–1997. Each spatial class was grouped by year, and formed the area–year groupings. The model used a hurdle design with a gamma distribution (see Bürkner 2017). The area–year groups were modelled as an interaction with sex (Model 2). To accommodate known differences in the likelihood of empty pots across area–year \times sex groups, the hurdle probability of an empty pot (hu) was modelled using the area–year \times sex interaction. To reduce complexity and computational loads, seasonal data (autumn, winter, spring) were modelled independently.

Model 2: Catch rate \sim Area–year \times Sex, $hu \sim$ Area–year \times Sex

Differences in the size distributions of male lobsters in commercial offshore catch from 1995–1997 (size data from 1994 were not available) and the 2018–2019 survey data (separated into reef, sand and 100 m from offshore boundary areas) were tested using the unequal variance model recommended in Kruschke (2013) with a Gaussian distribution (Model 3):

Model 3: CL \sim Group, sigma \sim Group

Here, 'Group' is the survey year and area group, and 'sigma \sim Group' indi-

cates that sigma was allowed to vary between groups. Posterior pairwise differences between groups were assessed by testing the 95% HDIs of group means.

3. RESULTS

3.1. Seasonal catch rate

Across all surveys, catch rates were higher within marine reserves than in adjacent fished areas (Fig. 2). In both marine reserves, catch rates for male and female lobsters were lower in autumn and higher in spring. Variation in catch with sex across seasonal surveys differed between marine reserves. Male catch and differences between seasons were higher in CROP, while overall female catch and seasonal differences in catch were higher in TAWH. Analysis of male catch data indicated consistent effects of sampling year (2018 and 2019) and location (CROP and TAWH) but found a significant interaction between status and season (95% log credible interval, CI, crossed 0), indicating that the effect of status varied between seasons (a full summary of Model 1 can be found in Table S2). Pairwise comparisons of posterior means showed significantly higher catch rates for male lobsters in

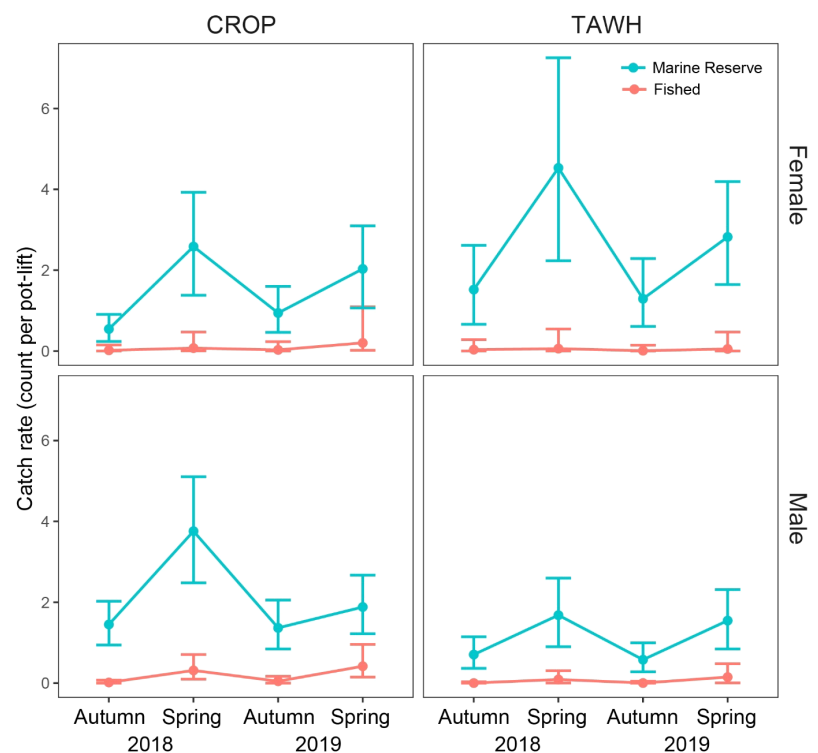


Fig. 2. Estimates of seasonal catch rates (\pm 95% credible interval) of female and male lobsters in marine reserves and fished areas at CROP and TAWH during 2018–2019. See Fig. 1 for marine reserve abbreviations

marine reserves than in fished areas across all surveys but insignificant differences between autumn TAWH marine reserve catch rates and spring fished area CROP and TAWH catch rates (95% HDI crossed 0; see Fig. S1 for full HDIs). Analysis of female catch rates found no interactions between tested effects, with status identified as the only significant effect (logCI: 0.886–5.91). However, pairwise comparisons did identify several weakly significant contrasts, suggesting a weak season and status interaction (see Fig. S1). Lastly, analysis of both male and female catch rates (Model 1) found that the standard deviations of random intercepts across the different 'date' levels were relatively small (male: 0.19; female: 0.21), indicating only modest levels of temporal variability not captured by the fixed effects.

3.2. Spatial distribution of catch

Across all surveys, catch rates were higher on reef than on offshore sand habitat. Only 6 and 1% of all male and female lobsters, respectively, were caught at potting stations on offshore sand habitat (male: Fig. 3; female: Fig. S2). All female lobsters captured on sand were caught during spring, only within TAWH and within 150 m of the reef edge. Four female lobsters were caught on deep (16.5 m depth) offshore patch reef within CROP. Of these, 2 were caught during spring surveys and 2 were caught during the winter survey and both were in berry (i.e. carrying eggs). The proportion of male lobsters caught on sand habitat was greatest during spring surveys (9.4% of total spring catch; Fig. 4). Fewer were caught on sand during the winter survey (3.6% of total winter catch) and only one male was caught on sand (55 m from reef edge) during all autumn surveys (0.4% of total autumn catch). Ten male lobsters were caught within 100 m of the offshore boundary, all during spring. Of these, 3 were caught on a shallow patch reef (5.5 m depth) at the western end of TAWH where the offshore boundary is within 350 m of the low tide margin. The remaining 7 male lobsters (3 from

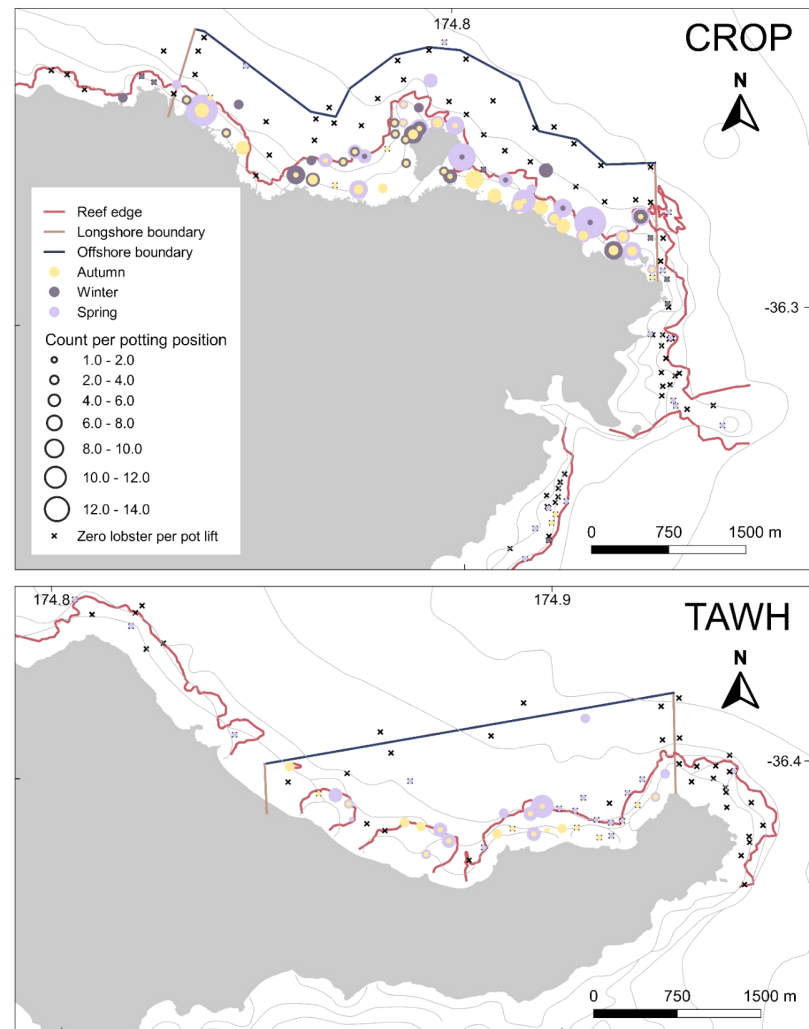


Fig. 3. Distribution of male lobster catch in CROP and TAWH and adjacent fished areas (see Fig. 1 for marine reserve abbreviations). Size of bubble indicates number of male lobsters caught in each pot for each season during the 2018–2019 surveys (see Fig. S1 for female catch distributions)

CROP, 3 from TAWH) were all large (CL >140 mm) and were caught on deep sandy habitat between 21 and 32 m depth and 472–800 m away from the reef edge. Only one was caught beyond the offshore boundary of CROP.

During each survey, 75 and 50% of female and male lobsters, respectively, were caught on shallow reef habitat. Despite this, seasonal patterns between broad habitat types were evident and similar between CROP and TAWH (Fig. 5). Proportions of male lobsters on deep reef and deep sand habitats were low in autumn and increased in spring over both surveying years. Proportionally more female lobsters were caught on deep reef during the winter survey, when most were in berry (Fig. S3).

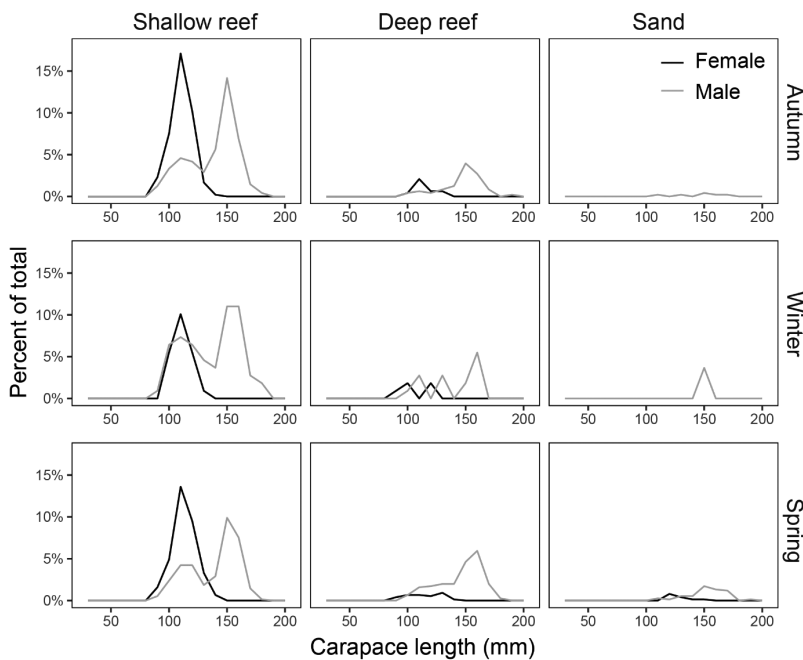


Fig. 4. Size distribution (carapace length) of female and male lobsters across broad habitat types (deep and shallow sand habitats have been pooled) and season. Frequencies scaled by percentage of total catch per season across the 3 habitat types and marine reserve (CROP and TAWH; see Fig. 1) pooled and years (2018 and 2019). Catch data from fished areas are excluded

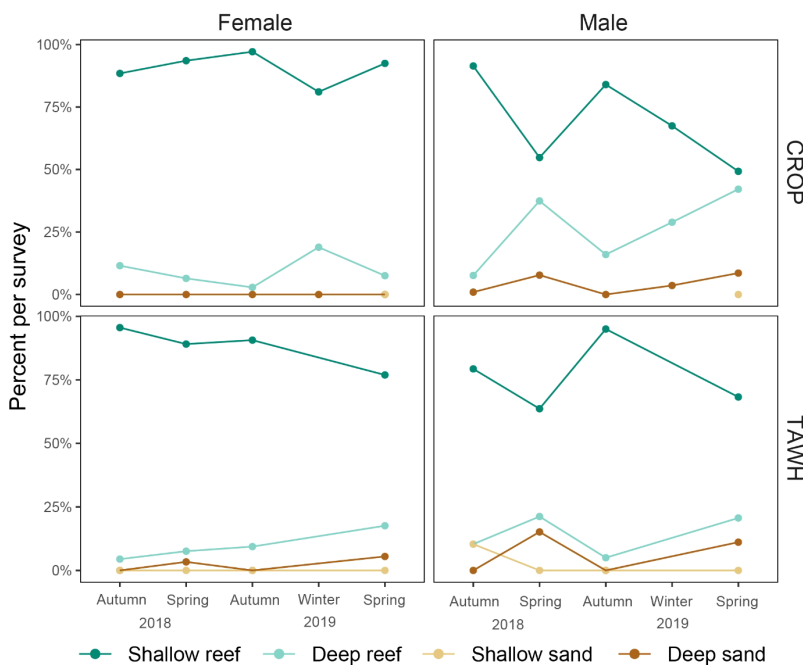


Fig. 5. Seasonal changes between autumn (March–April) and spring (November–December) during 2018–2019 and winter (August and CROP only) in 2019 in lobsters caught within marine reserves from different broad habitat types (expressed as percentage of total catch). See Fig. 1 for marine reserve abbreviations

3.3. Comparison of contemporary and historic catch

Seasonal differences in catch were evident across the 1994–1997 commercial catch data. In general, catch rates increased from autumn through winter into spring. Although both female and male lobsters were present across all seasonal periods, catch compositions shifted with season (Fig. 6). Proportionally more male lobsters were caught during autumn and winter, while more females were caught during spring. Overall, the 1994–1997 catch rates were considerably larger than the 2018–2019 catch rates from potting stations within 100 m of the offshore boundary. Within seasons, catch rates of male lobsters from 1994–1997 were similar to 2018–2019 catch rates from sand habitat within marine reserve boundaries. Catch rates of female lobsters from 1994–1997 were similar to or exceeded the 2018–2019 catch rates from reef habitat within marine reserve boundaries and were considerably greater than the 2018–2019 catch rates from sand habitat.

The size (CL) distribution of female lobsters in the 1994–1997 catch data was similar to that of the female lobsters caught on marine reserve reef habitat during the 2018–2019 surveys (Fig. 7). In contrast, pairwise comparisons indicated that the size distributions of male lobsters in the 1994, 1995 and 1996 commercial catch data were significantly smaller than male lobsters across all 2018–2019 area groups (Fig. 8; 95% HDIs associated with pairwise comparisons in Fig. S4). Across the 1994–1997 commercial data, pairwise comparisons indicated significant increases in mean size with each consecutive year. Within the 2018–2019 data, male lobsters caught on sand habitat within marine reserve boundaries were significantly larger than male lobsters caught on reef habitat.

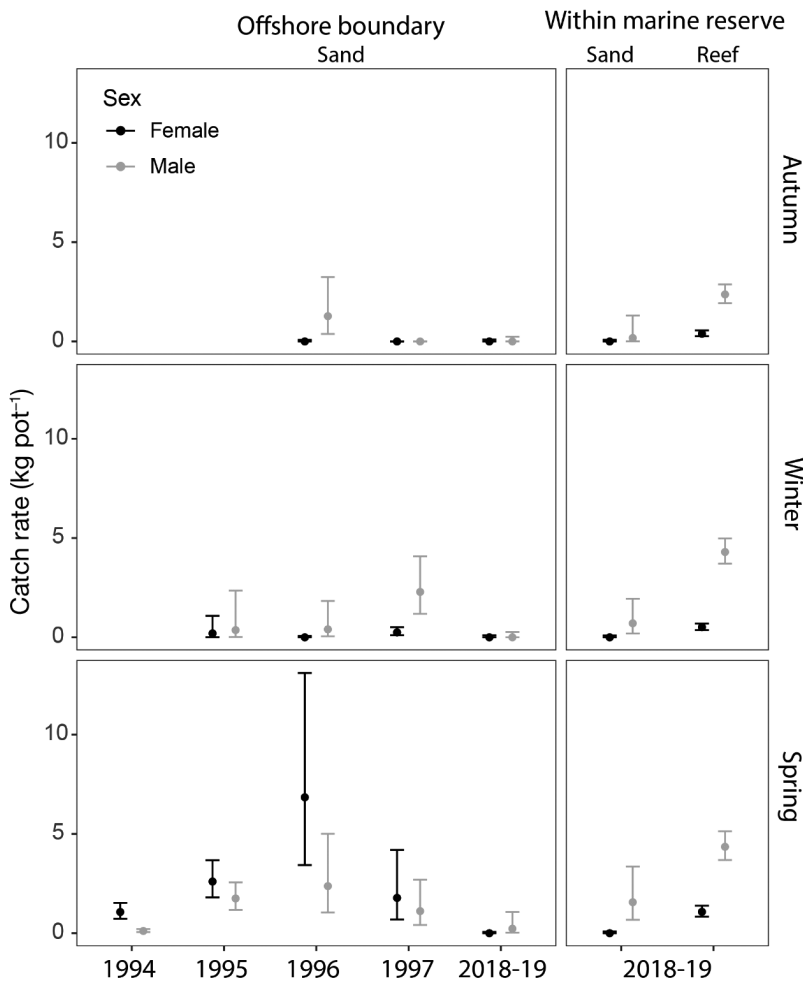


Fig. 6. Estimates of the 2018–2019 potting survey and 1994–1997 commercial catch data from within and offshore of CROP. For the 2018–2019 data, offshore boundary catch included lobsters caught within 100 m of the offshore, both inside and outside the marine reserve, whereas 1994–1997 catches are exclusively from outside the reserves. Sand habitat within marine reserves included all shallow and deep sand habitat outside of the 100 m offshore boundary buffer area

4. DISCUSSION

Following large-scale declines of the spiny lobster *Jasus edwardsii* across NENZ (LaScala-Gruenewald et al. 2021, Nessia et al. 2024), the present study shows that the sizes and proportions of male and female lobsters moving offshore of reef habitat within 2 small marine reserves have changed. We found that the frequency and abundance of lobsters moving offshore have reduced and distances travelled from the reef edge have declined. Catch rates during the 2018–2019 potting surveys on offshore sand habitats were very low compared to reef habitat, and were substantially lower than the 1994–1997 commercial catches from beyond the offshore boundary. The his-

toric capture of lobsters beyond the offshore boundaries showed that these marine reserves ineffectively encapsulated seasonal offshore movements and likely contributed to reductions in the protected population (LaScala-Gruenewald et al. 2021). The findings of the present study indicate that under reduced densities, these seasonal offshore movements no longer result in the spill-over of lobsters across offshore boundaries at levels previously reported (i.e. Kelly et al. 2002).

Seasonal movements in NENZ lobsters are associated with ecdysis, mating and egg release (MacDiarmid 1989, 1991). During ecdysis periods (October to early November for males; late April to early June for females), moulting individuals move to shallow (<10 m) reef habitat (MacDiarmid 1989). Likewise, during mating (late May to mid-July), sexually mature lobsters are mostly constrained to reef habitat, with courtship occurring within or near shelter structures. From late April to early July, female lobsters aggregate on deep reef or reef edge habitat (i.e. deepest extent of reef habitat) to release eggs (MacDiarmid 1989). This behaviour is suggested to promote the rapid dispersal of hatched larvae away from reef-dwelling planktivorous species (see McKoy & Leachman 1982). In between periods of ecdysis, mating and egg release, lobsters have been recorded moving away from reef habitat to deep sand habitat (Kelly 2001).

Seasonal variation in catch rates between shallow reef, deep reef and deep sand habitats can be attributed to variation in feeding activity associated with the seasonality of ecdysis and mating. Lower catch rates and catches concentrated on reef habitat during autumn in both the 2018–2019 survey data and the 1994–1997 offshore commercial catch data coincided with mating and lower consumption rates during the March to mid-June period (see Kelly et al. 1999). Likewise, higher catch rates and higher catches on deep reef and sand habitats in spring coincided with seasonal peaks in feeding between November and January, following male ecdysis and egg release (Kelly et al. 1999).

The relationship between feeding activity and offshore movements from reef habitats is thought to be

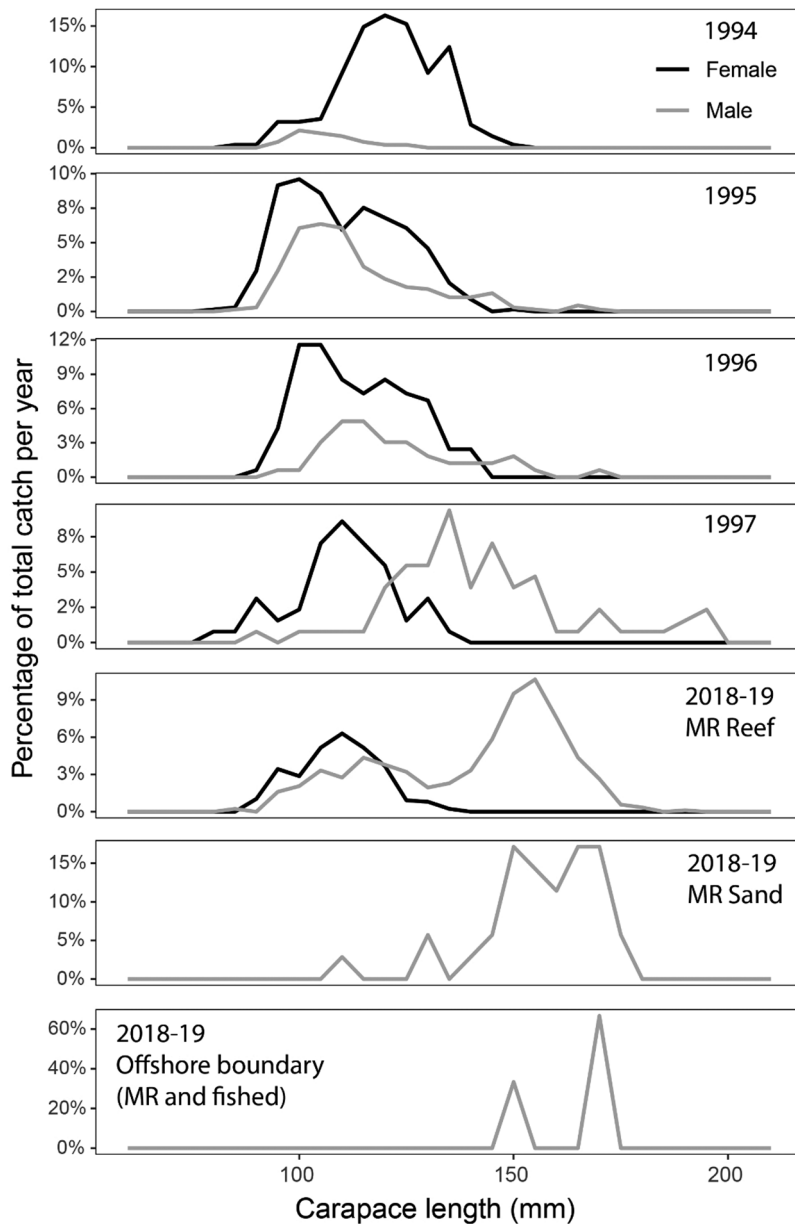


Fig. 7. Carapace lengths of lobsters from the 1994–1997 commercial catches and lobsters caught during the 2018–2019 potting surveys within CROP on reef and sand habitat, and potting station within 100 m of the offshore boundary (both within and outside of marine reserve [MR] boundaries)

driven by the need to compensate for metabolic deficiencies after ecdysis and mating (Kelly et al. 1999). During these periods, lobsters undergo prolonged sub-satiation (MacDiarmid 1989). Lobsters may therefore have ventured onto deeper, soft-sediment (i.e. sand) habitats to access higher-quality prey compared to what is available in reef habitats.

Although these lobsters are considered opportunistic omnivores (Pederson & Johnson 2006), with their diet being influenced by their surroundings, observa-

tions of individuals foraging on sand and carrying sand-habitat-associated prey (e.g. bivalve species) back to reef shelters suggest a preference for soft-sediment species over reef-associated prey (MacDiarmid 1991). This preference is further supported by feeding experiments showing that lobsters actively select infaunal bivalve prey over gastropods and sea urchins typically found in rocky reefs (Flood 2021). These experiments also found that lobsters had significantly shorter handling times for soft-sediment prey, indicating lower energy expenditure for higher caloric gain.

However, foraging in soft-sediment or sand habitats comes with greater risks. Unlike rocky reefs, which provide protective structures, offshore soft-sediment areas leave lobsters more exposed and vulnerable to predation. Observations of large aggregations of lobster on offshore soft-sediment habitats within the CROP marine reserve by Kelly et al. (1999) may indicate that movement offshore is aided by mutually beneficial social interactions. Gregariousness is a common behavioural feature among spiny lobsters (Zimmerfaust & Spanier 1987, MacDiarmid 1994), playing an important anti-predator defensive role (McKoy & Leachman 1982). Herrnkind et al. (2001, p. 1121) suggested that the Caribbean spiny lobster *Panulirus argus* 'in the open [deep sand habitat] benefit from increasing their number by joining together to make even larger groups' and noted that group sizes increased when predators were present. This was later demonstrated in field experiments (see Lavalli & Herrnkind 2009).

Population reductions within the surveyed marine reserves of 20.1 and 40.8% from peak abundances in CROP and TAWH, respectively, reflected wider regional declines (LaScala-Gruenewald et al. 2021, Nessia et al. 2024). While lobster populations initially recovered on reef across the 5.4 km (CROP) and 3.9 km (TAWH) longshore extents of both marine reserves (Kelly 1999), movements across the offshore boundaries (<1 km from the coastline) were soon recognised and exploited by fishers (Kelly et al. 2002).

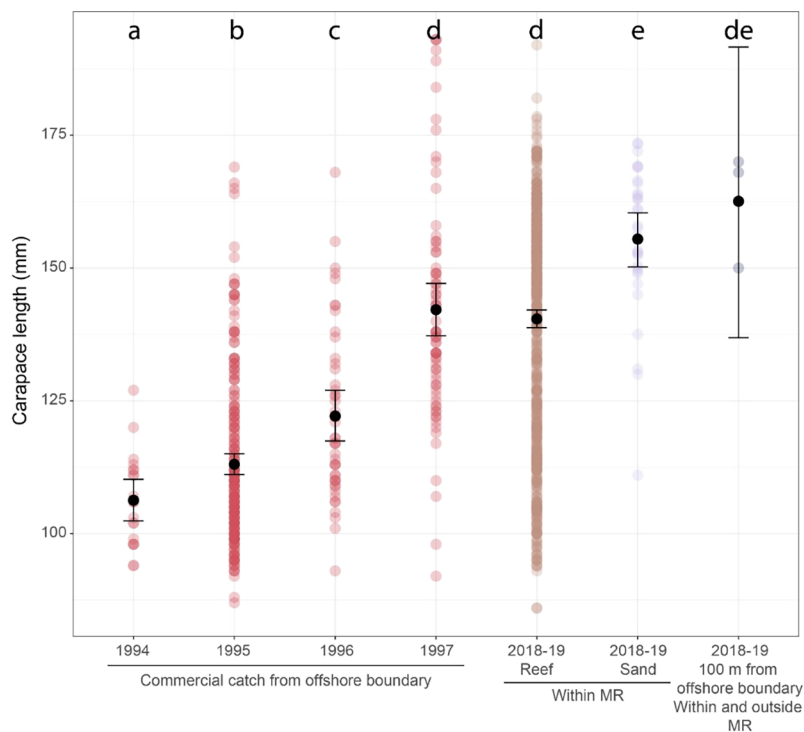


Fig. 8. Modelled comparisons of male carapace lengths (mm) from different year–area groups. Point colours refer to catch location (i.e. habitat) and data collection period — red: historical commercial catch data taken from beyond the offshore boundary; brown: contemporary catch from reef habitat within the marine reserve; purple: contemporary catch from sand habitat within the marine reserve; grey: contemporary catch from 100 m to the offshore boundary inside and outside the marine reserve. Predicted conditional means and 95% lower and upper credible intervals are shown. Groups (letters) are based on pairwise assessment of the highest posterior density intervals produced by Model 3; pairwise comparisons of groups are indicated by letters. Groups that share at least one letter are not significantly different from each other ($p \leq 0.05$)

The inability of these marine reserves to effectively encapsulate these offshore movements likely limited their ability to insulate protected populations from the impacts of overexploitation in the adjacent fishery.

Catch rates in both marine reserves, across all habitats, were expected to have declined in proportion with reductions in overall population sizes. However, catch rates on offshore soft-sediment habitats were exceptionally low and comparatively much lower than recorded declines in density on rocky-reef habitats. The relationship between population size and offshore distributions may therefore be non-linear and reflect more complex density-dependent-associated behaviours and/or mechanisms. It is possible that the movement to soft-sediment habitats is an adaptive response within the species, driven by intraspecific interactions like gregarious or aggregating behaviours, where individuals benefit from being in close proximity to conspecifics.

Aggregating behaviours are fundamentally density-dependent. If too few lobsters are present, the defensive benefits of aggregating, such as clustering appendages (i.e. antennae) (Barshaw et al. 2003, Lavalli et al. 2015) or 'selfish herd' mechanisms (Hamilton 1971) may be ineffective. The initial formation of aggregations may also be hindered by Allee effects (i.e. Gascoigne & Lipcius 2004). A lobster's ability to locate or detect chemical cues emitted by conspecifics may be limited at low densities (see Butler et al. 1999).

Our 2018–2019 survey data provided little evidence that lobsters were aggregating in offshore habitats at densities similar to Kelly et al. (1999). Catches from offshore sand habitats mostly comprised low numbers of large male lobsters, while female lobsters and smaller size classes of male lobsters appeared to maintain year-round associations with reef structure. When compared with size class information from the 1994–1997 commercial catch data, lobster caught on sand during the 2018–2019 surveys were significantly larger. Under lower density conditions, offshore movements beyond protective reef structures may now be constrained to large males, possibly reflecting better individual defences against predation (i.e. Wahle 1992).

In stark contrast to the 2018–2019 catches, female lobsters dominated the catch beyond the offshore boundary during 1994–1997. Kelly et al. (1999) reported that female lobsters were a constant feature of offshore aggregations on deep-sand habitat, but proportions of males and females varied seasonally in connection with periods of ecdysis, mating and egg release. They noted that peak consumptive rates in captive female lobsters followed ecdysis and egg extrusion, from late April to early July (MacDiarmid 1989). However, unlike male conspecifics, peak feeding in female lobsters did not coincide with greater numbers in offshore aggregations. Rather, female lobsters appeared to forfeit elevated foraging after ecdysis to protect recently extruded eggs. Female abundances subsequently increased over the following 3–4 mo egg-bearing period, peaking when larvae were expected to hatch around September (Kelly et al. 1999). During the 2018–2019 surveys, more female

lobsters were caught on deep reef during winter surveys than other seasons, and all female lobsters caught on deep reef during winter were in berry. As the winter survey (August) coincided with periods of egg maturation, these lobsters were likely caught while undertaking movements to or residing on deep reefs prior to egg release. The absence of female lobsters from offshore soft-sediment habitat in spring may reflect a failure to form effective defensive aggregations after egg release. For females and small males who maintain smaller sizes than male conspecifics (for size comparisons, see Hanns et al. 2022), rewards gained from travelling further offshore are likely not equitable to predation risks.

Our findings suggest that reductions in population densities within NENZ marine reserves have contributed to lower frequencies and abundances of lobsters moving offshore. The movement of lobsters beyond the offshore boundaries of the surveyed marine reserves and the subsequent spill-over fishery highlights the inability of these small marine reserves to effectively protect high-density lobster populations. These findings also highlight the broader indirect impacts of fishing extraction. Not only does fishing remove individuals, thereby depleting populations, but by doing so, fishing can also disrupt a targeted species' ecology. While a species can behaviourally adapt to the impacts of fishing, such behavioural adaptations may also facilitate other negative consequences, such as reduced access to key food resources. For NENZ lobsters, the physiological impacts of maintaining year-long associations with reef habitat require further consideration. If offshore movements in female lobsters are driven by feeding requirements (i.e. access to high-quality infaunal prey such as bivalves), lower densities may indirectly impact the overall nutritional conditions of reproductive females (for example, see Oliver & MacDiarmid 2001). Likewise, the co-occurrence of egg extrusion and peaks in feeding activity (Kelly et al. 1999) suggests that metabolic recovery following ecdysis and egg extrusion or larval release may benefit from access to bivalve prey of higher nutritional quality than that available on reef habitat (see Flood 2021).

The harvest of lobsters that spill over offshore boundaries coupled with a period of low recruitment have acted to reduce densities to where this spill-over no longer occurs. Under their current designs, the CROP and TAWH MPAs are too small and do not extend far enough offshore to effectively protect the species. If lobster densities were to recover within these marine reserves, the frequency and abundance of lobsters moving offshore and the distances trav-

elled offshore would be expected to increase. Assuming that the efficacy and/or formation of defensive aggregations are density-mediated, increased densities should permit greater exploration and a return to deep offshore sand habitats. It would therefore be prudent to extend the offshore boundary of both marine reserves to encompass offshore movements and provide more effective and longer-term protection for these lobsters. Without this change, the continuation of even low fishing activity on offshore boundaries will continue to prevent long-term recoveries within these marine reserves. Although our findings show that these small MPAs cannot sustain the spill-over of lobsters seasonally moving offshore, Hanns & Shears (2023) suggested that spill-over across the long-shore boundaries may increase if the population's offshore limits are effectively protected. Future research should aim to improve understanding of these reported distribution changes by making a concerted effort to monitor offshore movements and aggregations.

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LITERATURE CITED

- ✦ Abesamis RA, Russ GR (2005) Density-dependent spillover from a marine reserve: long-term evidence. *Ecol Appl* 15: 1798–1812
- ✦ Barshaw DE, Lavalli KL, Spanier E (2003) Offense versus defense: responses of three morphological types of lobsters to predation. *Mar Ecol Prog Ser* 256:171–182
- Booth J (2008) New Zealand's rock lobster fisheries. In: Phillips BF, Kittaka J (eds) *Spiny lobsters: fisheries and culture*, 2nd edn. Fishing News Books, Oxford, p 78–89
- ✦ Bürkner PC (2017) brms: an R package for Bayesian multi-level models using Stan. *J Stat Softw* 80:1–28
- ✦ Butler MJ IV, MacDiarmid AB, Booth JD (1999) The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Mar Ecol Prog Ser* 188:179–191
- ✦ Carpenter B, Gelman A, Hoffman MD, Lee D and others (2017) Stan: a probabilistic programming language. *J Stat Softw* 76:1–32
- ✦ Claudet J, Osenberg C, Domenici P, Badalamenti F and others (2010) Marine reserves: fish life history and ecological traits matter. *Ecol Appl* 20:830–839
- ✦ Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S and others (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216–220

- Flood AS (2021) Gut instincts: feeding behaviour of the rock lobster, *Jasus edwardsii*. PhD dissertation, University of Auckland
- Freeman D (2008) The ecology of spiny lobsters (*Jasus edwardsii*) on fished and unfished reefs. PhD dissertation, University of Auckland
- Freeman DJ, MacDiarmid AB, Taylor RB (2009) Habitat patches that cross marine reserve boundaries: consequences for the lobster *Jasus edwardsii*. *Mar Ecol Prog Ser* 388:159–167
- Gascoigne J, Lipcius RN (2004) Allee effects in marine systems. *Mar Ecol Prog Ser* 269:49–59
- Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Stat Sci* 7:457–472
- Giakoumi S, Scianna C, Plass-Johnson J, Micheli F and others (2017) Ecological effects of full and partial protection in the crowded Mediterranean Sea: a regional meta-analysis. *Sci Rep* 7:8940
- Goñi R, Quetglas A, Reñones O (2006) Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar Ecol Prog Ser* 308:207–219
- Goñi R, Hilborn R, Díaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 400:233–243
- Goñi R, Badalamenti F, Tupper M H (2011) Fisheries. Effects of marine protected areas on local fisheries: evidence from empirical studies. In: Claudet J (ed) *Marine protected areas: a multidisciplinary approach*. Cambridge University Press, Cambridge, p 72–98
- Grüss A, Kaplan DM, Guénette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biol Conserv* 144:692–702
- Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecol Lett* 5:361–366
- Halpern BS, Lester SE, Kellner JB (2009) Spillover from marine reserves and the replenishment of fished stocks. *Environ Conserv* 36:268–276
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Hanns BJ, Shears NT (2023) Modelling spatial variation in an exploited species across marine reserve boundaries. *J Appl Ecol* 60:1708–1719
- Hanns BJ, Haggitt T, Shears NT (2022) Marine protected areas provide unfished reference information to empirically assess fishery status. *Biol Conserv* 276:109775
- Herrnkind WF, Childress MJ, Lavalli KL (2001) Cooperative defence and other benefits among exposed spiny lobsters: inferences from group size and behaviour. *Mar Freshw Res* 52:1113–1124
- Hilborn R, Stokes K, Maguire JJ, Smith T and others (2004) When can marine reserves improve fisheries management? *Ocean Coast Manage* 47:197–205
- Jack L, Wing SR (2010) Maintenance of old-growth size structure and fecundity of the red rock lobster *Jasus edwardsii* among marine protected areas in Fiordland, New Zealand. *Mar Ecol Prog Ser* 404:161–172
- Kay MC, Lenihan HS, Kotchen MJ, Miller CJ (2012) Effects of marine reserves on California spiny lobster are robust and modified by fine-scale habitat features and distance from reserve borders. *Mar Ecol Prog Ser* 451:137–150
- Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* 17:1039–1054
- Kelly S (1999) Marine reserves and the spiny lobster, *Jasus edwardsii*. PhD dissertation, University of Auckland
- Kelly S (2001) Temporal variation in the movement of the spiny lobster *Jasus edwardsii*. *Mar Freshw Res* 52:323–331
- Kelly S, MacDiarmid AB (2003) Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *NZ J Mar Freshw Res* 37:149–158
- Kelly S, MacDiarmid AB, Babcock RC (1999) Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Mar Freshw Res* 50:409–416
- Kelly S, Scott D, MacDiarmid AB (2002) The value of a spill-over fishery for spiny lobsters around a marine reserve in northern New Zealand. *Coast Manage* 30:153–166
- Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Environ Biol Fishes* 55:65–79
- Krueck NC (2021) Marine conservation across protected area boundaries. *Nat Ecol Evol* 5:1203–1204
- Kruschke JK (2013) Bayesian estimation supersedes the *t* test. *J Exp Psychol Gen* 142:573–603
- LaScala-Gruenewald DE, Grace RV, Haggitt TR, Hanns BJ, Kelly S, MacDiarmid AB, Shears NT (2021) Small marine reserves do not provide a safeguard against overfishing. *Conserv Sci Pract* 3:e362
- Lavalli KL, Herrnkind WF (2009) Collective defense by spiny lobster (*Panulirus argus*) against triggerfish (*Balistes capricus*): effects of number of attackers and defenders. *NZ J Mar Freshw Res* 43:15–28
- Lavalli K L, Spanier E, Thiel M, Watling L (2015) Predator adaptations of decapods. In: Thiel M, Watling L (eds) *The natural history of the Crustacea. 2. Lifestyles and feeding biology*. Oxford University Press, Oxford, p 190–228
- Lenihan HS, Gallagher JP, Peters JR, Stier AC, Hofmeister JK, Reed DC (2021) Evidence that spillover from Marine Protected Areas benefits the spiny lobster (*Panulirus interruptus*) fishery in southern California. *Sci Rep* 11:2663
- Lenihan HS, Reed DC, Vigo M, Leiphardt C and others (2024) Regional differences in fishing behavior determine whether a marine reserve network enhances fishery yield. *Sci Rep* 14:1242
- Ley-Cooper K, De Lestang S, Phillips B, Lozano-Álvarez E (2014) An unfished area enhances a spiny lobster, *Panulirus argus*, fishery: implications for management and conservation within a biosphere reserve in the Mexican Caribbean. *Fish Manag Ecol* 21:264–274
- MacDiarmid AB (1989) Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda: Palinuridae) in northern New Zealand. *Mar Biol* 103:303–310
- MacDiarmid AB (1991) Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus edwardsii* on a coastal reef in northern New Zealand. *Mar Ecol Prog Ser* 70:129–141
- MacDiarmid AB (1994) Cohabitation in the spiny lobster *Jasus edwardsii* (Hutton, 1875). *Crustaceana* 66:341–355
- McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conserv Biol* 10:1187–1199
- McKoy J, Leachman A (1982) Aggregations of ovigerous female rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae). *NZ J Mar Freshw Res* 16:141–146
- Moland E, Olsen EM, Knutsen H, Garrigou P and others (2013) Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study. *Proc R Soc B* 280:20122679

- Murawski S, Rago P, Fogarty M (2004) Spillover effects from temperate marine protected areas. *Am Fish Soc Symp* 42: 167–184
- ✦ Nessia HR, Hanns BJ, Haggitt TR, Shears NT (2024) Using marine protected areas to assess the status and recovery of the spiny lobster *Jasus edwardsii* fishery in the Hauraki Gulf, Aotearoa New Zealand. *Front Mar Sci* 11:1440350
- Nillos Kleiven PJ, Espeland SH, Olsen EM, Abesamis RA, Moland E, Kleiven AR (2019) Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area. *Proc R Soc B* 286:20182455
- ✦ Ohayon S, Granot I, Belmaker J (2021) A meta-analysis reveals edge effects within marine protected areas. *Nat Ecol Evol* 5:1301–1308
- Oliver M, MacDiarmid A (2001) Blood refractive index and ratio of weight to carapace length as indices of nutritional condition in juvenile rock lobsters (*Jasus edwardsii*). *Mar Freshw Res* 52:1395–1400
- Paterson NF (1968) Anatomy of the Cape rock lobster, *Jasus lalandii* (H. Milne Edwards). *Ann S Afr Mus* 51:1–232
- ✦ Pederson HG, Johnson CR (2006) Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. *J Exp Mar Biol Ecol* 336:120–134
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. *Science* 294:1920–1923
- ✦ Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142
- Shears NT, Babcock RC (2004) Community composition and structure of shallow subtidal reefs in northeastern New Zealand. *Science for Conservation* No. 245. Department of Conservation, Wellington
- ✦ Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take marine park. *Biol Conserv* 132:222–231
- ✦ Spanier E (2024) Marine protected areas — a review of their potential effects on lobster population size & structure and fisheries management. *Fish Res* 275:107025
- ✦ Wahle RA (1992) Body-size dependent anti-predator mechanisms of the American lobster. *Oikos* 65:52–60
- Webber D, Starr P, Haist V, Rudd M, Edwards C (2018) The 2017 stock assessment and management procedure evaluation for rock lobsters (*Jasus edwardsii*) in CRA 2. *New Zealand Fisheries Assessment Report* 2018/17
- ✦ Zimmer-Faust RK, Spanier E (1987) Gregariousness and sociality in spiny lobsters: implications for den habitation. *J Exp Mar Biol Ecol* 105:57–71

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