



FEATURE ARTICLE

Bias in lobster tethering experiments conducted for selecting low-predation release sites

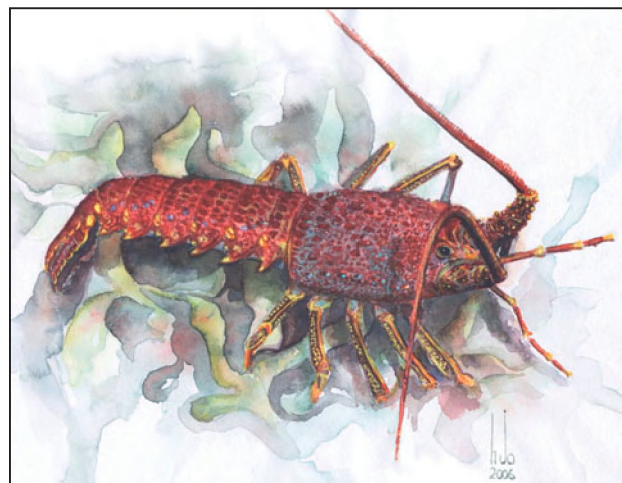
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ABSTRACT: Juvenile spiny lobsters *Jasus edwardsii*, grown in tanks for 1 yr following capture as pueruli, may be released to coastal reefs in Tasmania, Australia, to offset possible stock depletion resulting from the harvest of pueruli for commercial culture. We assessed the utility of tethering experiments for selecting sites with low predation pressure appropriate for lobster releases, and address a concern that experimental artefacts are likely to vary across sites, providing biased estimates of relative mortality. A multi-camera surveillance system used to observe tethered juvenile lobsters at 4 isolated reefs revealed low-diversity of predators, which included wrasse (45% of observed predation events), octopus (21%), crabs (17%) and large lobsters (16%). Wrasse and octopus were the dominant predators at 3 of the 4 sites, while crabs and large lobsters dominated the fourth. Survival rates in 48 h tethering trials varied substantially (24.4 to 62.2%) among sites. Tethers substantially increased the success rates of all predators in a reef mesocosm. The magnitude of the tethering effect was similar for wrasse and octopus, while large lobsters caught relatively few untethered juvenile lobsters, and crabs appeared incapable of catching untethered lobsters. Survival rates for each site were adjusted by applying a site-specific correction factor calculated using knowledge of predator suites at each site and magnitude of tethering bias for each predator. Corrected survival rates did not vary among sites, and the rank order of sites in terms of predation rates did not change following correction; overall, there was a significant correlation between adjusted and unadjusted values. Our results suggest that tethering trials are appropriate as a tool for selecting release sites only if complementary data on predator assemblages and tethering artefacts are collected with sufficient rigour to enable calculating site-specific correction factors.



Sites that are appropriate for release of juvenile southern rock lobster *Jasus edwardsii* can be identified by means of tethering experiments.

Painting: Hilary Oliver

KEY WORDS: Spiny lobster · *Jasus edwardsii* · Fishery enhancement · Tethering experiments · Predation · Experimental artefacts

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INTRODUCTION

The release of hatchery-reared juveniles of marine species for restocking or stock enhancement frequently results in poor survival (see reviews by Blaxter 2000, Brown & Day 2002). This is most often attributed to behavioural inadequacies induced by artificial feed-

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ing regimes and sensory deprivation during rearing (Berejikian 1995, Olla et al. 1998, Svåsand et al. 1998, Castro et al. 2001). Where behaviour is unaffected or problems can be redressed by changes in hatchery practices (e.g. Brown & Smith 1998, Hossain et al. 2002), the choice of optimal release sites is of primary importance (Leber et al. 1996, Kellison et al. 2003). Release sites must be selected to provide high quality habitats affording maximum protection and minimal predation pressure. As most mortality occurs in the hours to days immediately following release (Furuta et al. 1997, Blaxter 2000, Svåsand et al. 2000, van der Meeren 2000), experimental approaches that can compare short-term relative survival among sites are of value for site selection.

Mark-recapture studies are frequently used to gauge the success of enhancement operations (Bannister et al. 1994, Agnalt et al. 1999), and tag return rates from juveniles released at multiple sites have been used to define optimal release habitats (Leber et al. 1996). However, the inability to distinguish losses due to emigration and mortality can confound mark/recapture results, and large numbers of juveniles must be available to ensure sufficient returns from multiple sites. Tethering experiments have the potential to overcome these limitations by providing accurate data on the fate of a small number of juveniles with restricted mobility; however, they introduce a new set of potential pitfalls. When tethering highly mobile prey, at best, mortality rates will increase substantially due to reduced effectiveness of escape responses (Zimmer-Faust et al. 1994), and at worst, tethered prey may be captured by predators incapable of capturing untethered prey (Adams et al. 2004). Still more problematic is the potential for non-additive, or higher order, artefacts (Peterson & Black 1994). An example of a non-additive artefact relevant to our study is that the effect of tethering on capture rates may vary among predators (Curran & Able 1998), so that if the relative abundance of predators varies among sites, tethering results may be more a reflection of the nature of predator assemblages at particular sites than a measure of relative predation rates. Following spirited debate (Peterson & Black 1994, Aronson & Heck 1995, Kneib & Scheele 2000, Aronson et al. 2001), more recently backed by substantial empirical evidence, it is now widely acknowledged that tethering experiments must be accompanied by rigorous tests of associated artefacts. This is particularly important for highly motile prey that manifest rapid or unpredictable movements to escape predators. Key to a robust interpretation of tethering data is information on the identity of the predators (Peterson & Black 1994, Micheli 1996), behaviour of tethered prey (Barbeau & Scheibling 1994, Curran & Able 1998), and predation mechanisms

(Zimmer-Faust et al. 1994, Adams et al. 2004). Here we report an experiment using novel techniques to quantify and account for artefacts associated with tethering juvenile *Jasus edwardsii* (southern rock lobsters) on spatially isolated rocky reefs.

The potential for aquaculture of spiny lobsters is attracting much attention globally, and where successful (notably Vietnam; Thuy & Ngoc 2004), is progressing through the captive rearing of pueruli (first benthic post-larval stage) captured from the wild. In Tasmania, Australia, concerns that the harvest of *Jasus edwardsii* pueruli may harm wild lobster stocks are being addressed through reseedling (Gardner et al. 2006). This involves on-growing harvested pueruli in tanks or seacages for 1 yr, then releasing a proportion estimated to be equivalent to the number that would have survived naturally back to the area of capture. This system of management is underpinned for the year following settlement by a large discrepancy in field survival (3 to 5%; Herrnkind & Butler 1994, Edmunds 1995) and captive survival (85 to 95%; Phillips et al. 1983, Kington 1999, Crear et al. 2003) so that, following reseedling, a large proportion of juveniles are still available for on-growing in captivity to a marketable product. The success of management by reseedling is contingent on a high survival of released juveniles.

Field and laboratory observations have shown that behaviour relating to predator avoidance, shelter use, and feeding of released captive-reared juvenile *Jasus edwardsii* are largely indistinguishable from those of wild juveniles (Mills et al. 2004, 2005a, Oliver et al. 2005). Accordingly, identification of suitable release sites prior to commercial-scale releases became a priority. While mark-recapture trials (Mills et al. 2005a) provided evidence of equivalent survival among captive-reared and wild juveniles across multiple sites, they failed to provide a measure of relative predation rates among sites because of site-specific emigration rates. The present study assesses the potential of tethering experiments to indicate spatial variability in relative predation, employing a multi-camera surveillance system to observe predator/prey interactions in the wild, and mesocosm experiments to quantify artefacts.

MATERIALS AND METHODS

Study sites. Because juvenile *Jasus edwardsii* may be released in southeast Tasmania as a licence requirement associated with the harvest of pueruli, we selected representative areas of accessible reef in this region (Fig. 1). We did not target sites with obvious variability in habitat characteristics, but rather restricted our choice to areas we judged to be suitable for lobster release. Sites were selected based on the presence of

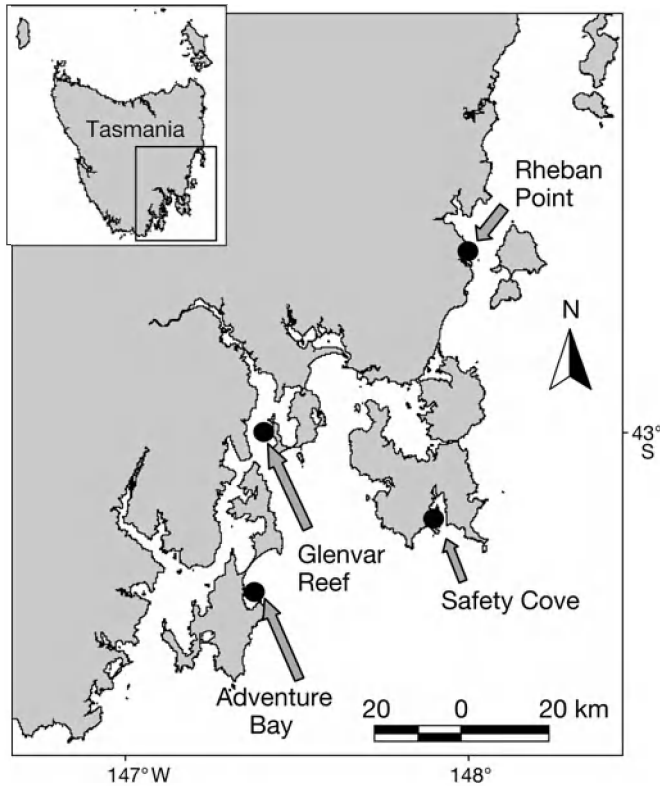


Fig. 1. Location of tethering sites in southeastern Tasmania

wild juvenile lobsters, an obvious abundance of appropriate-sized shelter (Edmunds 1995), moderate to high macroalgal abundance to provide cover for released lobsters and accessibility for deploying camera equipment and performing regular dive surveys.

To permit regular dive surveys, all experimental reefs were in water less than 13 m deep, and were sheltered from prevailing strong southerly weather patterns (Table 1). A site at Adventure Bay was the most exposed, experiencing oceanic swell from the east, and frequent strong north-westerly wind. The biota of this reef reflected a relatively high-energy environment. While separated from coastal fringing reef by ca. 200 m of sandy sea floor, patchy low-profile

reef extended 50 to 80 m north of the reef to a depth of 13 to 14 m. The Glenvar Reef site was a discrete area of moderately sheltered reef within the Derwent Estuary. The reef was ca. 100 m offshore from a rocky headland. There were further areas of patch reef ca. 100 m to the west, and shelving reef extended some 800 m south along the shoreline. Although fetch at the Safety Cove site did not exceed 3 km (to the northeast), the site receives considerable reflected swell from the adjacent cliffs to the east in southerly conditions. Accordingly, the fish assemblage at Safety Cove is more typical of high exposure habitat than would be expected given the limited fetch (Jordan et al. 1998). The Safety cove reef was isolated from adjacent fringing reef by a minimum of 200 m of sandy sea-floor. Rheban Point was the deepest of the sites and was moderately exposed. Extensive areas of sand and unstructured rock platform at least 250 m wide separated this site from adjacent fringing reef.

Experimental lobsters. *Jasus edwardsii* individuals for tethering trials were captured as pueruli in crevice collectors (Booth & Tarring 1986) deployed off southern and eastern Tasmania (Gardner et al. 2001) and grown in conditions similar to those likely to exist in a commercial grow-out facility. Lobsters were grown in fibreglass tanks supplied with flow-through water (ca. 250 l h⁻¹) at ambient temperatures (11 to 19°C) and held at densities as high as 200 ind. m⁻³ for pueruli, reducing to ca. 60 ind. m⁻³ for 1 yr old juveniles. Lobsters were fed daily on fresh, opened blue mussels *Mytilus edulis planulatus* or commercial prawn pellets, and lobsters attained sizes of 28 to 37 mm carapace length (CL) after 12 mo. Lobsters for field tethering and mesocosm trials were selected haphazardly from tanks, avoiding the largest and smallest individuals.

Tethering and deployment. Tethering techniques were refined using tank trials until we were confident that escape from tethers was highly unlikely. On the day prior to field experiments, spiny lobsters were 'saddled' for tethering. After drying the lobster carapace with compressed air, a short length of 6 kg breaking strain nylon monofilament was tied around the

Table 1. Summary of reef characteristics at tethering sites. Reef dimension (reef dim.) is given as the longest reef axis × the longest axis perpendicular to the first. Relief describes the rise of the reef from the seafloor and is categorized as low (L: small boulders or shelving reef rising no more than 1 m from the seafloor), medium (M: large boulders or rock slabs rising 1 to 2 m from the seafloor) or high (H: large boulders or rock slabs rising more than 2 m from seafloor)

Site	Position	Reef dim. (m)	Depth (m)	Relief	Fetch
Adventure Bay	43° 21' 254" S, 147° 21' 28" E	60 × 25	6–9	H	40 km NE
Glenvar Reef	43° 00' 11" S, 147° 23' 46" E	150 × 150	5–7	M	15 km N
Safety Cove	43° 11' 5" S, 147° 51' 45" E	150 × 80	4–9	M	3 km NE
Rheban Point	42° 36' 57" S, 147° 56' 28" E	100 × 50	11–13	L	40 km NE

lobster between the 2nd and 3rd pair of walking legs, and a small fishing swivel with a snap-hook tied at the dorsal centre of the carapace using this line. The knot and swivel were secured with a drop of cyanoacrylate glue, and the lobsters remained in air for ca. 5 min to allow the glue to reach partial-cure. Recovery to apparently normal behaviour was rapid after the lobsters were returned to water. The snap-hook allowed the tether to be attached to lobsters by divers in the field, and the swivel minimised the likelihood of the tether becoming tangled. Each lobster was identified by a number printed on waterproof paper, which was glued to the dorsal carapace surface using cyanoacrylate glue.

In the field, lobsters were tethered to 200 g cylindrical lead weights using a 250 mm length of 6 kg breaking-strain nylon monofilament. This length of tether permitted lobsters to move in and out of selected and adjacent shelters while minimising entanglement and retaining lobsters within the field of view of cameras. Lead weights had protruding galvanised wire hooks to allow them to be secured in rock crevices.

At each tethering site, a 30 m weighted transect line marked in 0.5 m increments provided a spatial reference in which to determine lobster positions. Lobsters were deployed within 4 m either side of the transect line at spacings of not less than 3 m from each other. Position of lobsters was ultimately determined by the location of appropriate shelters. Lobsters were placed within a crevice or hole in the reef judged by divers to be appropriate to lobster body-size and provide good shelter from predation. Occasionally, individual macroalgal stipes were removed from the range of the tethered lobster where divers identified a risk of entanglement. We aimed to deploy 15 tethered lobsters per replicate trial, although on 2 occasions (1 at Rheban Point, 1 at Safety Cove), sample size was reduced to 14 due to a lobster escaping during the deployment process. At each site, 3 replicate trials were performed, the transect line being moved to a different area on the reef for each trial. Ideally, the order of replicates would have been randomised among sites; however, this was not feasible within the project budget due to the time taken to deploy the camera system. All trials lobsters were deployed within 1 h of dusk, providing consistency between trials and limiting exposure of newly released lobsters to visual predators.

Dive surveys were conducted 24 and 48 h post deployment and surviving lobsters then recovered. During each survey, the presence or absence of each lobster was noted, along with any evidence of lobster remains. This evidence has previously been used to identify predators responsible for individual kills (Micheli 1996), and we wished to assess the robustness of such evidence using video surveillance. Differences

in tethering mortality rates among sites were examined by 1-way ANOVA, with Site treated as a random factor. Conformity to distributional assumptions were examined graphically through plotting mean versus standard deviation and distribution of residuals. Log transformation stabilised errors appropriately.

All field tethering trials were conducted during the periods November 2002 to March 2003, and November 2003 to March 2004. Mesocosm experiments were conducted between April and June 2004. At the time this study was conducted, ethics approval was not required in Australia for field-based or laboratory experiments on lobsters.

Remote surveillance. A time-lapse video system was used to monitor 6 tethered lobsters simultaneously throughout the 48 h tethering trials. The system comprised 6 cameras paired with 12 infrared (IR) lights (845 nm wavelength) connected to a surface pontoon which provided power and capacity to process and transmit video signals (Mills et al. 2005b). The use of IR light for night surveillance allowed observation free from biases associated with the use of visible light. Camera signals were either transmitted to the remote monitoring station via a microwave video link, or, where no suitable monitoring station could be established, recorded directly on the pontoon. Time-lapse recording resulted in a frame rate of ca. 1 frame s^{-1} for each camera.

Once the tethered lobsters were in place, divers positioned each camera and pair of lights to provide a clear image of the area of seafloor accessible to a single randomly selected tethered lobster. Due to the high absorption of IR light in water (Kirk 1994), this represents the maximum area that could be effectively illuminated by 2 lights. When the 24 h dive survey revealed that a lobster under a camera had been taken, that camera was moved to a nearby surviving lobster to maximise the number of predation events recorded.

Videotapes from field trials were reviewed in the laboratory. Once a predation event was located on the tape, the identity and estimated size of the predator, time of predation, and other relevant factors such as tether entanglement were recorded.

Baited underwater video surveys. An independent census of the abundance of predatory fishes was conducted at each site using a baited underwater video station (Willis & Babcock 2000). This technique is efficient at sampling larger mobile fish species (Cappo et al. 2004), does not require additional dive effort, and is non-extractive and therefore did not bias nearby tethering trials. An underwater colour video camera was mounted on a tripod with an 80 cm extension arm on which was placed a bait pot (500 ml plastic jar with numerous holes in the top and sides). A 30 m cable returned the camera signal to a 12 V videocassette

recorder on the research vessel. A census was conducted at the completion of each tethering trial prior to divers entering the water for the final census. The bait pot was filled with crushed juvenile lobsters and the system lowered to the seafloor for 20 min. Recording commenced as soon as the camera system reached the seafloor. Video footage was later reviewed and scored for the maximum number of fishes and the maximum number of potential predatory fishes seen in any single frame, and the total number of species seen in the 20 min of footage for each replicate. Fishes scored as potential lobster predators were of a species and size previously observed as successful predators in video-monitored tethering trials.

Mesocosm trials. Once the identity of predators at each site was established from monitored tethering trials, we compared the relative magnitude of tethering artefacts for each predator in mesocosm trials. A reef was constructed from natural reef rock in a large outdoor raceway tank measuring $18 \times 5 \times 2$ m depth (volume 180 000 l). Rocks ranged in size from 8 cm in diameter to large slabs ca. $0.8 \times 0.5 \times 0.3$ m, and many were heavily encrusted with algae and invertebrate communities, while some supported one or more macroalgal plants. Once assembled, the reef covered an area ca. 3.5×2.5 m and rose a maximum of 0.8 m from the tank floor, and macroalgal abundance was at a level similar to that of natural reefs used in tethering trials. The reef provided shelter of varying morphology as seen on natural reefs, including large 'dens', as well as crevices and holes suitable for habitation by individual lobsters. The mesocosm was supplied with unfiltered seawater at ambient temperature at a rate of ca. 6000 l h^{-1} .

As experiments progressed, some macroalgae became detached, and heavy grazing of encrusting biota by lobsters became apparent. Accordingly, each time the reef was reassembled after a replicate trial, we replaced a small percentage of rocks, including any that had lost macroalgae, with new rocks supporting similar species and sizes of algae.

Experiments compared predation rates with different predators under 2 conditions: (1) a mixed population of tethered and untethered lobsters, and (2) an equivalent untethered population. Condition 1 experiments approximated a tethering experiment in the wild, where tethered lobsters supplemented an existing population at sites chosen because of the presence of resident juvenile lobsters. Condition 2 experiments provided an independent measure of mortality in a wholly untethered population under identical conditions. The comparison between the 2 trial conditions directly reflects the aim of the mesocosm trials, which is to produce a correction factor allowing field-based tethering trials to be used to predict predation of released untethered lobsters. Control experiments with

no predators present were conducted to quantify mortality due to uncontrolled causes such as cannibalism.

After the reef was assembled and the tank filled, a single species of predator was released into the tank and given a 48 h acclimation period in the mesocosm prior to commencing experiments. Preliminary observations using the surveillance system in the mesocosm revealed that predators became acclimated quickly; lobsters and wrasses were observed 'grazing' on epiphytes within a few hours of release. A single meal of blue mussels *Mytilus edulis*, equivalent to ca. 5–8% body mass for each predator, was provided 24 h after release; all predators consumed this meal rapidly. The number of predators used in each trial reflected their abundance in the wild as interpreted from video footage. For trials with octopus and fish as predators, a single predator was used. The dominant fish predator (male blue-throated wrasse *Notolabrus tetricus*) is fiercely territorial, protecting ranges of 400 to 775 m² (Barrett 1995), and accordingly lobsters were unlikely to be subject to attack by more than 1 of these fish simultaneously in the wild. For trials with adult lobsters, 2 lobsters of 100 to 105 mm, i.e. the size seen to attack juvenile lobsters, were used. Video footage from field tethering trials regularly showed several red swimmer crabs *Nectocarcinus tuberculosis* attacking or feeding on tethered lobsters, and accordingly, 4 *N. tuberculosis* were used in each trial. Individual predators were used in only a single replicate trial, with one exception; capturing octopus of the small size observed attacking tethered lobsters in the field proved difficult, and so the same octopus was used in all trials. The order of trials, including control trials, was randomised with respect to predator type.

A total of 18 juvenile lobsters were released in each replicate trial, with 9 of these being tethered in Condition 1 trials. All lobsters were measured and sexed prior to release, and released at dusk. The duration of experiments was 4 d for Condition 1 trials, and 10 d for Condition 2 trials. Equivalent durations would have been preferable, but mortality rates were often zero after 4 d in Condition 2 trials, and 100% after 10 d in Condition 1 trials. Mortalities of 100% are not useful results, as the time over which mortalities occurred is not known. The mesocosm reef was inspected daily by a diver, and remains of any lobsters were removed, a process that would have been carried out by scavengers on natural reefs.

At the completion of each replicate trial, the mesocosm was drained, predators captured, and the reef disassembled. All surviving lobsters were captured, counted and measured. The reef was reassembled in a different configuration for each replicate, effectively providing a new mesocosm environment. This was particularly critical for trials using the (same) octopus.

Standardisation. We used the results of mesocosm trials to calculate a standardised correction factor C for each predator i :

$$C_i = \frac{U_i}{T_i \cdot c_{\max}} \quad (1)$$

where U_i is the average number of mortalities of untethered lobsters in the Condition 2 mesocosm trials, T_i is the average number of mortalities of tethered lobsters in the Condition 1 mesocosm trials, and c_{\max} is highest ratio of $U_i:T_i$ amongst the 4 predators.

This factor accounts for the differences in tethering artefacts caused by different search and attack behaviour among predatory species. Incorporating this factor into calculation of corrected relative mortality rate enables results of field tethering trials to be adjusted for artefacts according to the observed suite of predators at each site.

Using this correction factor and the known composition of the predator assemblage at each site, the corrected number of mortalities (M) for each replicate at each field site was calculated as:

$$M_{jk} = m_{jk} \sum_{i=1}^n C_i P_{ij} \quad (2)$$

where m_{jk} is the number of mortalities at site j in replicate k after 48 h, P_{ij} is the proportion of mortalities at site j attributed to predator i , and n is the number of different predator species responsible for mortalities at site j .

While M provides a relative measure of the number of mortalities per replicate trial corrected for tethering artefacts, a further adjustment is required to calculate the corrected relative mortality rate over 48 h. We cannot assume that lobsters killed due to the presence of the tether would have, in the absence of the tether, survived for the entire 48 h trial. Rather, these lobsters would have been subjected to the same predation pressure (corrected for tethering artefacts) as all other lobsters in the population. By removing these lobsters entirely from the trial, we in effect assign to them the average predation rate of the remaining lobsters. To achieve this, N_{jk} (the number of lobsters released in each replicate trial k at each site j) must be reduced by the same factor as the calculated reduction in number of mortalities; thus:

$$\hat{N}_{jk} = N_{jk} - (m_{jk} - M_{jk}) \quad (3)$$

and the corrected relative mortality rate over 48 h (\hat{M}) for each replicate calculated as:

$$\hat{M}_{jk} = \frac{M_{jk}}{\hat{N}_{jk}} \quad (4)$$

Due to differing binomial probability distributions associated with mortality rates of tethered and untethered

lobsters in the mesocosm trials, we were unable to directly derive errors associated with the calculation of C . Errors for the corrected mortality estimates from tethering trials in the wild were derived by applying correction to individual tethering replicates, then averaging these corrected results. This approach is likely to underestimate total error for corrected mortality rates at each site, and will therefore be conservative with respect to Type II errors.

RESULTS

Field tethering experiments

The pattern of differences in mortality rates among sites observed after 24 h (Fig. 2) was accentuated after 48 h, resulting in significant differences (ANOVA, $F_{3,8} = 5.404$, $p = 0.035$). A post-hoc Ryan-Einot-Gabriel-Welch test revealed that mortality at Adventure Bay was significantly higher than that at Safety Cove.

Camera observations indicated that tethered lobsters utilised the shelters into which divers released them. Lobsters often responded when first released with rapid swimming (tail flicking). Divers were instructed that in such cases they should persist and replace the lobster in the shelter until the lobster remained there. When a lobster would not settle in a chosen shelter, the lobster was moved to an alternative shelter. Once settled, behaviour patterns of tethered lobsters were consistent with those of wild lobsters. Lobsters emerged from shelters soon after dusk, moving and feeding within the range provided by the tether. Occasionally lobsters were observed pulling persistently against the tether; however, this involved a continuous pull on the tether rather than rapid activity (such as tail-flicking) likely to attract predators, and rarely persisted beyond a few minutes. Shelter occupancy by tethered lobsters was sporadic throughout the night, and surviving lobsters invariably returned to shelters before dawn.

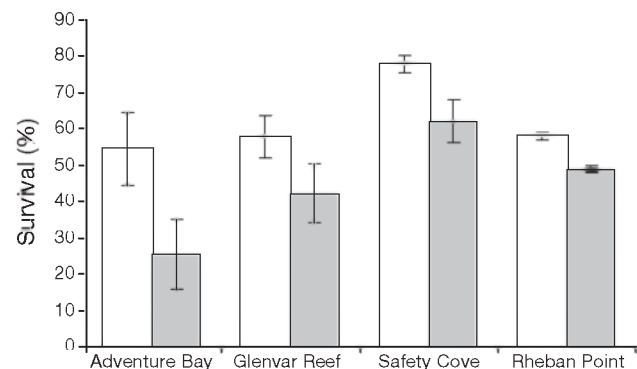


Fig. 2. *Jasus edwardsii*. Percent survival (\pm SE) from 24 h (open bars) and 48 h (shaded bars) dive surveys at tethering sites

Overall, 41 predation events were recorded from 98 lobsters monitored by the remote surveillance system; 2 events were clearly the result of entanglement in camera equipment and were not included in analyses. One predator remained unidentified, as the event occurred between camera frames. Of the remaining 38 predation events, 17 (45%) were predation by fishes, 8 (21%) by octopus *Octopus maorum*, 7 (18%) by red swimmer crab *Nectocarcinus tuberculosis*, and 6 (16%) were cannibalism by larger (>80 mm CL) *Jasus edwardsii*. Of the fishes, 12 were blue-throated wrasse *Notolabrus tetricus* (5 female, 7 male), 3 were purple wrasse *Notolabrus fucicola*, 1 was an unidentified leatherjacket (family Monacanthidae) and 1 kill occurred on the edge of the field of view of a camera, providing only enough evidence to identify the predator as a fish.

Successful predators were within defined size ranges for each species. Blue-throated wrasse are site-attached protogynous hermaphrodites (Barrett 1995) exhibiting sexual dimorphism. A single large fish (35 to 45 cm total length, TL) within a well-defined territory becomes a male. A ratio of ca. 20 female or immature fish to one male fish of this species is typical for Tasmanian reefs (N. Barrett, TAFI, pers. comm.). The female:male ratio of 5:7 among successful predators indicates that large size is important for predatory success with lobsters of the size tethered. Successful females were also among the largest seen on the reef. Conversely, while *Octopus maorum* can attain 1.2 m TL (Edgar 1997) only octopus estimated at 0.3 to 0.45 m TL were successful predators in our study. Octopus up to 1 m TL were observed by divers at Safety Cove and Adventure Bay. All predatory red swimmer crabs were amongst the largest present on the reef (80 to 90 mm carapace width), while predatory lobsters were 80 to 110 mm CL. No lobsters larger than 110 mm CL were seen by divers in the areas where cannibalism was observed.

Video footage revealed that the presence of the tether directly contributed to capture in 22 of the 30 predation events where the entire capture sequence was clearly visible to a camera. Of the 8 captures that did not appear to directly involve the tether, 7 were attacks by fish, and one was by octopus. Attacks by fish occurred in daylight (Fig. 3), when lobsters were sheltering. When the tether was not directly involved, capture was the result of a direct frontal attack, and escape by the lobster was restricted by the shelter rather than by the tether. Where the tether contributed to capture, often a first 'strike' by the predator was unsuccessful, and the lobster was then pursued to the end of its tether where it was captured. Octopus attacks, which occurred at night (Fig. 3), were only observed on lobsters within shelters. See Videoclip#1 available at www.int-res.com/articles/suppl/m364p001_app/. The reasons for this are unclear. Most attacks

involved the octopus disturbing the lobster through physical contact with the extremity of an arm, and then capturing the lobster as it attempted to flee. In contrast, attacks by red swimmer crab and larger lobsters occurred only when tethered lobsters were feeding away from shelter during the night. A single exception, involving predation by a lobster during the day (see Fig. 3), occurred when a newly released tethered lobster walked into the den of a large lobster and was captured. In attacks by red swimmer crabs the tether often became entangled in the crab's chelae, and as the lobster attempted to escape, the tether became wound around the chelae, eventually resulting in capture. Alternatively, the crab would progressively reduce the lobster's range of movement by walking towards the lobster along the tether (see Videoclip#2 available at www.int-res.com/articles/suppl/m364p001_app/).

In 2 cases (1 octopus, 1 crab) the tether aided escape by a juvenile lobster, when the predator attack led to the tether anchor being dislodged from an elevated crevice. The momentum of the falling anchor was sufficient to pull the lobster from the grasp of the predator.

All predation events initially involved a single predator except in one case where 2 crabs were involved. After a successful attack by a large lobster, it was common for several red swimmer crabs to later aggressively procure the dead prey, the lobster then moving away from the kill.

After a lobster was captured, the octopus fed at the site of capture for the longest period, remaining unsheltered in the field of view of the camera for up to 231 min ($\bar{x} = 66.3 \pm 32.8$ min). Similarly, crabs (maximum 87 min, $\bar{x} = 46.7 \pm 17.9$ min) and lobster (maximum 30 min, $\bar{x} = 18.7 \pm 6.0$ min) tended to consume prey at the site of capture. Fishes (maximum 10 min, $\bar{x} = 1.1 \pm 1.0$ min) dislodged the anchor and carried the lobster and anchor away, broke the tether, or applied sufficient pressure to pull the tethering saddle off the

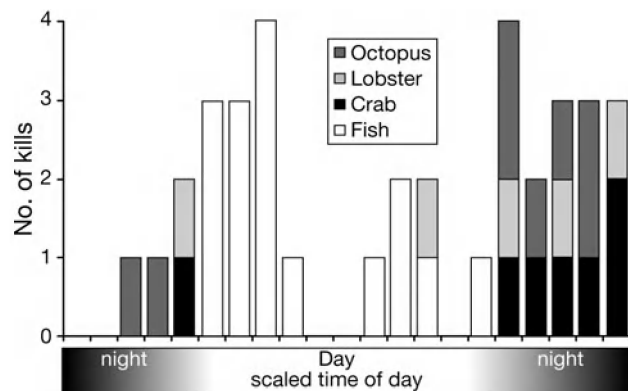


Fig. 3. Predators of *Jasus edwardsii*. Time of day at which predation events by different predators occurred. As trials were conducted over 3 mo, times are re-scaled around the time of sunrise and sunset to accommodate for changing day lengths

lobster carapace. Divers rarely found any remains at the site of lobster kills, with the exception of remnants of the carapace attached by glue to the tether. There was no correlation between the evidence remaining after a predation event and the identity of the predator. Video footage revealed that scavengers (hermit crabs *Trizopagurus strigimanus*; red swimmer crabs *Nectocarcinus tuberculosis*; and small shrimps, family Palaemonidae, at night, and a diverse range of small fishes during the day) removed any remains after predators had finished feeding.

The composition of the predator assemblage and the number of predation events for which predators were positively identified varied among sites (Fig. 4). Of particular note is that cannibalism was only evident at Adventure Bay, and predation by crabs was also most prevalent at this site. Blue-throated wrasse was the dominant fish predator at all sites except for Glenvar Reef, where 2 of 3 predation events by fish were attributable to purple wrasse.

Abundance of predatory fishes

The number of species observed feeding at baited underwater video stations (Fig. 5) varied among sites (ANOVA, $F_{3,8} = 6.485$, $p = 0.016$), while the maximum number of fish observed in any frame was highly variable within sites, and no differences were detected among sites (ANOVA, $F_{3,8} = 0.314$, $p = 0.815$). It was rare to see more than 2 potential lobster predators in a camera frame simultaneously, and where multiple predators were present, they tended to be different species. The maximum number of predators seen in a frame did not vary significantly among sites (ANOVA, $F_{3,8} = 1.331$, $p = 0.331$).

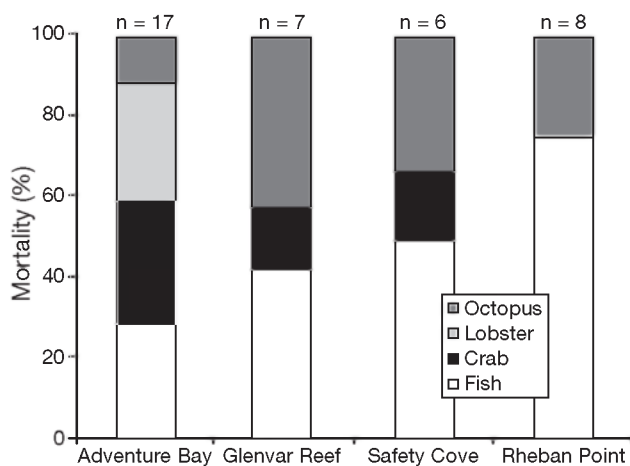


Fig. 4. Predators of *Jasus edwardsii*. Composition of predator suite at each site as determined by analysis of video footage from monitored tethering trials

Mesocosm experiments

Rates of predation on tethered and untethered lobsters were similar between wrasse and octopus (Fig. 6), the 2 most numerous predators observed in the field trials, but both predators consumed tethered lobsters at a much higher rate than untethered lobsters. Red swimmer crab caught the highest number of tethered lobsters, but proved ineffective at capturing untethered lobsters. A single lobster from a Condition 2 crab trial had 1 antenna and the associated antennal base removed, suggesting that this lobster had been captured by a crab but had escaped. Adult lobsters proved less effective than fish and octopus at catching tethered juvenile lobsters, and only a single untethered lobster was killed by a large lobster during the 3 Condition 2 trials.

The use of the same octopus for all trials raised concerns that learning by the octopus (Fiorito & Scotto 1992) may compromise the independence of trials. While this concern is to a degree alleviated by the random order of Condition 1, 2 and control trials, we also note that the highest successful predation rate occurred in the second of 6 (non-control) octopus mesocosm trials, rather than the later trials. There was no evidence of increasing predation success as trials progressed.

Standardisation

Site-specific mortality corrections produced minor changes to relative survival estimates at the 3 sites where fish and octopus were the predominant predators (1.5 to 11.7% increases) but produced a larger change for Adventure Bay (49% increase), where can-

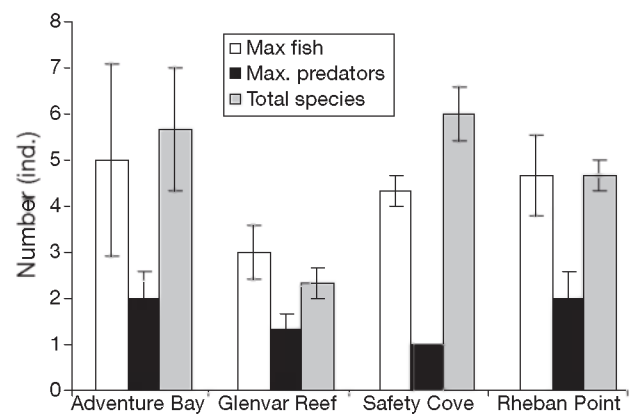


Fig. 5. Maximum number of fish (Max. fish) and potential predators (Max. predators) (\pm SE) seen simultaneously in any single frame during replicate 20 min baited video drops at tethering sites, and the total number of fish species seen in each replicate. All numbers are averaged across replicates

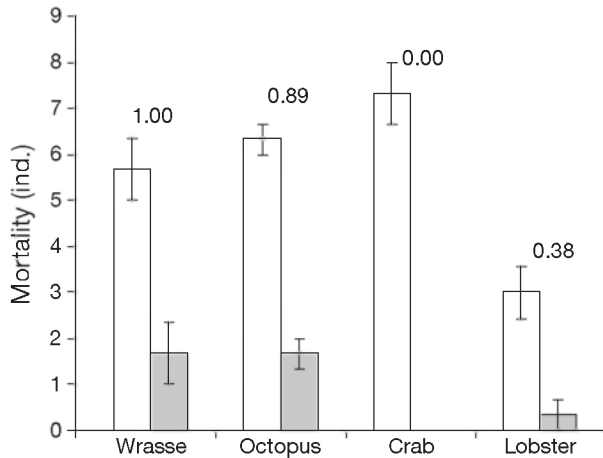


Fig. 6. *Jasus edwardsii*. Mean rates of mortality (\pm SE) for tethered lobsters from mesocosm Condition 1 trials (open bars) and untethered lobsters from mesocosm Condition 2 trials (shaded bars). Standardised species correction factors (C) from mesocosm results are shown above bars

nibalism and predation by crabs was common (Fig. 7). There was a significant correlation between unadjusted and adjusted survival rates ($R^2 = 0.92$, $F_{1,2} = 24.3$, $p = 0.039$), and corrections for tethering artefacts did not alter the rank-order of sites based on predation rates. The negative relationship ($R^2 = 0.48$) between uncorrected survival rate and the maximum number of fish predators seen at bait stations was strengthened ($R^2 = 0.68$) following correction for tethering artefacts. While this relationship remained non-significant ($F_{1,2} = 3.36$, $p = 0.21$), power to detect significance given the observed difference was low (0.2) at least in part due to the small number of sites, and we would expect these correlations to improve with the addition of further sites.

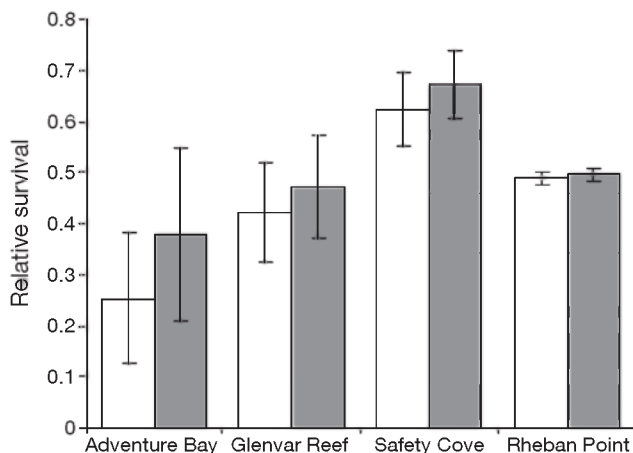


Fig. 7. *Jasus edwardsii*. Relative survival (\pm SE) of tethered lobsters in the field over 48 h (open bars) and corrected values after allowing for tethering artefacts (shaded bars)

Due to the decrease in the effective number of released lobsters in each replicate (\hat{N}_{jk}) for adjusted estimates, errors associated with survival estimates increased in comparison to unadjusted values. As errors associated with C could not be incorporated into calculations, these remain underestimates of total error and thereby increase the probability of committing a Type I error. Despite this, no significant difference between corrected relative survival estimates was detected (ANOVA $F_{3,8} = 2.10$, $p = 0.179$).

DISCUSSION

Predation on tethered lobsters

Vigorous discussions of the merits of tethering experiments have led to a better understanding of the potential pitfalls of this technique and increasingly sophisticated methods of improving data quality. Beyond simple survival data, chronographic tethering devices (Minello 1993, Haywood & Pendrey 1996, Peterson et al. 2001) provide additional data on survival time, which can greatly aid the investigation of artefacts (Haywood et al. 2003). Single video cameras have been deployed to identify predators and monitor survival over periods of minutes to hours (Wahle & Ste-neck 1992). Our video system with the capacity to monitor multiple tethered animals over periods of several days used in combination with mesocosm experiments has provided an unprecedented level of information on the identity and behaviour of predators and behaviour of prey, ultimately facilitating meaningful interpretation of results despite predator- and site-specific artefacts.

In contrast to tethering trials with some fishes (Curran & Able 1998, Adams et al. 2004) and crustaceans (Barshaw & Able 1990, Haywood et al. 2003), the behaviour of tethered and wild lobsters in our trials was indistinguishable. Once settled in a shelter, normal diel patterns of shelter use were assumed, and normal defensive behaviour was observed on approach by predators. Entanglement of tethers (see Adams et al. 2004) was largely eliminated by careful choice of shelters and occasional removal of macroalgae. Despite the apparent absence of these artefacts identified as confounding factors in previous studies, video footage showed that the preconditions for site-specific artefacts existed at our study sites. These include differences in the effect of the tether on rate of predatory success by various predators and variation in predator abundance among sites.

The lack of diversity amongst predator assemblages was surprising, but greatly simplified the process of quantifying and comparing tethering artefacts. The vulnerability of lobsters to predation decreases dra-

matically with small increments in body size (Wahle & Steneck 1992), and the size of lobsters we released excluded predation by a diverse array of smaller fish species observed by divers and baited video stations on study reefs. In addition to the observed finfish predators, we expected to see predation by a range of other species present at the sites such as conger eel *Conger verreauxi*, red cod *Pseudophycis bachus* and gurnards (family Triglidae). The prevalence of crabs as a predator was unexpected, as was the high apparent rate of cannibalism. While wild juveniles of the size that we tethered are less gregarious than larger *Jasus edwardsii* (Macdiarmid 1994, Edmunds 1995), they were seen to cohabit shelters with large lobsters at tethering sites, suggesting that cannibalism does not play a large part in structuring wild lobster populations. This is supported by evidence that moulting lobsters avoid predation by con-specifics through behavioural adaptations (Lipcuis & Hernkind 1982). The predator assemblage at Bruny Island was distinctive from those at other sites, with lobsters and crabs responsible for ca. 60% of predation events. Octopus and fishes were the dominant predators at the other 3 sites, and cannibalism was absent.

While diversity at the species level was low, the 4 main predatory species represent 3 taxonomic classes (Malacostraca, Cephalopoda and Osteichthyes), each with distinct prey detection and capture methods. Variability in capture technique can lead directly to differences in the effect of the tether on the rate of predatory success (Barbeau & Scheibling 1994, Curran & Able 1998). All predation by fishes occurred during daylight hours and visual detection was clearly important. Tactile detection appeared to be important to octopus and crabs, which were only seen feeding at night. It was unclear from the video footage how lobsters were detecting prey. Large lobsters were seen to 'pounce' on tethered juveniles from a distance, suggesting remote sensing, which is likely to be olfactory (Derby et al. 2001). Camera footage showed that the tether was directly involved in all captures by crab and lobsters, ca. 90% of captures by octopus and ca. 40% of captures by fishes. In these instances the lobster was captured because escape responses were directly impeded by the tether. It has been suggested that field-based video surveillance can provide the most complete evaluation of the tethering artefacts and variability of artefacts among sites (Peterson & Black 1994, Micheli 1996) and superficially the percentage of predation events where the tether appears to contribute to capture could be taken as a direct measure of tethering artefacts. However, there is potential for artefacts that cannot be detected or quantified visually, and for this reason we pursued an independent measure of tethering artefacts through the mesocosm experiments.

Quantifying the artefacts of tethering

The paradox of experimental tests for artefacts is that the tests themselves will undoubtedly induce further artefacts (Micheli 1996, Kraufvelin 1999). Quantifying the artefacts of tethering on natural reefs with the full range of biotic and physical interactions present would clearly minimise the introduction of further artefacts; however, if this were achievable tethering would not be required. Where the mobility of predators is considerably greater than that of their prey, this may be possible through comparisons with alternative methods for prey restraint that maintain access for predators (e.g. buried fences constraining clams; Micheli 1996). The same cannot be achieved where both predators and prey are highly mobile. Tank trials have been widely employed to observe the effects of tethering on prey behaviour and predation rates (Barbeau & Scheibling 1994, Zimmer-Faust et al. 1994, Curran & Able 1998, Kneib & Scheele 2000, Kellison et al. 2003, Haywood et al. 2003) but have been criticised for providing artificially simplified biological conditions under which to observe behaviour (Aronson et al. 2001). In our reef mesocosm we did not attempt to recreate the diversity of biotic interactions occurring on natural reefs, but rather were concerned with replicating physical structure and direct interactions between predator and prey. This emphasis is appropriate, as the artefacts of tethering are a direct result of physical interactions involving the prey, the tether and the reef structure. We acknowledge that predators in mesocosms may not behave naturally due to the absence of higher order predators (Aronson et al. 2001), although behavioural observations suggest this is unlikely to be a significant factor in the present study. Field video footage showed that fish preying on tethered lobsters were amongst the largest present on the reefs and accordingly were unlikely to be subject to frequent threat of predation. Invertebrates seen preying on tethered lobsters fed only at night and did not appear to forage in a risk-averse manner, often remaining exposed for long periods following the capture of tethered lobsters.

Undoubtedly the most significant artefact of tethering relates to the reduction in the effectiveness of the escape responses of the prey (Barbeau & Scheibling 1994, Zimmer-Faust et al. 1994). Accordingly, our objectives for the mesocosm trials were best served by maximising mesocosm size, and we assume that in the very large mesocosm we employed the natural escape response of lobsters was not hindered. Other potential artefacts are associated with unnatural behaviour by predators due to containment, and unnatural feeding behaviour by predators or prey due to a lack of diversity of potential food items. Our Condition 1 mesocosm trials, with tethered and untethered lobsters present,

were designed to remove biases associated with learning behaviour in predators. Reinforcement of particular feeding behaviour through increased yield can lead to rapid improvements in efficiency of prey recognition, attack and handling in fishes (Warburton 2003 and references therein). Assuming that fish were unable to differentiate between tethered and untethered lobsters, substantial reward from successful attacks on tethered lobsters would lead to increased attacks on tethered and untethered lobsters in the wild. Given that success rate will be higher for tethered lobsters, the absence of untethered lobsters from mesocosm trials could lead to an inflated estimate of relative predation rates on tethered lobsters. Although we cannot rule out the presence of further artefacts from the use of a mesocosm, we are confident that the mesocosm reef was sufficiently large and the reef sufficiently realistic to provide a meaningful relative estimate of tethering artefacts on natural reefs.

The mesocosm experiments confirmed that tethering engendered a greater increase in predation rates by crab and lobster than by fish and octopus. Crabs have previously been observed 'reeling in' tethered prey (Haywood et al. 2003), while Wahle & Steneck (1992) note that crabs were particularly clumsy at handling tethered lobsters, and suggested most would likely have escaped without the tether. Differences in outcomes from field observations and mesocosm trials confirmed the presence of artefacts that cannot be assessed directly from video-based observations. In contrast with results obtained from experiments in the mesocosm, in which effects of tethering on lobster capture were similar for octopus and fishes, observations by video on natural reefs showed that the tether was involved in a much higher proportion of successful captures by octopus than by fishes. Where the tether was directly implicated in a lobster capture, it is still possible that the lobster would have been captured had the tether not been present, and the probability of this will vary with predation mechanism. Foraging by octopus has been described as 'tactile and speculative' (Forsythe & Hanlon 1997), and our video footage confirms this. The response of a lobster to contact from an octopus arm was invariably to flee, which in turn triggered a high speed 'pounce' by the octopus. While lobsters were normally captured once the tether restricted movement, the speed of the octopus attack suggested that there was a high probability of capture in the absence of a tether, albeit further from the point of initial contact. Attacks by fish were focused rather than speculative, and noticeably slower than those by octopus, with lobsters responding by withdrawing to shelter. Their escape was ultimately restricted by the confines of the shelter rather than by the tether. The suitability of shelters chosen by divers may induce

further artefacts that cannot be visually assessed; these likely vary between predators employing visual or tactile detection methods.

Utility of tethering trials for selecting release sites

For selecting amongst the sites investigated in this study the implications of accepting the uncorrected tethering results are minor. In this instance we would have rejected Adventure Bay as a site for lobster releases (Type I error) and favoured Safety Cove. While corrected relative mortality rates did not differ significantly among sites, critically, the rank order of sites in terms of relative mortality rates did not change following correction for artefacts. While the significant relationship between corrected and uncorrected results should be confirmed by detailed investigations at a greater number of sites, this relationship suggests that on Tasmanian inshore reefs, tethering trials provide a good indication of site suitability for the release of juvenile lobsters.

Importantly, we have shown that this outcome is entirely a result of the dominance of fishes and octopus as predators at most sites, and the similarity in the magnitude of tethering artefacts for these 2 predators. In this example, the outcomes of tethering trials are not dominated by artefacts, but rather by the abundance of the major predators. A different balance of predators among sites could lead to entirely different outcomes. Therefore, tethering is only appropriate as a technique for selecting release sites if complementary data on predator assemblages and the magnitude of tethering artefacts are collected. While it is labour and equipment intensive, the use of video-monitored tethering trials in combination with appropriate mesocosm experiments presents a way forwards for determining the magnitude of artefacts, and potentially establishing predictive relationships between easily quantifiable variables (e.g. predator abundance, tethering mortalities) and relative predation rates.

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