A large-scale experiment finds no evidence that a seismic survey impacts a demersal fish fauna

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Edited by William Hallowell Satterthwaite, University of California, Berkley, CA, and accepted by Editorial Board Member James A. Estes May 29, 2021 (received for review January 20, 2021)

Seismic surveys are used to locate oil and gas reserves below the seabed and can be a major source of noise in marine environments. Their effects on commercial fisheries are a subject of debate, with experimental studies often producing results that are difficult to interpret. We overcame these issues in a large-scale experiment that quantified the impacts of exposure to a commercial seismic source on an assemblage of tropical demersal fishes targeted by commercial fisheries on the North West Shelf of Western Australia. We show that there were no short-term (days) or long-term (months) effects of exposure on the composition, abundance, size structure, behavior, or movement of this fauna. These multiple lines of evidence suggest that seismic surveys have little impact on demersal fishes in this environment.

BRUVS | predatory fish | telemetry | MBACI | community

The exploitation of oil and gas reserves in much of the world's oceans focuses on continental shelves, which for many nations are also the region of the most productive fisheries. Exploration for petroleum resources involves the use of seismic surveys, a major source of high-intensity, impulsive underwater sound that can persist for weeks to months. The effects of this noise on commercial fisheries are a subject of intense debate, with significant economic implications (1). At present, the scientific evidence that catch rates are impacted by seismic surveys is often contradictory, with experimental studies providing contrasting results (*SI Appendix*, Table S1). However, fishers suggest that some commercial species may decline in abundance for a prolonged period (up to several months to a year) following a survey. Since it is generally agreed that there is no obvious evidence of the mortality of fishes, declines in abundance might occur for reasons including displacement due to noise, reduction in feeding on baits, and/or indirect causes such as prey displacement or loss (1, 2).

Experimental field studies of the impacts of seismic surveys are typically hampered by several important constraints. These include the expense and difficulty of chartering and tasking seismic vessels dedicated to experimental work and the confounding effects of studying species that are also the target of commercial fisheries and thus likely to be subject to depletion, irrespective of the potential effects of seismic surveys. Furthermore, given the distances sound may travel underwater, there is a major issue with the scale of experimental studies, which must encompass hundreds of square kilometers to monitor target species at places that might act as control locations (1, 3–5). This invariably requires the use of large vessels with high costs and complex logistics. The need for large experimental arenas also brings with it the possibility of changes in benthic habitats and composition across the study area and thus variation in sound transmission properties and species distributions among sites. Compromises in the experimental design associated with these problems have confounded the results of most published studies of the effects of seismic surveys (1).

We addressed these issues in a large-scale, long-term study that quantified the impacts of exposure to a full-scale, commercial seismic source on the distribution, abundance, size structure, behavior, and movement of an assemblage of tropical demersal fishes targeted by commercial fisheries on the North West Shelf of Western Australia.

Results

Exposure Levels. The effective source level of the airgun array was estimated as 231 dB relative to (re) 1 μPa at 1 m mean square pressure, 228 dB re 1 $\mu Pa^2/m^2/s$ sound exposure level (SEL), 247 dB re 1 μPa m peak-to-peak pressure, and at 15° below the horizontal (6). Most of the acoustic energy occurred below 100 Hz and almost all of it below 1,000 Hz, with peaks at 10 and 50 Hz above an average ambient mean square pressure of 84 dB re 1 μPa. The maximum modeled SEL values received at each sampling site are shown in Fig. 1 [see *SI Appendix*, Table S4 for propagation loss (PL) model coefficients, *SI Appendix*, Fig. S15 for examples of SELs against horizontal range, *SI Appendix*, Fig. S17 for the variation in sound levels with range and azimuth from the airgun array, and

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Significance

Seismic surveys are used to locate deposits of oil and gas in seabeds throughout the world's oceans. There are conflicting views on the impact of these surveys on fish fauna and whether they harm commercial catches. To resolve this issue, we conducted an experimental seismic survey and monitored the composition, abundance, behavior, and movement of an assemblage of commercially important demersal fishes on a shelf habitat using acoustic telemetry and underwater video. We found that the seismic survey did not alter fish abundance or behavior in multiple before-after-control-impact and dose–response experimental frameworks. Our work may allay some of the concerns of stakeholders about the negative impacts of seismic surveys on demersal fishes in tropical shelf environments.

Author contributions: M.G.M., C.W.S., R.D.M., R.F., L.M.C.-R., J.M.S., S.J.N., and M.J.G.P. designed research; M.G.M., C.W.S., R.D.M., R.F., M.J.B., L.M.C.-R., J.M.S., S.J.N., K.C., M.S., B.V., and M.J.G.P. performed research; M.G.M., C.W.S., R.D.M., R.F., M.J.B., L.M.C.-R., J.M.S., S.J.N., K.C., M.S., B.V., and M.J.G.P. analyzed data; and M.G.M., C.W.S., R.D.M., R.F., M.B., L.M.C.-R., J.M.S., S.J.N., K.C., M.S., B.V., and M.J.G.P. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. W.H.S. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2100869118/-/DCSupplemental.

Published July 19, 2021.

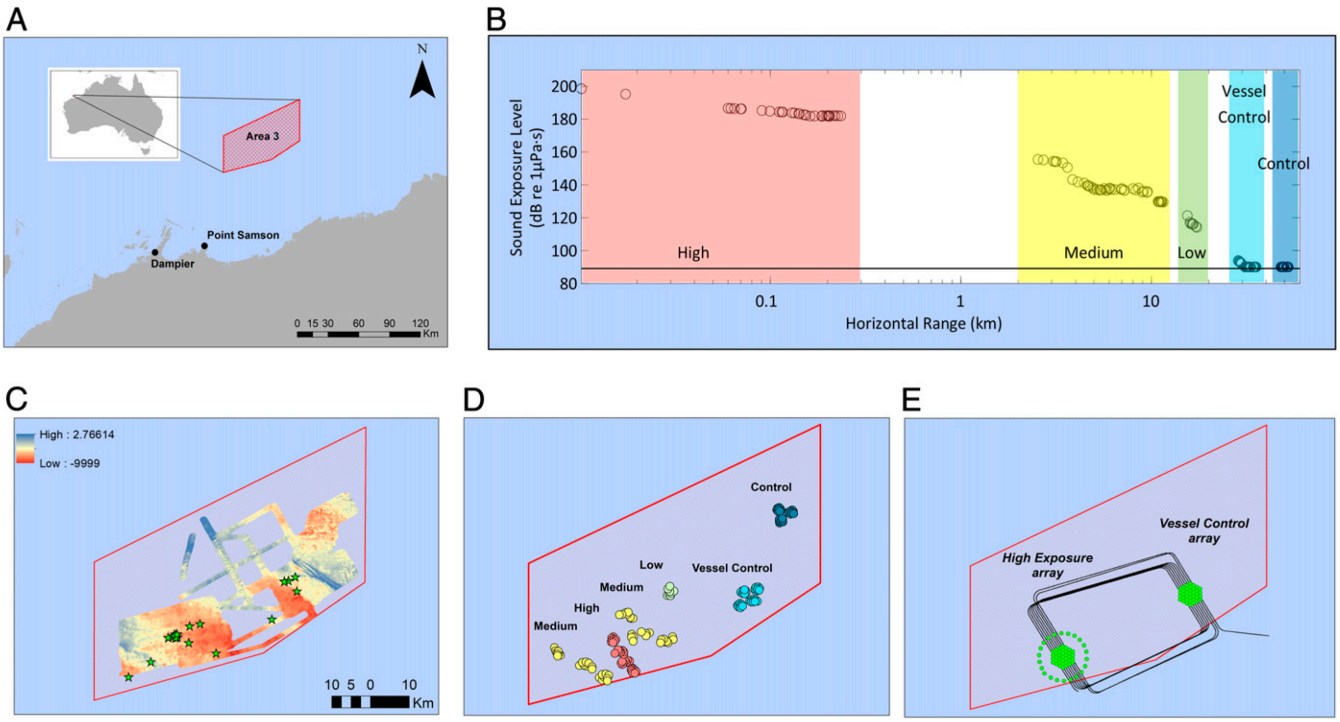

Fig. 1. Setting and layout of a large-scale experiment to examine the effects of seismic exposure on fish assemblages. (*A*) Map of study area within the fishery management location Area 3, where all fishing is prohibited. (*B*) Modeled maximum SELs at sampling sites in the high-exposure (red), medium-exposure (yellow), low-exposure (green), vessel control (light blue), and control zones (dark blue). The black horizontal line shows ambient sound pressure levels. (*C*) Locations of sensors for passive acoustic monitoring (green stars) deployed at and near the high-exposure and vessel control zones during the period of seismic exposure, overlaid on a map of backscatter from a multibeam survey of the seafloor (backscatter levels in decibels shown by color bar; *SI Appendix*, Fig. S3). (*D*) Locations of BRUVS sample sites in exposure zones (high—red, medium—yellow, low—green, vessel control—light blue, and control—dark blue). (*E*) Locations of acoustic receiver arrays (green points) and seismic vessel sail lines (black lines) in Area 3.

McCauley et al. (6) for further details on the generation, measurement, and propagation of the airgun array pressure, particle acceleration, and ground motion components of the signal].

Baited Remote Underwater Video Systems. Analysis of the videos provided by the baited remote underwater video systems (BRUVS) in our multiple before-after-control-impact (MBACI) experimental design found no evidence for major changes in the assemblage structure or species richness of fishes that could be attributed to seismic source exposure (Fig. 2 and *SI Appendix*). The maximum number of species recorded in a single BRUVS deployment was 33, with a maximum of 140 species recorded across high-exposure, control, and vessel control zones (*SI Appendix*).

The relative abundances of all demersal species and all target species remained consistent across sampling surveys at an overall mean of 31.61 h^{-1} and 19.66 h^{-1}, respectively (*SI Appendix*, Fig. S20). We found no consistent trends in the changes of abundance through time at any zone. The variability through time in the relative abundance of all demersal and target species, particularly in the vessel control and high-exposure zones, was driven by the numerically dominant species *Lethrinus punctulatus*, *Lutjanus sebae*, and *Lutjanus vitta* (*SI Appendix*, Fig. S21).

Data from a total of 418 BRUVS deployments were included within the MBACI models. Of these, 269 were spread across seven sets of deployments in control zones, and 149 were spread across four sets of deployments in exposure zones over five sampling periods. There was no evidence for a significant decline in the relative abundance of any species or group of fishes in the high-exposure zone re control zones following exposure to the seismic source. There were no changes in the abundance of the entire assemblage, in combined species targeted by commercial fisheries or key families of commercial importance (Lutjanidae, Lethrinidae, and Epinephelidae), after exposure to the seismic source (Fig. 3). Analysis of individual species that were abundant and/or targets of commercial fishing also showed no significant declines in abundance (Fig. 3). There was a trend of a slight increase in abundance of all species combined and all target species in the high-exposure zone following exposure to the seismic source. There was either no change in abundance at the level of families or species or small, nonsignificant trends indicating either increases or declines following exposure. Analyses of all demersal and target species had the highest power to detect a change in relative abundance (*SI Appendix*, Fig. S26). Analyses of these two categories had >70% probability of detecting an effect size of a 40% change in relative abundance. At the level of species, the analysis of *Abalistes stellatus* had the greatest power to detect a change in relative abundance, which was >80% probability to detect a 50% change. In comparison, *L. sebae* had slightly lower power, with an 80% probability to detect a 60% change (*SI Appendix*, Fig. S27). Our dose-dependent analysis also found no significant trend in the abundance of fishes with increasing distance from the seismic source (Fig. 4). Overall, there was a slight, nonsignificant trend of increasing abundance with increasing exposure for commercially targeted species.

There was no consistent change in the mean sizes of species that were abundant and valuable targets of the commercial fishery (*L. punctulatus*, *L. sebae*, *L. vitta*, *Epinephelus areolatus*, *Epinephelus multinotatus*, and *Plectropomus maculatus*) following exposure to the seismic source (Fig. 3). The sizes of two species were nearly identical before and after exposure, whereas three showed a small trend to larger size (<2 cm on average) (*SI Appendix*, Fig. S29). There was also no change in time to first feeding on BRUVS baits by the commercially important and/or abundant species *Nemipterus furcosus*, *A. stellatus*, *L. punctulatus*, *L. sebae*, *L. vitta*, *E. areolatus*, *E. multinotatus*, *Argyrops notialis*, and *P. maculatus* or any change in

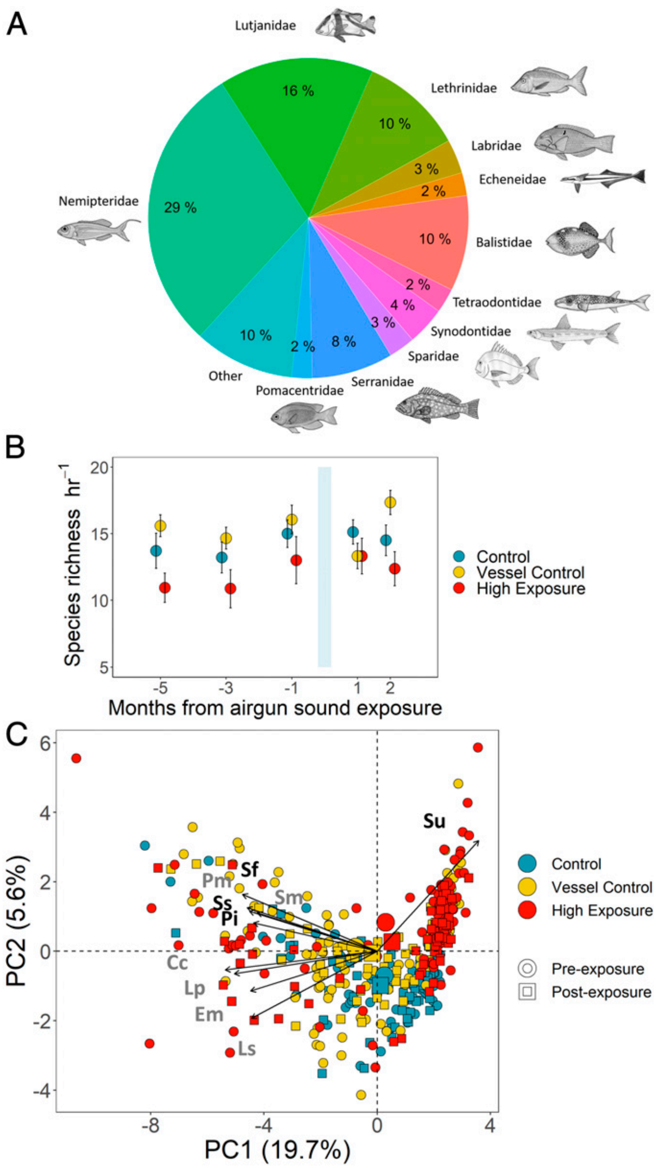

Fig. 2. (*A*) Proportional abundance of demersal fish families observed on all BRUVS surveys. (*B*) Mean number of species (± SE) seen per hour on BRUVS videos in each seismic exposure zone by sampling survey. Light blue bar denotes the period when seismic exposure occurred. (*C*) Biplot of PCA on PC1 and PC2 of the abundance of demersal fishes occurring in 5% or more of BRUVS deployments. Preexposure includes data from sampling surveys 1 to 3 before the seismic source exposure; postexposure includes data from sampling surveys 4 and 5 after the seismic source exposure. The top 10 contributing species are shown, including the following: Su = *Saurida undosquamis*, Sf = *Sufflamen fraenatum*, Sm = *Scolopsis monogramma*, Pm = *P. maculatus*, Ss = *Scarus sp3* (yet to be formally named *Scarus hutchinsi*), Pi = *Parupeneus indicus*, Cc = *Choerodon cauteroma*, Lp = *L. punctulatus*, Em = *E. multinotatus*, and Ls = *L. sebae*. Initials of commercially important species are in gray font.

the distance that *L. punctulatus*, *L. sebae*, *L. vitta*, *E. areolatus*, *E. multinotatus*, and *P. maculatus* were likely to approach the BRUVS following exposure to the seismic source (Fig. 5). In all cases, changes in mean range averaged <0.5 m within the ~10-m field of view of the cameras (depending on water visibility) (Fig. 5). There was also no change after exposure in the likelihood of feeding on the bait bag of the BRUVS by the species *L. vitta*, *E. areolatus*, *E. multinotatus*, and *A. notialis* (Fig. 5).

Tagging. In June 2018, 151 and 146 *L. sebae* were captured, tagged, and released in the high-exposure zone and vessel control zone arrays, respectively. A further 45 fish were captured, tagged, and released in each array in August 2018. Of these, ~57% were detected by our receivers, providing over four million detections. The number of tagged fish retained for analysis (*SI Appendix*) was greatest in the high-exposure array, with 35% of individuals providing patterns of detections consistent with tags inside living fish, compared with 22% of individuals in the vessel control array.

Individual *L. sebae* tagged with acoustic transmitters stayed in the high-exposure and vessel control zones, with no evidence of any long-term displacement during or following the seismic source exposure (Fig. 6 and *SI Appendix*, Figs. S32 and S33). Indeed, most *L. sebae* generally remained within 0.15 km^2 of their first detection in the high-exposure and vessel control zones (Fig. 6).

Discussion

Multiple lines of evidence from our study suggested that seismic surveys have little to no impact on the composition, abundance, behavior, and movement of demersal fishes in the coastal shelf environment off northwestern Australia. The community structure and species richness of fishes sampled by BRUVS was comparable before and after the seismic source exposure, and we did not detect any changes in abundance (as measured by MaxN, the maximum number of a species seen on a video at any point) of all demersal fishes combined or when data were grouped into species targeted by commercial fisheries, families, or individual species that were either very abundant or relatively high-value targets of commercial catches.

Our study focused on a tropical shelf environment within a depth range of 50 to 70 m, where habitats are patchy at multiple spatial scales. In this system, the fishery targets a very diverse range of species; none of which exclusively dominates catches (7). This contrasts to temperate environments, where fisheries usually target one or two species that overwhelmingly dominate species abundance curves or focus on times and places such as spawning sites, where single species aggregate predictably and can be captured with greatest efficiency. Because of the multispecies nature of the fish catch and the sparse distribution of habitat, our principal aim in this study was to examine evidence for impacts of seismic surveys in the assemblage rather than the responses of a few abundant species. The latter scenario has typically been the focus of studies of impacts of seismic surveys on the behavior and abundance of fishes in temperate waters (*SI Appendix*, Table S1).

Our MBACI analyses of data grouped into all species, or all target species, had appropriate levels of power for this task, despite the relatively high spatial and temporal variability in abundance data we observed, even in the absence of any impacts (*SI Appendix*). We had >70% chance of detecting a 40% change and a >90% chance of detecting a 50% change in abundance for all species combined and all target species combined. Despite our focus on assemblages, we still retained sufficient power in the MBACI analyses to reliably detect major changes in the abundance of one of the key species targeted by the fishery, *L. punctulatus* (77% chance of detecting a 50% change), and a species that was abundant as bycatch, *A. stellatus* (92% chance of detecting a 50% change). Importantly, we found no consistent trend of lower abundance in the high-exposure zone following the exposure in individual families or species for which the experimental design had less power to detect change.

Similar to the results of the MBACI analysis, we found no changes in abundance when data were analyzed in a dose–response experimental design re any acoustic metric of the seismic signal. Again, there was a slight positive, albeit nonsignificant, trend in relative abundances of species that were targets of commercial fishing, with increasing exposure to the seismic source.

Our MBACI analyses did not detect any major change in the size–frequency distributions of six species of commercial importance

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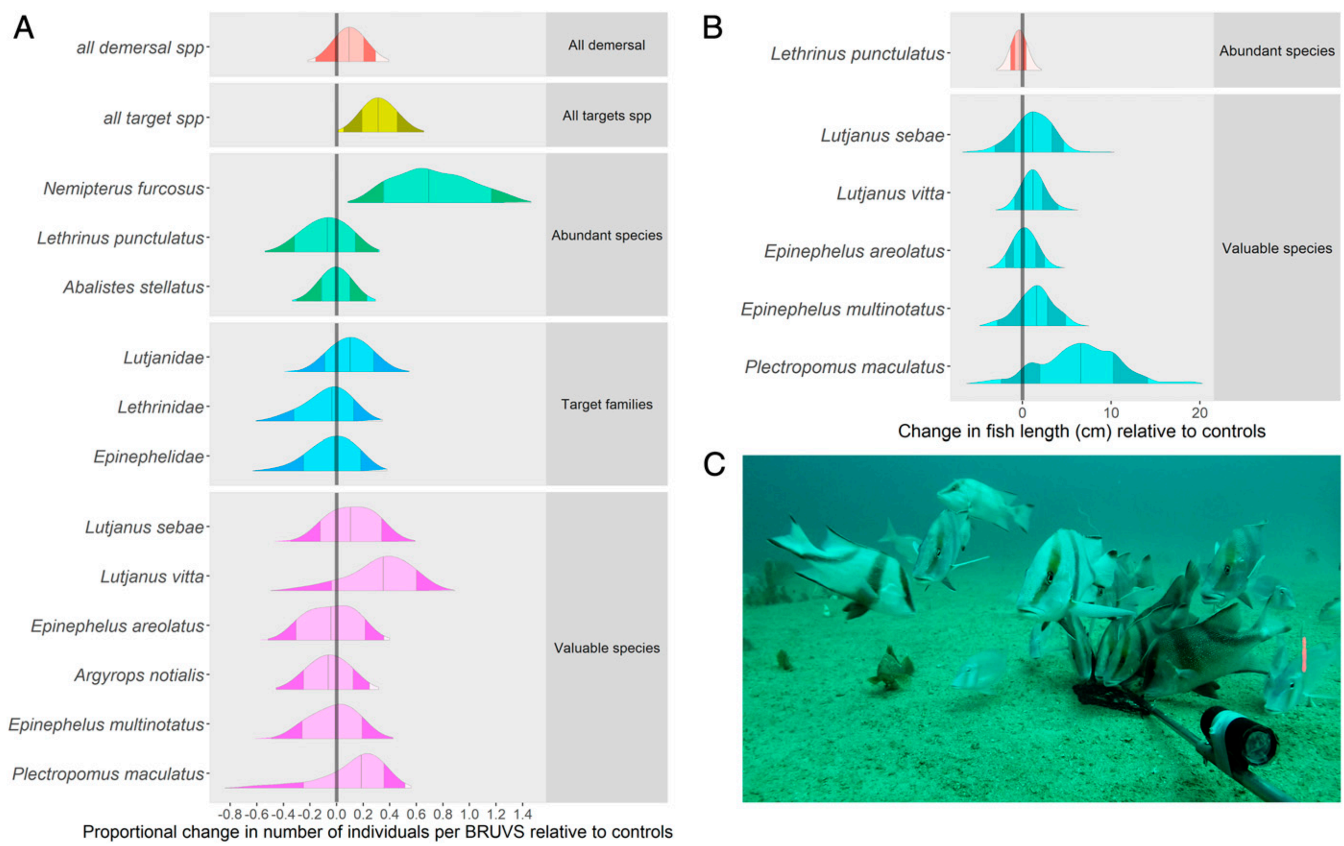

Fig. 3. Comparison of the abundance of demersal fishes in high-exposure and control zones following exposure to the seismic source. (*A*) MBACI posterior distribution plots of all demersal fishes recorded on BRUVS, all species targeted by commercial fisheries, families of commercial importance, and individual species that were of high commercial value and/or abundant. A shift in a distribution above zero (black vertical line) indicates an increase in relative abundance in the high-exposure zone compared with control zones, whereas a shift below zero indicates a decline in relative abundance in the high-exposure zone compared with control zones after seismic exposure. (*B*) MBACI posterior distribution plots for length of target species observed on BRUVS. A shift in the distribution above zero (black vertical line) indicates an increase in fish length in the high-exposure zone compared with control zones, whereas a shift below zero indicates a decline in fish length in the high-exposure zone compared with control zones. (*C*) An image captured from a BRUVS video showing a school of *L. sebae* and surrounding habitat.

following exposure to the seismic source. The sizes of two species were nearly identical before and after exposure, whereas three showed a small trend to a larger size (<2 cm on average). For all species, BRUVS videos were dominated by adult-size classes that are targeted by fisheries, although the technique tends to sample individuals of a wider range of sizes than commercial fish traps (8).

We argue that it is a reasonable assumption that the behavioral responses of demersal fishes to the bait cue provided by the BRUVS are a realistic proxy of the likely response of these species to baited hooks or traps (8). There was little evidence that exposure to the seismic source altered the behaviors of demersal fishes in response to the presence of BRUVS. We found no major changes in time to first feeding for any abundant or key species of commercial importance, with some showing a small decline in time and others a small increase following exposure. We also found no evidence for a change in mean distance from the cameras of six species of commercial importance, although there was a trend for *E. areolatus* and *P. maculatus* to be closer to the bait bag after exposure. In all cases, changes in mean range averaged <0.5 m within a field of view of the cameras of 10 m (depending on water visibility). Given these results, it seems unlikely that exposure to the seismic source would affect the likelihood of capture by hook and line or in baited trap fisheries.

Fishes can show immediate behavioral reactions (startle reflex, schooling, flight, etc.) (e.g., refs. 5, 9, and 10) to seismic surveys or airguns (9, 11–13), although these responses can be inconsistent (14), and some species appear to habituate rapidly (15, 16). If these behaviors did take place in our study, they had no measurable short- (days to weeks) to long-term (months) impacts on abundance or the behavior of demersal fishes in our experimental area.

Consistent with our results from the BRUVS surveys, acoustic telemetry found little evidence that *L. sebae* was displaced by the exposure to the seismic source. Movements of these fish occurred over a limited area focused on two or three receivers, and there was no evidence for the departure of tagged fish after exposure. Other acoustic tagging studies also show that fishes of the same family, such as the Gulf red snapper (*Lutjanus campechanus*), can show strong site fidelity, with individuals of this species residing on artificial structures and single reefs for periods of weeks to months (17). BRUVS provided further supporting evidence of strong site fidelity in *L. sebae*, with a very consistent pattern in the sightings of this species in deployments across sites within zones during the many months of surveys (*SI Appendix*, Figs. S22 and S23). This result showed that there were predictable patterns in the distribution of this and other species (*SI Appendix*, Figs. S23–S25) of commercial importance over time that were most likely driven by the sparse distribution of reef-like or benthic habitats (<2% observed on BRUVS) that provide a suitable habitat for these demersal fishes (*SI Appendix*, Fig. S3).

We recorded high rates of mortality of tagged fish (~33% of fish detected), which is typical of acoustic telemetry studies, particularly when fish are caught in deeper water (18–22). In many

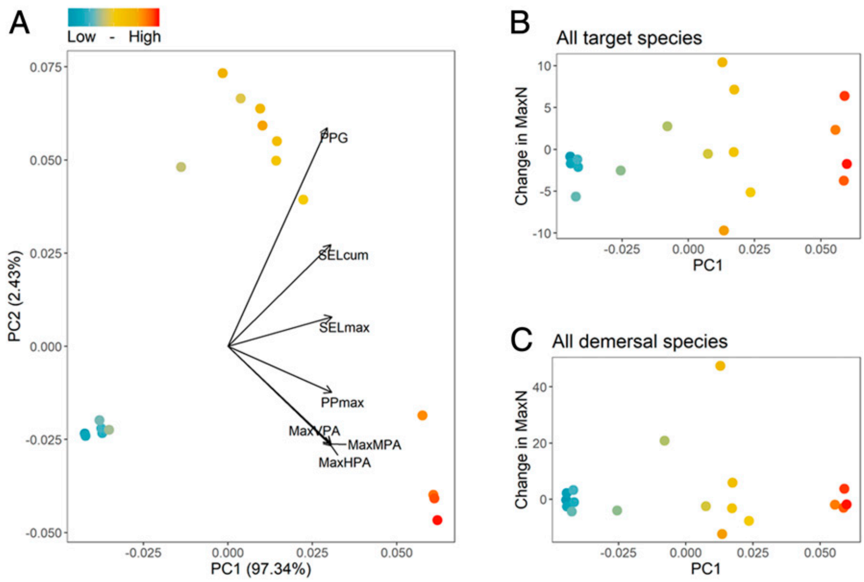

Fig. 4. The relationship between sound metrics and the abundance of fishes that received different levels of seismic exposure. (*A*) PCA plot of various seismic exposure metrics including: the maximum horizontal, vertical, and magnitude components of particle acceleration (MaxHPA, MaxVPA, and MaxMPA, respectively); maximum and cumulative sound exposure levels (SELmax and SELcum, respectively) and maximum peak to pressure levels (PPmax); and one relating to the peak pressure gradient (i.e. the maximum rate of change in acoustic pressure; PPG), overlaid with BRUVS sampling sites (dots) color coded by level of exposure metric from low to high (see color bar). (*B* and *C*) The relationship between combined seismic exposure metrics (PC1) and the change in relative abundance (MaxN) between pre- and postseismic exposure for species targeted by fishing (*B*) and all demersal species (*C*) at each sampling site. Sites are color coded by the level of combined seismic exposure metrics (PC1) (see color bar).

cases, this mortality was likely the result of predation. Fish consumed by predators displayed a distinctive pattern of detections across many receivers from 2 to 7 d after tagging, followed by detection on only a single receiver, implying that after consumption by a wide-ranging predator, such as a shark, the tag had then passed through the gut and had not moved from where it had been deposited on the seafloor (23) (*SI Appendix*, Fig. S14). Despite these losses, we retained enough tagged fish in vessel control ($n = 23$) and high-exposure zones ($n = 43$) to adequately characterize movement patterns of the target species in response to the seismic source.

Measurements of the exposure levels experienced by fishes, together with source modeling of the airgun array signature and sound PL, confirmed that demersal fishes in our experiment experienced exposure to a seismic source that was as close as possible to industry surveys operating in similar water depths (24–26) and included energy at frequencies detectable by almost all fishes that are capable of hearing (27). PLs from the survey through the experimental area conformed to our initial modeling and mapping study and were typical of environments with similar water depths (50 to 70 m), uniform bathymetry, and seafloor composition of a thin layer of sand over limestone pavement (26) and were thus representative of shelf waters off Australia's northwest coast. A lack of directionality in the airgun array source, combined with the comparatively uniform depth and seafloor structure, allowed the calculation of reliable estimates of exposure levels.

We argue that it is unlikely that other, earlier seismic surveys in the general region of our study area may have influenced our results (*SI Appendix*, Fig. S2). With the exception of one survey that occurred 6 y before our experiment (*SI Appendix*, Fig. S2*D*), all of this activity took place more than 10 y prior to our work. This most recent survey overlapped one set of BRUVS sampling sites in the control location, but the majority of other sites were over 10 km from the survey boundary. At these distances, none of the study species would have experienced more than a temporary shift in hearing thresholds, and most study sites would have received noise levels similar to or less than those emitted by passing vessels. Furthermore, if any impacts had occurred, the interval between this recent survey and our experiment was sufficient for considerable population turnover in our study species [generation times of *L. sebae* are estimated to be ∼7 y (28)] and the immigration of multiple, new age classes of many fishes [e.g., *L punctulatus* (29)] into the study area from shallow, inshore nursery habitats that have never been subjected to seismic operations.

In addition to the large spatial scale and use of a dedicated seismic vessel to apply the experimental treatment, the relatively sedentary and demersal nature of the fishes we studied may account for the consistency of our results in comparison with the outcomes of earlier work. The extension of our approach to more mobile and pelagic species presents a significant logistic challenge, as shown by an earlier study of small sharks and epibenthic species that was hampered by the departure of tagged fish prior to experimental treatments (14). Sonar surveys offer an alternative, nondestructive means to monitor the abundances of mobile and midwater fishes; however, these must sample at large scales commensurate with the movement patterns of target species, and will require very high levels of replication because of the inherently patchy distributions of schooling fishes. Determining the impacts of seismic surveys on sessile fauna, such as shellfish (30), awaits targeted experimental studies that more closely mimic real-world conditions.

Our study shows that careful experimental design and the use of appropriate sampling techniques can provide robust data to answer key questions about the effects of seismic surveys on the demersal fish assemblages of coastal shelf waters. Given similar physical environments (notably water depths) and life history stages, it is likely that our results are applicable to other locations and species of the same families of fishes; many of which form an important part of the fauna targeted for food in coastal and reef environments across tropical and subtropical regions. Our results may allay, to some extent, the concerns frequently voiced by commercial fishing stakeholders over the negative impacts of seismic surveys on catches of demersal fishes in this environment, at least for the suite of site-attached species that were the subject of our study.

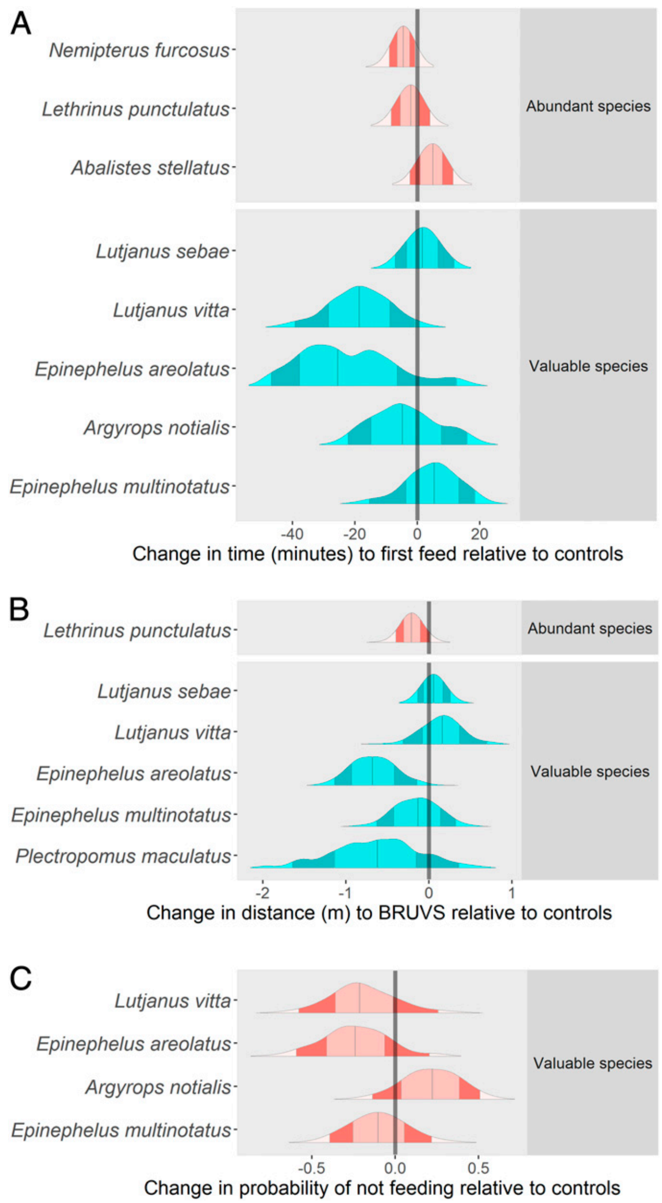

Fig. 5. Comparison of behaviors of demersal fishes in high-exposure and control zones following exposure to the seismic source. (*A*) MBACI posterior distribution plots for the change in time (minutes) to the first feeding of selected species on the BRUVS baits following seismic exposure. A shift in a distribution above zero (black vertical line) indicates an increase in time to the first feeding in the high-exposure zone compared with control zones, whereas a shift below zero indicates a decline in time to the first feeding in the high-exposure zone compared with control zones after seismic exposure. (*B*) MBACI posterior distribution plots for the change in the range (or distance to the BRUVS) of selected species following seismic exposure. A shift in a distribution above zero (black vertical line) indicates an increase in range to the BRUVS in the high-exposure zone compared with control zones, whereas a shift below zero indicates a decline in range to the BRUVS in the high-exposure zone compared with control zones after seismic exposure. (*C*) MBACI posterior distribution plots for the probability of selected species not feeding on BRUVS baits following seismic exposure. A shift in a distribution above zero (black vertical line) indicates an increase in the probability of not feeding in the high-exposure zone compared with control zones, whereas a shift below zero indicates a decline in probability of not feeding in the high-exposure zone compared with control zones.

Materials and Methods

Experimental Design. Our experiment was conducted from April 4 to December 15, 2018, within the "Area 3" fishery management zone of the Pilbara Fish Trawl Fishery, ~90 km north of Point Samson, and off Western Australia's Pilbara coast (Fig. 1). The area, covering ~2,500 km^2 of gently sloping seabed from 50 m in the south to 80-m depths in the north, has been closed to fishing since 1998 and, because of the distance from shore, is subject to little recreational fishing. The area is of similar environment (depth, habitat, and biogeography) to adjacent and nearby commercial trap and trawl fishery zones. The most recent seismic survey in this region occurred 6 y prior to our experiment and covered only the northernmost part of the experimental area. The remainder of the area (including treatment zones) had not been subjected to a seismic survey in over a decade (*SI Appendix*, Fig. S2). Previous studies using nonextractive techniques (8) indicated the presence of high densities of fishes targeted by commercial fisheries, particularly red emperor (*L. sebae*) and their preferred habitat. Placement of the experiment within this management zone ensured results would not be confounded by the capture and removal of fishes by any commercial fishery.

We used a combination of MBACI and dose–response experimental designs (31) to monitor fishes within high-exposure (impact) and control sampling zones and at multiple sites that experienced varying levels of exposure to the seismic source within Area 3 (Fig. 1). In April 2018, multibeam sonar, sediment grab samples, and video transects documented the seafloor habitat (Fig. 1 and *SI Appendix*, Fig. S3). The 100-kHz operating frequency of the multibeam survey was significantly higher than the hearing thresholds reported for most fishes (32), including *L. sebae*, and was not expected to impact fish behaviors. A single airgun and the passive acoustic monitoring (PAM) of pressure (33), particle velocity, and ground motion sensors characterized PL in the study area (*SI Appendix*, Figs. S4, S16, and S17). PLs across the experimental area were confirmed following protocols developed by McCauley et al. (5, 6) and were then used to determine the required distances between the high-exposure, vessel control, and control zones and estimate the distances from the seismic lines at which fishes would experience given exposure levels for the dose–response model. Three parts of the study area were identified that met habitat and dimension criteria to be suitable sampling zones in the MBACI design (*SI Appendix*, Fig. S3). Suitable habitats at distances expected to experience medium and low exposures were uncommon but present, and sampling sites were grouped at similar distances from the seismic source to provide multiple replicates receiving similar exposures.

Exposure to the three-dimensional seismic source occurred over 5 d in September 2018 using a commercial seismic vessel, the *BGP Explorer*, equipped with two 2,600-in^3 (41.6l, comprising 10 Sercel G Gun II) airgun arrays operated at 2,000 psi (13.8 MPa). The *BGP Explorer* sailed a racetrack pattern with eight operational (high exposure) and eight inactive (vessel control) sail lines, with 500-m sequential line separation and 12.5-m shot point spacing, creating two sampling zones separated by 36 km (Fig. 1 and *SI Appendix*, Fig. S3). During the exposure, PAM sensors were deployed at 19 locations of differing range from the seismic sail lines, providing ~70,000 measurements of airgun signals, from which PLs were verified and updated (Fig. 1). All analyses used purpose-built software run in MATLAB (https://www.mathworks.com). We followed standard protocols to characterize the received airgun pressure signals in several acoustic metrics (5, 34). For impulsive signals, such as those generated by the airguns being discharged, the most common is the SEL, a measure of peak level (5). For brevity, and as no response by fishes to any exposure level was observed, details are only provided for SELs [*SI Appendix*, see McCauley et al. (6) for further details on all acoustic components of the seismic noise]. Modeling techniques estimated maximum levels for every time the array was discharged and cumulative SELs for each sail line and the total survey, as they would be received by each sampling site.

Sampling cruises to monitor fishes were conducted 5, 3, and 1 mo before and then 1 and 2 mo after exposure to the seismic source. The MBACI sampling design provided a binary comparison between exposed and control zones (vessel control and control samples were pooled for analysis). The potential impact of exposure was measured as the difference in the response variable (e.g., abundance and length) before and after the seismic source exposure at a high-exposure (impact) zone, compared with the difference in the variable before and after the exposure at the vessel control and control zones (31). To demonstrate an impact, there must be statistical evidence for a significant difference in the measured variable between the high-exposure and control zones, after accounting for natural variability through time. To understand how responses varied with differing levels of exposure, we also sampled in zones that received different levels of exposure to the seismic source (high, medium, low, vessel control, and control), providing a dose–response experimental design for analysis (35).

The experiment examined the impacts of exposure to a seismic source on assemblages and individual species of demersal fishes (*SI Appendix*, Table S2).

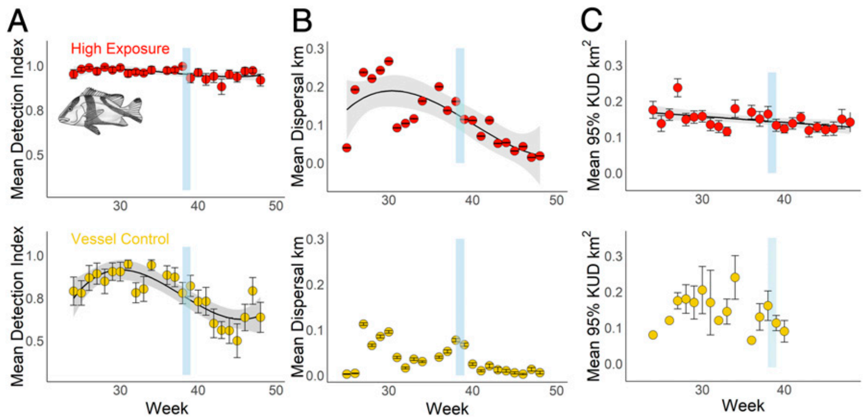

Fig. 6. Detection metrics of tagged *L. sebae*. (*A*) Mean detection index (± SE). (*B*) Mean consecutive dispersal (± SE). (*C*) Mean 95% (± SE) KUDs per week for tagged fish in receiver arrays in the high-exposure (*Top*, $n = 43$ individuals) and the vessel control (*Bottom*, $n = 23$ individuals) zones. The light blue bar in each panel denotes timing of the seismic exposure. Lines show significant linear or polynomial regressions fitted to the data (*SI Appendix*, *Materials and Methods*).

We aimed to determine whether there had been a measurable change in the abundance of all demersal species, all demersal species that are targets of commercial fisheries, and in the abundance of three families of fishes (Lethrinidae, Lutjanidae, and Epinephelidae) of commercial importance (7). Additionally, we aimed to determine if there had been changes in the number, size, and behavior of individual species that were of commercial importance and/or relatively abundant (*SI Appendix*, Table S2). Because of logistics and cost, only *L. sebae* was selected for acoustic tagging. This species is a broadly distributed, high-value target of commercial (7) and recreational fisheries, abundant within the study area, resilient to capture from depth, and brief housing in tanks before release at depth (36), site attached with a limited home range [based on anecdotal evidence from previous studies and commercial fishers (37)], which reduced the likelihood of dispersal into areas subject to commercial fishing beyond the boundary of the study. The species is a member of a family of fishes (Lutjanidae) likely to be sensitive to sound in the environment (36).

We sampled the fish assemblages for composition, relative abundance, size, and behavior using stereo BRUVSs, a fishery-independent, nonextractive technique that facilitated repeated sampling of the same sites. Over the five sampling surveys, we deployed a total of 629 BRUVS at 144 sampling sites in water depths of 60 to 70 m to document changes in demersal fish assemblages as a result of the exposure (Fig. 1). BRUVS were deployed during daylight hours, separated by 400 m, and set to record for ∼1 h. Totals of 24 or 32 BRUVS (grouped into three or four sets of eight) were deployed in the control, vessel control, and high-exposure zones on each sampling occasion, six sets of eight in the medium-exposure zone and one set of eight in the low-exposure zone over 5-d periods (Fig. 1*D*). The initial positions of deployments were allocated randomly within habitats found within each zone and redeployments occurred in approximately the same location in following surveys (*SI Appendix*).

Principal components analysis (PCA) was used to assess whether there was an effect of the seismic source on the assemblage structure of fishes. A biplot was constructed from the PCA to illustrate the pre- and postexposure structure by zone and run in the statistical program R (38) using the base function *prcomp*. Permutational multivariate ANOVA+ using Primer (39) tested whether there had been a change in assemblage structure pre- versus postseismic exposure using the MBACI design. This analysis included all demersal species that occurred in 5% or more of deployments and used a Bray–Curtis similarity matrix based on square root–transformed, relative abundance data. We structured our model by treating replicates nested in sets as random effects and by fitting an interaction term with the fixed effects control versus impact and before versus after. This analysis was run over 9,999 permutations. A P value of ≤ 0.05 was deemed to indicate a significant change in fish assemblage structure.

The average number of species per hour was calculated for each BACI zone and through time. The number of new species encountered per deployment was used as a measure of how efficient our sampling had been at capturing species richness present within each zone, presented as a species accumulation curve, in which an asymptote implied that sampling has adequately captured species richness (*SI Appendix*, Fig. S19).

Fish abundance data were recorded using the metric MaxN, the maximum number of a species seen on a video at any point per deployment (8), extracted using EventMeasure (https://www.seagis.com.au). Relative abundances (MaxN) were standardized to the soak time (1 h per deployment) to produce a rate of fish sightings per hour of soak time (MaxN h^{-1}). Abundance data were modeled using combined MaxN h^{-1} for each analysis group using the R package "Epower" (31) that implements a generalized Bayesian hierarchical-mixed MBACI analysis based on Laplace approximation via the integrated nested Laplace approximation (INLA) package (40). Epower provides a convenient means of specifying all elements of an MBACI design and provides an associated power analysis specifically for the BACI interaction term (31). Assessment of an impact is achieved by comparing two fitted Bayesian-generalized, linear-mixed models (one with and one without the BACI interaction term), with evaluation of the strength of evidence of a BACI interaction effect based on the posterior model probability of one model compared with the other. In this approach, a probability ratio of >0.5 provides more support for the BACI interaction model over a model with only the two noninteracting fixed effects (31). Further details of the models and formulae used in the analysis through Epower are provided in *SI Appendix*.

A Poisson distribution was used as the family for the abundance response and was found to have equal or better fits to the data, compared with a negative binomial. For all BACI analyses, probability integral transform (PIT) value plots were assessed for each model, such that a uniform distribution was expected if the model was appropriate for the data (31). A hierarchical model based on the sampling design was fitted. The best hierarchical structure was determined to be BRUVS deployment locations nested within sets. Thus, we had seven sets of BRUVS at the control area (three at the control zone and four at the vessel control zone) and four sets at the high-exposure zone, with each set containing eight BRUVS replicates (*SI Appendix*, Fig. S6). As this structure had the highest power to detect change and yielded more robust model fits (according to PIT histograms), this was also maintained for subsequent MBACI analyses of fish length and behavior. Posterior distribution plots were built using a posterior sample of 200, extracted using the posterior sample function in INLA (40) that provides a Laplace approximation of the posterior from the fitted model. Epower was also used to calculate power of the analysis to identify a range of effect sizes (0, 10, 20, 30, 40, 50, and 60% declines) on the relative abundance of the target species, the three genera, all target species, and all demersal species.

Relative Abundance Dose–Response Analysis. We used a range of approaches to account for uncertainty in deriving dose–response relationships for the potential effects of seismic exposure on targeted fish abundance, based on estimates of the probability of a decline in fish abundance (*SI Appendix*). Our approach to develop dose–response relationships involved calculating a change in fish abundance for each BRUVS set (four high-, six medium-, and one low-exposure zone(s) and seven control zones), combining these as dose–response relationships and evaluating these against a range of seismic metrics. Both fish abundance data and acoustic metrics were subjected to the same clustering method used to group deployments through time, based on latitude and longitude. PCA was then run-on acoustic metrics to extract the primary axes (PC1 and PC2). PC1 was used to assess the relationship with change in relative abundance of 1) all target species and 2) all demersal species pre- and postseismic exposure. The PCA was run in R using the base package function *prcomp*.

MBACI Analysis of Size Structures and Behavior. Size measurements were recorded for *L. punctulatus*, *E. areolatus*, *E. multinotatus*, *L. vitta*, *P. maculatus*, and *L. sebae* at the time of MaxN for each species, when possible (fish at oblique angles to the camera could not be measured accurately). Fork length measurements (tip of snout to caudal fork) for each individual were made on screen for each of the two cameras using the EventMeasure software. We only kept measurements that had a rms error below 20, as determined by the software. The lengths of the six species were analyzed using the same MBACI framework as described for abundance (*SI Appendix*) to assess whether there had been a change in mean size of each species using the Epower package (as described for abundance in *Experimental Design*). Size models were fitted using a gamma distribution with a log link, as they were continuous variables on a scale of 0+ to infinity. Here, we assumed that fish size was independent (i.e., fishes did not aggregate by size classes).

Three behavioral metrics were extracted from BRUVS videos and compared before and after the seismic exposure using the same MBACI analysis framework: 1) the time taken for individuals of each species to begin feeding on the bait bag; 2) changes in the mean distance ("range") of fish from the BRUVS; and 3) the probability of fish feeding on the bait bag. These metrics were included in our analyses as any changes in whether a species fed or not, the time it took to feed, and the distance the fish maintained to the BRUVS could all be related to the potential opportunity for a catch in a fishery. The time of first feeding analysis only included fish that were present and fed on the bait bag in each BRUVS deployment, whereas the range analysis could only be applied to those six species whose length of individuals was measured in the BRUVS videos. Range was modeled using the methods described for abundance in *Experimental Design*, then fitted using a gamma distribution with a log link, as this was a continuous, positive variable. As time to first feeding was bounded by the maximum soak time of the BRUVS deployments, this was modeled using a beta with logit link function. The probability of feeding analysis made use of a binomial dataset (fed = 1 and not fed = 0). If fish were not present on the video at all, they were labeled "NA" and omitted from this analysis. The probability of feeding analysis was modeled using a binomial (or zero inflated binomial) distribution with a logit link.

Tracking Array. To describe the movement patterns of demersal fish in more detail, we deployed two Vemco VR2AR acoustic telemetry-tracking arrays, one in each of the high-exposure and vessel control zones, containing 39 and 37 receivers, respectively. The receivers were separated by ~900 m (distance defined during a range test; *SI Appendix*) in a hexagonal arrangement that covered ~32 km^2 detection range at each zone (Fig. 1). The high-exposure zone array also included an outer ring of 22 receivers, which was designed to detect any movement of tagged fishes out of or into the array (Fig. 1). Sentinel tags and receiver metrics developed by Simpfendorfer et al. (41) were used to assess consistency of receiver performance throughout the duration of the project (*SI Appendix*).

Because of logistics and costs, we selected only one species, *L. sebae*, for acoustic tagging. We followed established protocols for capture and handling of fish and surgical implantation of tags (42). Briefly, fishes were captured using short deployments (3 h) of fish traps (43), slowly brought to the surface, and held in tanks onboard. Healthy fish were anesthetized and a tag inserted into the gut cavity. Fish were allowed at least 2 h of recovery in tanks before being returned to the seabed in the fish trap. Detailed information on tagging procedures can be found in *SI Appendix*. A decision tree was developed to aid the identification and removal of tags of fish that suffered postrelease mortality within the receiver arrays (*SI Appendix*, Fig. S13), following methods outlined by Khan et al. (23), which enabled us to classify potential mortality events (e.g., *SI Appendix*, Fig. S14). After the removal of tags of fish that were suspected to have been eaten or died because of unknown causes, detections of tagged fish were converted to a mean "detection index" per week, which was the total number of days detected divided by seven (https://vinayudyawer.github.io/ATT/docs/ATT_Vignette.html). A score of 0 indicated no detections throughout the week, whereas a score of 1 indicated detections on every day of the week. The detection index was analogous to a residency index, which was the proportion of days detected in the array divided by the total number of days since tagging (44). To investigate diel patterns in residency, we combined hourly detections of individuals at the high-exposure and vessel control zones. The average number of detections for all individuals were calculated per hour, local time (Coordinated Universal Time +8), and we used detections from sentinel tags to correct data for background noise to average the hourly detections of fish (45).

Changes in the spatial patterns of residency were assessed using the metric consecutive dispersal, which was a measure of the distance moved between each detection location. Any tag that had a consistent mean weekly dispersal lower than 0.1 km was removed from the dataset, as this was considered too low to be representative of a tagged fish, based on similar studies of tropical lutjanids and lethrinids (46). Kernel utilization densities (KUDs) were also calculated based on hourly centers of activity (COA) (47). COAs rely on the multiple, simultaneous detections of tag signals; therefore, only tags that had overlapping detections could be included in KUD analyses. Average detection range in the high-exposure zone was >480 m, suggesting that there should be sufficient overlap of detection ranges by receivers to allow the calculation of COAs and resulting KUDs.

Data Availability. Acoustic data, abundance and length data and acoustic tracking data for fish is publicly available from AIMS; see https://apps.aims.gov.au/metadata/view/12f7edac-050f-42b9-9d6b-8eac55d102a1 (48). All other study data are included in the article and/or *SI Appendix*.

ACKNOWLEDGMENTS. AIMS acknowledges the Ngarluma, Yindjibarndi and Kariyarra People as Traditional Owners of Country adjacent to the areas where this study occurred. We recognise these People's ongoing spiritual and physical connection to Country and pay our respects to their Aboriginal Elders past, present and emerging. We acknowledge and thank the crew of the *R.V. Solander*, Jamie Colquhoun, Shaun Hahn, Iain Parnum, Chris Teasdale, Brett Taylor, Josh Baker, Audrey Schlaff, Michael Taylor, Gabby Mitsopoulos, Colby Bignell, Matthew Rees, Neill Roberts, and Simon Spagnol, for assistance with field work. We also thank Iain Parnum, Alaa Mufti, and Simon Spagnol for geophysical data collection and analysis of multibeam sampling. We thank Rachel Przeslawski and Andrew Carroll of GeoScience Australia and anonymous reviewers for constructive comments that improved the manuscript. We also thank Peter Farrell and Michaela Dommisse for project management. This study was conducted as part of Australian Institute of Marine Science's (AIMS) North West Shoals to Shore Research Program and was supported by Santos as part of the company's commitment to better understanding Western Australia's marine environment. Additional funding was provided by Woodside Energy Ltd.

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