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Habitat use and movements of Japanese spiny lobster (*Panulirus japonicus*) in a proposed offshore wind farm area: Implications for the coexistence of offshore wind energy development and coastal fisheries

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ABSTRACT

As Japan accelerates offshore wind farm (OWF) development to achieve carbon neutrality by 2050, it is crucial to understand the impacts of OWFs on local fisheries. To provide baseline data for the assessing these impacts on fisheries, we tracked the movements of Japanese spiny lobsters (*Panulirus japonicus*), a commercially important species, using acoustic telemetry in an area that was designated by the government as a promotion zone for OWF development. Acoustic tags were attached to 23 adult lobsters (CL = 97.9 ± 17.7 mm), which were then released in an isolated rocky reef frequently used by local fishermen as a lobster fishing ground. The tagged lobsters were detected within the reef for 7–97 (mean ± SD = 52 ± 29) days, with five individuals remaining within the reef > 90 days. The duration of home-area occupancy during which lobsters likely occupied the same or adjacent shelters within the reef ranged 2–42 (mean ± SD = 5.7 ± 5.8) days. Movement network analyses revealed that lobsters often relocated shelters both within and between habitat patches, with some traveling over 1-km per night to reach another patch. These findings suggest that if OWF structures function as new habitats for this species, the structures' introduction could alter the lobsters' spatial distribution and movement network. We believe that a comparative approach examining the space use of commercial species before and after OWF development is essential for determining the precise impacts of OWF introduction on local fisheries.

1. Introduction

With the growing demand for renewable energy, the introduction of offshore wind farms (OWFs) is expanding globally (Perveen et al., 2014). Japan's government, aiming to achieve carbon neutrality by 2050 (Prime Minister of Japan and His Cabinet, 2020), is accelerating the adoption of renewable energy sources. Among these energy sources, offshore wind power is positioned as a key energy source for Japan, as the islands that comprise the country are surrounded by rich marine resources. The government has set a target to establish up to 45 GW of offshore wind power projects by 2040 and is leading the development efforts. Ten areas have already been designated as 'promotion zones' for OWF development, with construction underway in four of these zones.

When the construction of an OWF is proposed, it is essential to consider and coordinate the many uses of marine resources for a wide array of end-users. This is especially true of a country like Japan, where local fisheries are prevalent; it is essential to discuss the potential impacts of an OWF and reach a consensus with the local fishermen. A fundamental concept in this process is "cooperativeness with local fisheries," which aims for the coexistence of OWF development and the fisheries (Kiyota, 2022; Roach et al., 2022; Kubo and Kiyota, 2023). Local fisheries are operated using a variety of fishing gear tailored to the target species and the characteristics of the fishing grounds. The introduction of an OWF can be expected to be perceived differently by fishermen depending on what type of fishing gear they use. For example, based on interviews with local fishermen, longliners and anglers may expect an OWF to serve as an artificial reef, while those who engage in set-net fishing near the shore expressed concerns about ensuring

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ecological connectivity between the OWF and the coastal fishing grounds. The coordination between OWF development and local fisheries should thus be tailored to the specific fishing characteristics of each local area.

Several studies in Europe have shown that underwater infrastructure associated with offshore wind turbines (such as wind turbine foundations and scour protection structures) can function as artificial habitats, increasing the abundance of benthic fish and crustaceans around the turbines (Wilhelmsson et al., 2006; Reubens et al., 2013a; Krone et al., 2017; van Hal et al., 2017). On the other hand, high-intensity underwater sounds and vibrations produced during the construction phase, as well as electromagnetic fields (EMFs) generated during the operational phase, may alter or restrict the behavior and movement of marine animals (reviewed in Gill et al., 2020). However, in East Asia, including Japan, only a few studies have examined the responses of commercially important species in tandem with the presence of such offshore wind power facilities (Karama et al., 2021; Mitamura et al., 2022), and thus the impacts of OWF introduction on local fisheries in Japan remain poorly understood.

Knowledge about commercial species spatiotemporal habitat use is essential for determining the distribution and abundance of fishery resources (Heupel et al., 2006; Crossin et al., 2017). This information supports the understanding of the impacts of changes on fisheries before and after the development and installation of energy infrastructure and helps predict the areas and ranges that might be affected beforehand. One of the most effective tools for studying aquatic animal space utilization and movement is acoustic telemetry (Hussey et al., 2015), which has been widely applied in conservation projects for endangered species and those under intense fishing pressure (e.g., Giacalone et al., 2006; Bertelsen and Hornbeck, 2009; Bertelsen, 2013; Giacalone et al., 2015). More recently, this method has been increasingly employed to examine the responses of commercially important species to the presence of marine infrastructure such as OWFs (e.g., Reubens et al., 2013b; Karama et al., 2021; Thatcher et al., 2023; Buyse et al., 2023; Berges et al., 2024). However, most of the current acoustic telemetry studies related to OWFs were conducted only during the operational phase after development. Due to the lack of comparative data obtained before the development of OWFs, it is challenging ascertain how the space use of commercial species inhabiting these areas has been affected by the developments.

In 2023, a corporate entity was selected to implement an offshore wind power generation project in the waters surrounding Enoshima Island in Saikai City, Nagasaki. The OWF to be installed here is a bottom-mounted type which is expected to be introduced and expanded in Japan's coastal waters. A total of 28 wind turbines with an output of 15 MW will be installed around the island. The development area includes fishing grounds for Japanese spiny lobster (*Panulirus japonicus*), and most of the area's local fishermen make their living by conducting bottom-fixed gillnet fishing for this species. Once the wind turbines are introduced, fishing activities in the vicinity of the facility are expected to be restricted due to the presence of submarine power cables and the facility itself. In addition, if the underwater structures of the facility begin to function as new habitats, they may alter the existing commercial species habitat use and movements. Gillnet fishing is a passive fishing method whose effectiveness is closely linked to the target animal's movement (Rudstam et al., 1984), and it is thus essential to compare the movement ecology of the target species before and after development to assess the impact of OWF introduction on the target animal catch (Methratta, 2020). However, in Japan, there is an overwhelming lack of information regarding the movement ecology of commercial species in the coastal areas where the introduction of OWFs is expected, and the coastal areas' existing users, i.e., the local fishermen, have asked that at least preliminary data be obtained before the full-scale introduction of the facilities.

In the present study we tracked Japanese spiny lobsters using acoustic telemetry over a 3-month period (from May to August) in the coastal waters of Enoshima Island, an area designated as a promotion zone for OWF development. The study period was determined to align with the availability of target species and to minimize conflicts with ongoing fishing activities. Palinurid lobsters typically exhibit high site fidelity and are known to be nocturnally active while retreating to shelters during the day; they may regularly relocate their shelters, and they occasionally undertake large-scale movements of several tens of kilometers due to ontogenetic or seasonal factors (Herrnkind, 1980; Childress and Jury, 2006). However, the movement ecology of *P. japonicus* remains poorly understood (Sasaki et al., 2021). Consequently, the current lack of sufficient information on the habitat use and movements of *P. japonicus* makes it difficult to evaluate the potential impacts of OWF installation on lobster fishing, both before and after construction. In addition, as the present study period overlaps with the spawning season for *P. japonicus* (Nakamura, 1994), their movements during this period may be related to reproduction, potentially leading to sex differences in behavior (MacFarlane and Moore, 1986; Waddington et al., 2005; Bertelsen, 2013). Such differences should be considered in future assessments of OWF impacts. The objective of this study was to investigate *P. japonicus* habitat use and movements in the planned OWF development area in order to accumulate pre-development data concerning the coexistence of OWF development and local fisheries. Specifically, we assessed (*i*) the residency of the lobsters in one of the important lobster fishing grounds; and (*ii*) their movement patterns and the connectivity between habitat patches within and around the fishing ground.

2. Materials and methods

2.1. Study site

We conducted the field survey in the coastal waters of Enoshima Island in Saikai City, Nagasaki, Japan (33.000° N 129.329° E) from May to August 2021 (Fig. 1A). The primary fishery in this region is a bottom-fixed gillnet fishery targeting *P. japonicus*, primarily operating on the western and southern sides of the island. The fishery operates year-round except during the closed fishing period (~May 21st–August 20th), which is the reproductive season for *P. japonicus*. In 2023, the waters surrounding Enoshima Island, including the fishing grounds for the gillnet fishery, were designated as a promotion zone for OWF development by Japan's government.

The acoustic monitoring area is located to the southwest of the island, centered on a large rocky reef zone covering approx. 170,000 m^2, consisting of a cluster of flat reefs (Fig. 1B). Surrounding this reef zone were substrates primarily composed of sand, gravel, and smaller rocky outcrops (Suppl. Table S1, Suppl. Fig. S1). The water depth in the monitoring area ranges from 13 m in the east to 33 m in the south. Since the central reef is considered one of the most commonly used lobster fishing grounds in this region, we designated it as the main monitoring area. Hereafter, we refer to the main monitoring area as the central area (CA) and the other area surrounding the CA as the surrounding area (SA).

The SA predominantly consisted of gravel and small rocky reefs, with rougher rocky reefs closer to the eastern shoreline. Between the CA and these rocky areas, sandy substrates were the dominant feature. During the survey period, the rocky reefs within the CA were colonized by soft corals, while several smaller reefs to the northeast were covered with red algae. Most of the rocky reefs in the survey area were flat, with reef heights generally less than 3 m.

2.2. Receiver array design and acoustic monitoring

From May 22 to August 30, 2021, ten acoustic receivers (69 kHz; model VR2Tx, Innovasea, Halifax, Nova Scotia, Canada) were deployed in the main monitoring area (Stns. C1–C10), arranged in a grid of triangles and squares with 200 m spacing between adjacent receivers. An

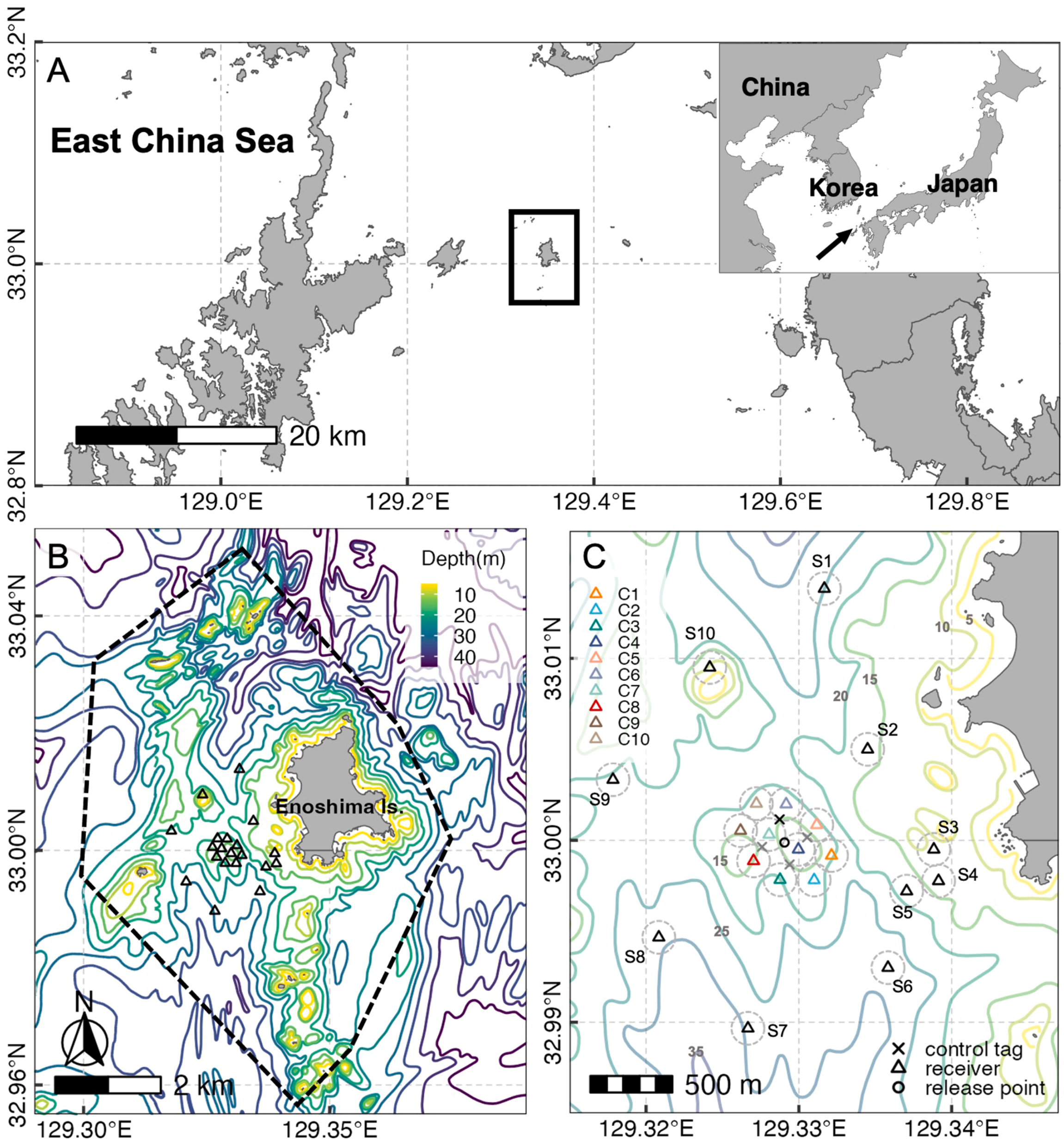

Fig. 1. Survey location and acoustic array. **(A)** The survey was conducted in the coastal area of Enoshima Island that faces the East China Sea. Japanese spiny lobster is one of the most important commercial species in this region. **(B)** The promotion zone of offshore wind farm (OWF) development designated by the Japanese government, and the bathymetry. *Dashed line:* the promotion zone. *Triangles:* acoustic receivers. **(C)** The acoustic array and the station names for each receiver. *Gray dashed circles:* the detection ranges of the receivers. *Black cross:* the control tag used for analyses. *Gray crosses:* the control tags which were lost. *Circle:* the release location. *Triangles:* acoustic receivers; Stns. C1–C10 belong to the central area (CA), and Stns. S1–S10 belong to the surrounding area (SA).

additional ten acoustic receivers (69 kHz; model VR2W, Innovasea) were deployed around the area (Stns. S1–S10) to assess the connectivity between the reef and surrounding habitats (Fig. 1C). Each receiver was wrapped by vinyl tape and attached to the mooring system's rope with the hydrophone directed to the surface, connected to buoys on one end and weights on the other. The receivers were positioned at approx. 1.75 m above the seafloor. The mooring system of the receiver array consisted of a 12-mm-dia. rope, a pressure-resistant buoy with 2-kgf buoyancy, and four sandbags weighing approx. 30 kg each. The survey area includes a route for fishing boats and a ferry. To prevent the monitoring boat from tangling the rope and the system getting lost, all of the mooring systems were designed so that the floats were ≥ 5 m below the sea surface, except for some mooring systems installed in shallower waters.

Four fixed position control tags (Innovasea V9–2H transmitter; 27.5 mm length, 9 mm dia., 4.5 g weight in air and 2.7 g weight in water, 108 days expected battery life, 540- to 660-sec random delay interval, 151-dB power output) were deployed inside the CA array to investigate the influence of distance on the detection probability throughout the survey period (Fig. 1C). To simulate the detection records of the animal tags, the control tags were attached to concrete anchor poles 0.5 m above the seafloor. Due to the loss of three of the tags, data from only one tag was used in the analyses. Detection histories from the control tag during the survey period were used to calculate the hourly detection probability at various distances between the control tag and the receivers. A generalized linear model with a binomial distribution was applied to model the detection probability by distance (Selby et al., 2016). The results indicated that the detection probability at a distance of 100 m between the transmitter and receiver was 18 % during the day and 8 % at night (Suppl. Fig. S2). The detection probability of the control tag appeared to decrease over time, likely due to the accumulation of biofouling and other environmental factors (Suppl. Fig. S3).

During the deployment period of the receiver array, water temperature (°C) was logged hourly and collected from each VR2Tx receiver. The temperature data from each receiver were averaged and used for analysis. Lunar phases were obtained using the *getMoonIllumination* function from the "suncalc" package in R.

2.3. Acoustic tagging

We tagged a total of 23 lobsters in May 2021: 11 males (mean ± SD carapace length [CL] = 103.3 ± 20.8 mm, mean ± SD body weight [BW] = 758.8 ± 359.4 g) and 12 females (CL = 92.9 ± 13.3 mm, BW = 731.7 ± 259 g) (Table 1). Five of the 12 females were egg-bearing at the time of tagging. "Egg-bearing" means a lobster which is carrying eggs attached to its tail. Female lobsters carrying eggs at the time of release are referred to as "berried," while those without eggs are designated as "non-berried." The egg clutches of the lobsters were vividly orange in color and lacked visible eye spots, suggesting that the eggs were in the early to mid-developmental stages (Lewis et al., 2022). The egg-bearing period for the Japanese spiny lobster is estimated to last approximately one month (Inoue and Nonaka, 1963). Therefore, it is likely that their eggs hatched during the study period.

All lobsters were caught in the main monitoring area during the period May 18–20 using gill nets operated by local fishermen. Lobsters were kept for ≤ 10 days in a circulatory tank and tagged with a transmitter the day before their release. During the tagging, lobsters were kept in a shallow tray filled with sea water, allowing them to maintain water flow over their gills (Sasaki et al., 2021). The transmitters used in this study were Innovasea V9–2H coded tags (27.5 mm length, 9 mm dia., 4.5 g weight in air and 2.7 g weight in water, 274 days expected battery life, 60- to 120-sec random delay interval, 151-dB power output) which transmitted coded acoustic signals for identifying each individual.

Each tag was glued onto the lobster's carapace with fast-setting plumber's epoxy resin (Konishi, Osaka, Japan). After the resin had cured, lobsters were acclimated overnight in the tank before being released. All individuals were released by divers on May 23rd at the center of the CA (Fig. 1C).

2.4. Data analyses and statistics

All of the data analyses were conducted in R 4.3.1 (R Core Team, 2023), and the statistical analyses were carried out at the 95 % level of significance. The detection data downloaded from receivers were filtered for false detections using the short-interval criterion. The short-term interval used in this study was calculated based on the minimum delay of tags used, with the methods outlined in Pincock (2012). To minimize potential biases associated with the lobsters' handling (e.g., tagging), the data of the initial 24 hr of detections were removed before the analyses (Farmer and Ault, 2011).

Acoustic detections from each individual were binned every 2 min (i.e., the maximum transmission interval) and labeled with a value of 1 for at least one reception in that time bin and 0 for no reception. All analyses were performed using binned presence/absence binary data. The total duration (TD) was calculated for each lobster as the period for which a lobster was free-ranging from the first detection after 24 hr of release until the tag was detected for the last time. The total duration in the CA (TDC) was also calculated as the period from the first detection after 24 hr post-release until the last day of detection in the CA.

We used the TDC data and a residency index (RI) to calculate the individual lobsters' residency within the CA. The RI was calculated by dividing the total number of days a lobster was detected in the CA by the TDC (Thatcher et al., 2023). The values ranged from 0 (complete absence) to 1 (complete presence) and are presented as the percentage of individuals present/absent in the CA. We also examined the correlation between residency (TDC and RI) and carapace length (CL) in the males and females, respectively.

The location of a lobster's home shelter within the CA was defined as being within the detection range of the receiver that recorded the highest number of detections within a 24-hr period. Given that *P. japonicus* is known to engage in low activity during the day (Sasaki et al., 2021) (and thus fewer detections by receivers), we divided the lobsters' day at noon (i.e., the 24-hr period was from 12:00 p.m. to 11:59 a.m. the following day). If a station with the highest number of individual detections did not change on consecutive days, we assumed that the lobster was likely exhibiting homing behavior to return to shelters in the same general area as the previous day. In this context, the detection range of this receiver was referred to as the "home area." We examined the duration of consecutive days on which each individual

Table 1
Information about the individual Japanese spiny lobsters (*Panulirus japonicus*) (n = 23) that were released on 23rd May 2021.

Lobster ID	CL, mm	BW, g	Sex	Total detections, n	Filtered detections, n	TD, days	TDC, days	RI	Home-area occupancy, days	Last detected station
M01	76.4	430	M	7735	2116	15	15	1.00	6 ± 4	C3
M02	77.5	390	M	2981	2500	38	33	0.85	5 ± 3	S2
M03	81.9	450	M	2538	1945	93	7	1.00	8	S2
M04	83.5	460	M	768	679	67	18	1.00	3 ± 1	S1
M05	94.4	740	M	3153	2716	57	57	1.00	3 ± 1	C3
M06	110.9	1100	M	16,994	14,183	97	97	0.88	14 ± 15	C6
M07	117.3	1300	M	3137	2805	53	51	1.00	7 ± 6	S4
M08	118.1	1200	M	2152	1903	74	41	0.46	9 ± 7	S1
M09	122.2	1550	M	736	624	78	67	0.87	8 ± 8	S2
M10	123.3	1360	M	1362	1142	41	41	1.00	4 ± 2	C6
M11	131.1	1720	M	939	732	28	8	1.00	8	S4
F01	77.3	450	F	2097	1720	70	37	0.97	3 ± 1	S10
F02	77.3	460	F	3418	2828	55	55	0.96	4 ± 3	C10
F03	81.6	460	F	1794	1626	92	92	0.80	5 ± 3	C4
F04	82.7	490	F	4831	4030	57	57	0.91	7 ± 7	C5
F05	96.0	740	F	3607	3249	56	54	0.94	5 ± 5	S8
F06	110.9	1070	F	1439	1231	43	42	0.93	19 ± 0	S5
F07	114.2	1180	F	4121	3537	58	57	0.98	6 ± 5	S2
E01	79.7	480	F (E)	1150	945	99	94	0.71	6 ± 5	S5
E02	90.1	640	F (E)	7252	6100	90	90	0.79	6 ± 5	C7
E03	96.6	880	F (E)	12,401	9705	95	95	0.91	6 ± 9	C7
E04	103.8	940	F (E)	4494	3774	99	12	1.00	3 ± 1	S1
E05	104.6	990	F (E)	1167	964	86	67	0.97	5 ± 5	S1

BW: body weight, CL: carapace length, F (E): egg-bearing female, TD: the total duration across the entire array, RI: residency index, TDC: the total duration in the CA.

used the same home area. Days without any detections were not counted, as the lobsters might have been sheltering or outside the detection range of the CA. We also compared differences in the TDC, RI, and the number of days of home-area occupancy between the males and females, as well as between berried and non-berried females, using the Wilcoxon rank-sum test.

We performed a network analysis to create spatial movement graphs to examine the connectivity and activity hotspots among the lobster habitats. A network analysis is a useful analytical tool that represents animals' spatial use by applying nodes and edges, based on the design of receiver arrays and their detection histories (Jacoby and Freeman, 2016; Whoriskey et al., 2019). This approach, which considers the connectivity of locations, facilitates the simulation, modeling, and intuitive visualization of animal movement interactions (Jacoby et al., 2012). In the present study, we created networks for all males, non-berried females, and berried females, combined separately, as well as for each individual lobster. The network's nodes represented the actual locations of the receivers, and the edges represented the movements of the lobsters between these locations.

To test for network differences between the males and females, we estimated the edge density and the eigenvector centrality from individual networks by using the "igraph" package (Csárdi and Nepusz, 2006; Jacoby et al., 2012). Edge density represents the percentage of available edges observed. Eigenvector centrality is a measure of connectivity and indicates not only the number of direct links a node has but also the relative importance of each node to which it is connected. We averaged the male and female eigenvector centrality values at each receiver (network node) and performed a Wilcoxon signed-rank test to compare differences between the males and females, as well as between berried and non-berried females. We also compared differences in edge density between the males and females, as well as between berried and non-berried females, using the Wilcoxon rank-sum test.

3. Results

A total of 90,266 detections were downloaded from the receivers, with a mean (± SD) of 3924 ± 3942 (range 736–16,994) detections per individual. A total of 88,757 filtered detections were used in the analyses, with a mean (± SD) of 3859 ± 3922 (range 694–16,840) detections per individual (Table 1). On average, an individual lobster was detected by 9.3 ± 2.2 receivers over the entire 3-month study period. The mean bottom water temperature for each month was 19.7 ± 0.1 (range 19.6–20.2) °C in May, 21.3 ± 0.8 (range 19.9–23.4) °C in June, 24.1 ± 0.8 (range 22.2–25.9) °C in July, and 26.2 ± 0.4 (range 25.3–27.3) °C in August (Suppl. Fig. S4).

The mean TD (± SD) was 67 ± 24 (range 15–99) days (Table 1). The mean TDC (± SD) was 52 ± 29 (range 7–97) days. Females tended to spend more time in the CA than males, but this difference was not significant (W = 96.5, p = 0.06). No significant differences in TDC were observed between berried and non-berried females (W = 9, p = 0.19) (Table 1, Fig. 2). The mean RI value (± SD) of the tagged individuals was 0.91 ± 0.13 (range 0.46–1.00), again showing no significant difference between the males and females (W = 42.5, p = 0.15) or between the berried and non-berried females (W = 22, p = 0.53) (Table 1). No significant correlations with CL were observed for the RI or TDC. The timing of detection loss in the CA varied among individuals, showing no synchronization. Additionally, no clear relationship with water temperature or lunar phase was observed.

The diel detection patterns of lobster tags exhibited three distinct trends: (i) higher detection rates during nighttime than daytime, (ii) similar detection rates between day and night, and (iii) higher detection rates during daytime than nighttime (Fig. 3). The pattern of higher daytime detections, also observed in the detection history of the control tag, suggests that environmental factors may affect detection probability (Suppl. Fig. S3). Furthermore, based on Fig. 3, the effect of environmental factors on detection probability appears to vary among receiver stations. For instance, Stns. C6 and C10 showed markedly reduced detection probabilities corresponding to tidal cycles. Consequently, it

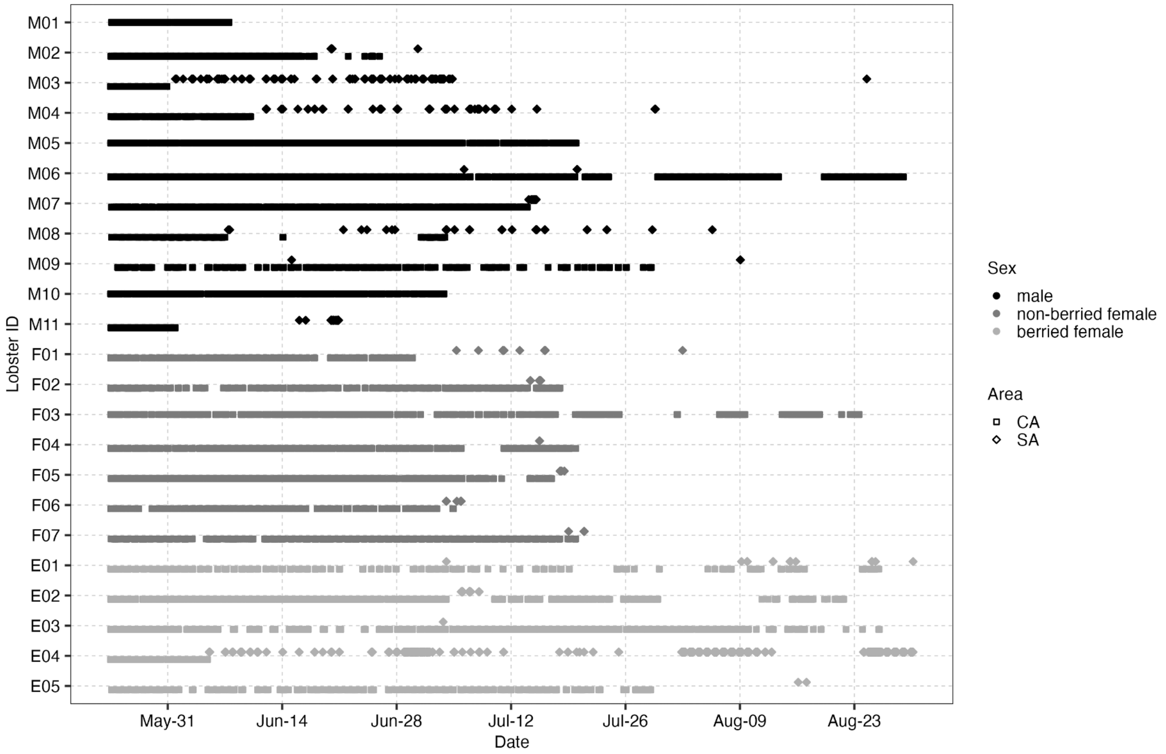

Fig. 2. Abacus plot depicting detections of each tagged lobster colored by sex and presence of egg-bearing (*black:* male, *gray:* non-berried female, *light gray:* berried female). *Squares:* a detection in the CA. *Diamonds:* a detection in the SA.

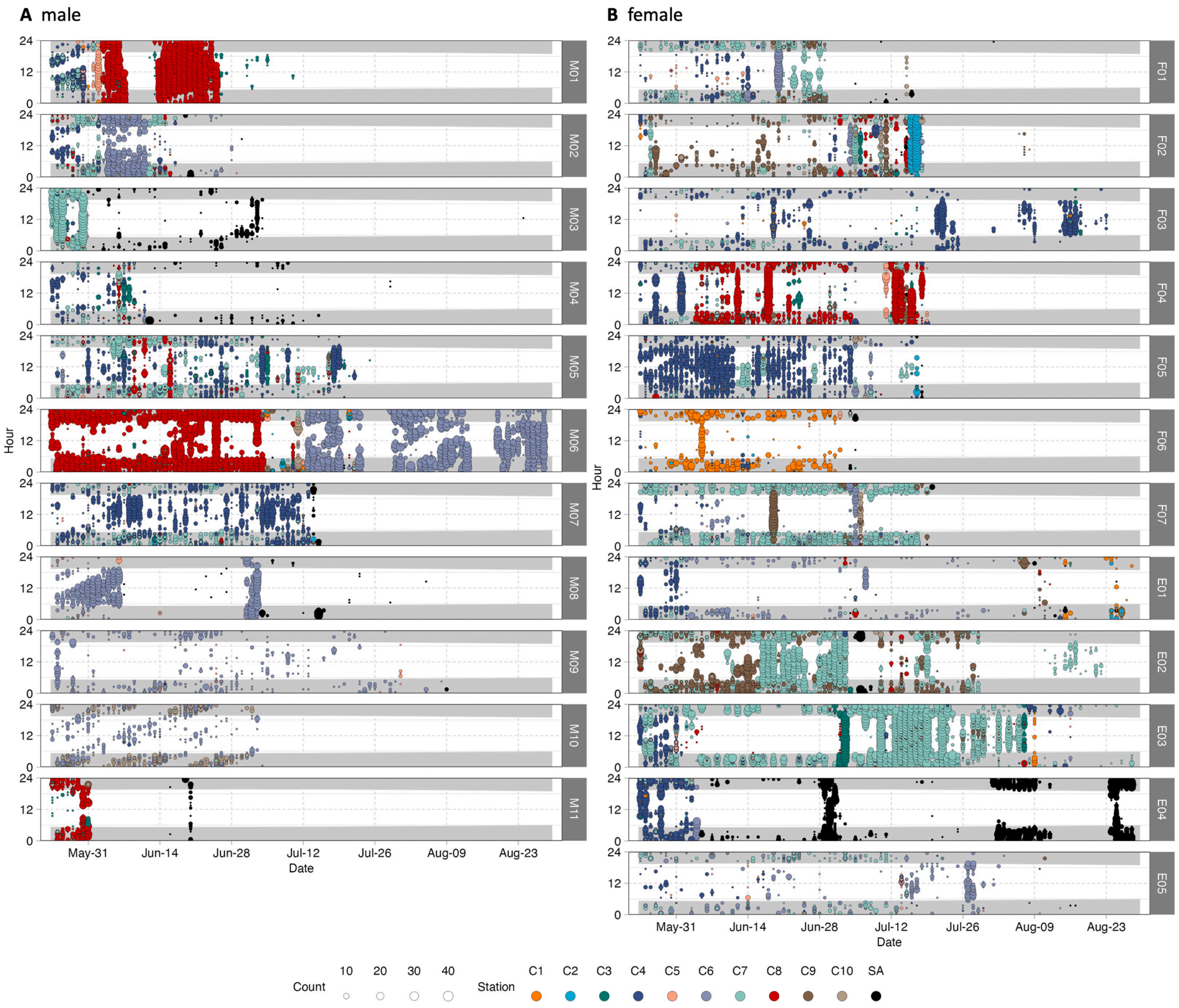

Fig. 3. Time series variation of individual diel activity patterns for males (A) and females (B) of Japanese spiny lobster. The bubble size indicates the number of hourly detections. Shading represents dark periods (dawn, dusk, and night). Colors represent each receiver station in the CA and aggregated SA stations.

was challenging to derive ecological interpretations of these patterns solely from the detection histories of individual lobsters. Nevertheless, trend (i) was most frequently observed pattern, indicating that the diel activity rhythm of lobsters was predominantly nocturnal.

Within the CA, for each individual, a receiver station with the highest number of daily detections often remained the same for several days, suggesting that lobsters were using the same shelter or adjacent shelters for consecutive days (Fig. 3). The mean number of consecutive days (± SD) spent in the same home area was 5.7 ± 5.8 (range 2–42) days, with no significant differences between the males and females ($W = 53$, $p = 0.44$) or between the berried and non-berried females ($W = 13$, $p = 0.53$) (Table 1).

Among all 23 tracked lobsters, 19 were detected in the SA, with 14 of them being last detected by the SA receivers. Of these 14 lobsters, 12 were last detected by receivers located closer to the shore of Enoshima Island (Stns. S1, S2, S4, and S5) (Table 1, Suppl. Fig. S5). Notably, three individuals moved to Stn. S1, approx. 1.5 km away from the center of the CA, with one individual (ID E04) covering this distance in a single night.

The movement network of the lobsters exhibited strong connectivity to SA stations characterized by rocky reef habitats (Stns. S1, S2, S8, and S10). Conversely, stations with gravel-dominated habitats (Stns. S6 and S9) showed limited connectivity. Stns. S4 and S5, primarily characterized by sandy habitats, detected four individuals temporarily, suggesting these stations may have been transitional pathways toward the rocky reef areas extending along the coastline. Males exhibited a stronger connectivity with the SA stations primarily to the east or north, while the network for females was more dispersed (Fig. 4). It is noteworthy that all eight individuals detected at Stn. S8 were females, and three of these were egg-bearing. This sex-specific movements indicated the possibility of a link to hatching events. However, all individuals detected at Stn. S8 visited the station after July, which did not align with the estimated timing of larval release (within one month after tagging, i.e. before the end of June). Despite these differences in movement networks, the mean eigenvector centrality scores, which indicate the connectivity of nodes within the network, showed no significant difference between the males and females ($W = 106$, $p = 0.98$) or between the berried and non-berried females ($W = 129$, $p = 0.39$). Similarly, the edge density, representing the proportion of available edges, did not show a significant difference between the males and females ($W = 84$, $p = 0.28$) or between the berried and non-berried females ($W = 20.5$, $p = 0.68$).

Three movement patterns were identified in the movement

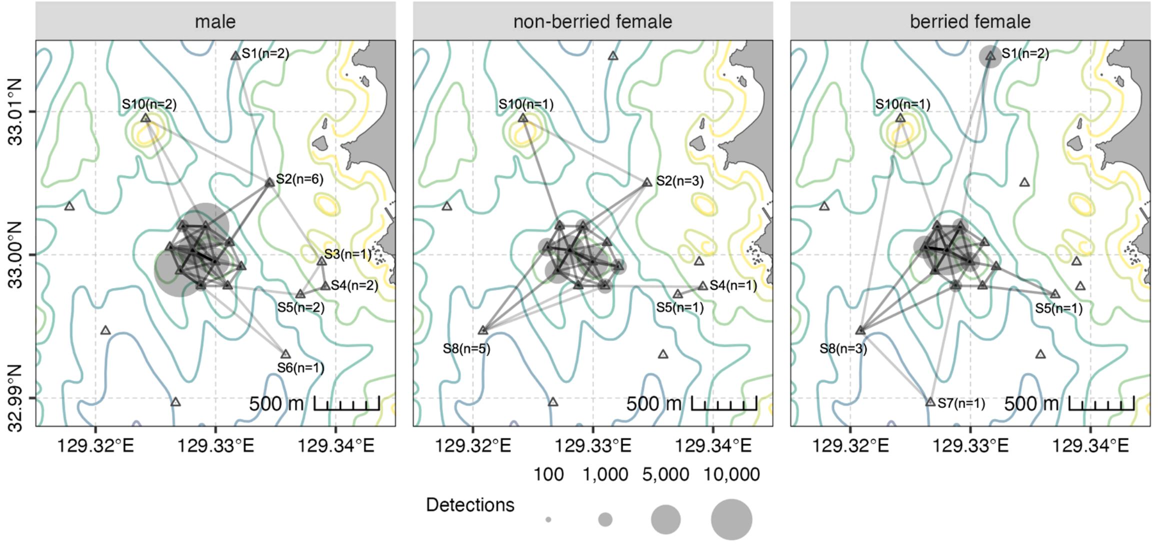

Fig. 4. Weighted network for male, non-berried female and berried female lobsters according to the spatial layout of acoustic receivers. The node size is proportionate to the number of detections for each receiver, and the color depth of each edge is proportionate to the density of movement. The names of the detected SA receivers and the number of individuals detected at each receiver are also presented.

networks. Pattern CA-CA was movements confined to the CA stations. Pattern CA-SA-CA was movements from the CA to the SA followed by a return to the CA. Pattern CA-SA was movements from the CA to the SA without a return to the CA (Fig. 5). Pattern CA-CA was observed in all tagged lobsters, indicating that it is a common and frequent movement pattern. The average number of receivers that detected each lobster within the CA during a single night was 2.1 ± 1.1 (range 1–7), suggesting that lobsters exhibiting this movement pattern traveled within an estimated radius of approx. 200 m per night. Pattern CA-SA-CA was observed in 11 lobsters, showing connectivity between the CA and SA stations located within 1 km of the CA (Stns. S2, S5, S8, and S10) (Suppl. Fig. S5). In this movement pattern, the lobsters' stay at the SA stations was mostly temporary, ranging from one to five nights, and after returning to the CA many individuals relocated to their previously used home area. Pattern CA-SA was observed in 14 lobsters that were eventually lost from detection in the SA (Table 1, Suppl. Fig. S5). Some individuals displaying the CA-SA pattern remained at a single SA station for extended periods; for example, individual M04 was detected at Stn. S1 for 48 days, and individual E04 was detected at Stn. S1 for 87 days. Additionally, some of the lobsters that moved in patterns CA-SA-CA and CA-SA exhibited non-directional movement paths. For instance, individual E02 moved nonlinearly over four nights in the western area of the CA, covering an estimated distance $>$ 4 km before returning to the CA (Fig. 4B).

4. Discussion

We tracked the movements of Japanese spiny lobsters by applying acoustic telemetry within an area planned for the installation of an OWF. In the context of OWF development in Japan, it is essential to predict the potential impacts of OWFs on fisheries and consider strategies for harmonizing OWFs with local fisheries. Knowledge about habitat use and movements of fishery species in the development areas will help predict the impacts of OWF development on the existing fisheries. The present study is the first to collect behavioral data of a commercially important species in an OWF promotion zone before the construction.

4.1. Presence and residence

Details concerning the presence and residency of animals in a habitat provide valuable insights into their habitat use patterns and selection (e.g., Lindberg et al., 2006). When a habitat is used as a fishing ground for a particular species, the residency within that area serves as an indicator of the fishing ground's quality, which is determined by factors such as the availability of food and shelter.

Our present survey revealed that the duration of lobster residency within the approx. 170,000-square-meter CA varied widely, ranging from 7 to 97 days (average 52 days), with only five individuals remaining for $>$ 90 days. This suggests that the CA does not encompass the entire spatial range used by these lobsters. However, more than half of the lobsters detected in the SA (11 of 19 individuals) returned to the CA at least once. In addition, most of lobsters within the CA exhibited a high residency index, continuously occupying the same home area for an average of 5.7 days and up to a maximum of 42 days. These findings suggest that this fishing ground meets the habitat requirements for *P. japonicus* (e.g., availability of shelters and food).

The research on the fine-scale residency of *P. japonicus* includes a study that tracked four adult spiny lobsters in a small (16,000 m^2) reef: three lobsters left the reef within 3 weeks, and one stayed throughout the 6-week study period (Sasaki et al., 2021). An investigation using mark-recapture methods reported that $>$ 90 % of recaptured lobsters were caught within a 5-km radius of the release site between 1 and 477 days (average 34.6 days) after their release (Takagi, 1972). These findings, combined with our present observations, suggest that Japanese spiny lobsters tend to remain within a 5-km radius for over a year but may frequently move within a more detailed spatial scale.

High site fidelity is a fundamental ecological trait of lobsters, including those in the Palinuridae family (Herrnkind, 1980). An investigation of the movements of the southern rock lobster (*Jasus edwardsii*) in Australia using a tag-recapture method revealed that 83 % of the released lobsters were recaptured within 1 km and 93 % within 5 km of their release site, with an average recapture time of 462 days post-release (Skeer et al., 2020). Similarly, Follesa et al. (2009) reported that 60.4 % of tagged European spiny lobsters (*Palinurus elephas*) were recaptured within 2 km of the release site center, on average 530 days post-release. On the other hand, Giacalone et al. (2015) reported that *P. elephas* regularly relocated shelters at an average interval of 5 days. This interval is similar to the 5.7 days average home-area occupancy observed herein. However, the duration of home-area occupancy varied both within and among individuals in this study, potentially influenced by the quality of the shelter and the availability of nearby food resources. These findings suggest that while *P. japonicus* exhibits high site

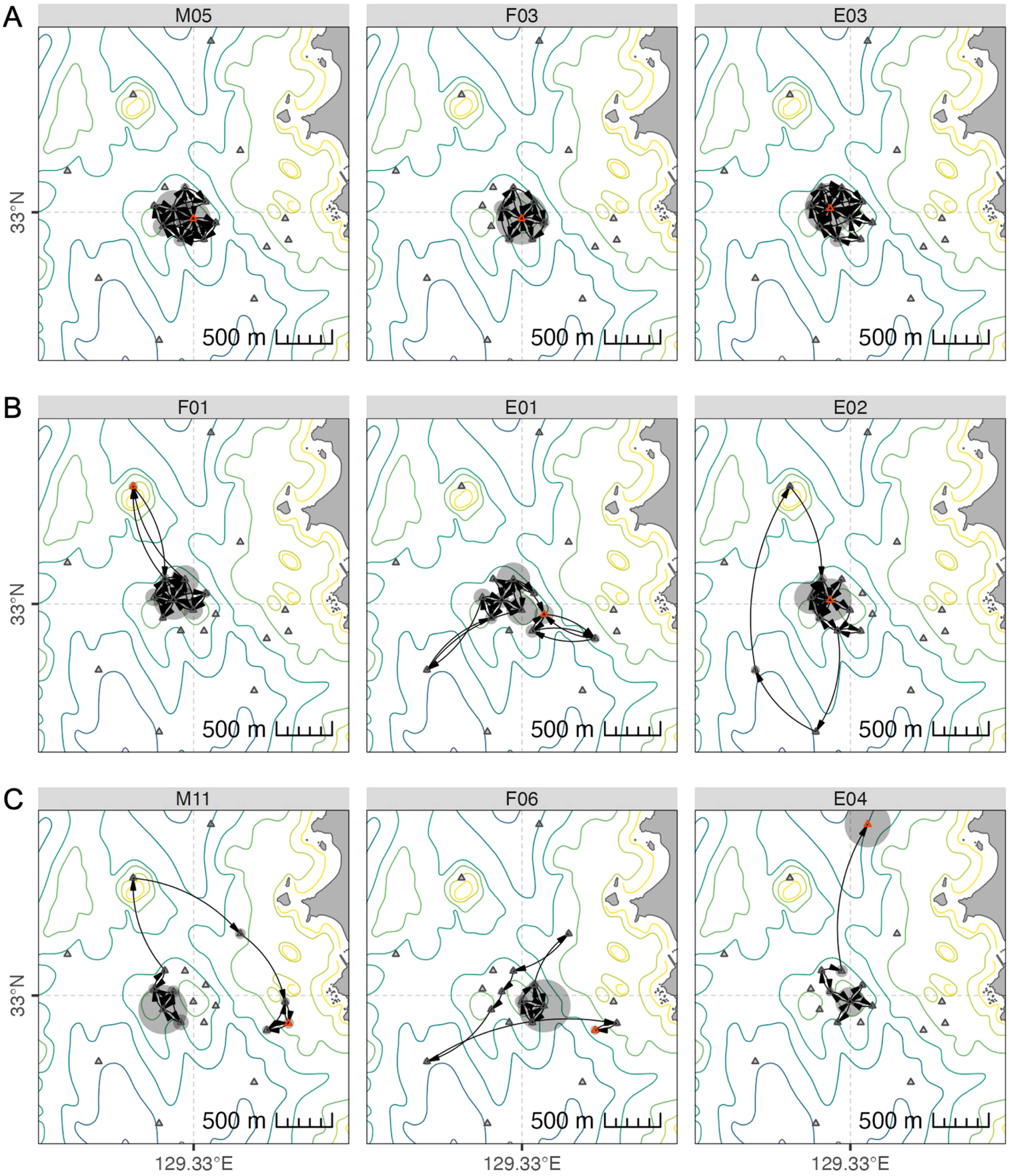

Fig. 5. Example of individual spatial graphs illustrating the three movement patterns in the CA and SA. (A) Pattern CA-CA: movements confined to the CA. (B) Pattern CA-SA-CA: movements from the CA to the SA, followed by a return to the CA. (C) Pattern CA-SA: movements from the CA to the SA without a return to the CA. The node size corresponds to the number of detections, with larger nodes indicating higher use. The edges show directed movement pathways. *Arrows* indicate the direction of movement. *Red triangles:* the receiver in which each individual was last detected.

fidelity similar to other members of the Palinuridae family, it also engages in regular short-distance relocations.

If the disappearance of individual lobsters from detection within the CA is associated with regular shelter relocation, it is possible that the individuals whose detection was completely lost may return to the CA in the future. To deepen our understanding of the movement ecology of this species, it is necessary to investigate how shelter relocations transition over the long term and how the lobsters select new habitats.

4.2. Movement patterns and habitat connectivity

The Japanese spiny lobster is a reef-dwelling crustacean whose habitat is strictly defined by the type of bottom substrate. For such species, movement between habitat patches signifies the exchange of resources between fishing grounds. Consequently, alterations to the lobsters' movement network could potentially influence catch rates in existing fishing grounds. Our findings revealed the connectivity between the CA and SA stations, highlighting frequent movements between habitat patches used by the lobsters. We also identified three movement patterns: the movements confined to the CA (CA-CA), those from the CA to the SA followed by a return to the CA (CA-SA-CA), and those from the CA to the SA without a return to the CA (CA-SA).

The movements of lobsters are primarily classified as: (1) homing–territorial, (2) nomadic–dispersive, and (3) migratory (Herrnkind, 1980). Homing consists of excursions of tens to hundreds of meters over familiar environments with lobsters returning to their home shelters. Nomadic movement is defined as non-directional movement without predetermined start and end points or temporal constraints, typically involving travel distances of several kilometers over multiple nights. The migration of lobsters is defined as large-scale directional movements at the population level, over several kilometers within a limited period, typically associated with seasons, life stages, or reproductive events.

The CA-CA movement pattern identified in this study is likely associated with homing behavior. Specifically, lobsters occupied the same home area within the CA for an average of 5.7 consecutive days, suggesting a reliance on the same shelter, or shelters in close proximity, as a base for daily activities. This pattern aligns with homing behavior, wherein individuals consistently return to the same shelter over consecutive days. The daily movements of a related species, the Caribbean spiny lobster (*Panulirus argus*), follow a homing routine of shelter-move-feed-move-shelter, with movement distances sometimes reaching several hundred meters (Bertelsen and Hornbeck, 2009; Bertelsen, 2013). Although the exact movement distances of the *P. japonicus* lobsters in our study remain unclear due to spatial resolution limitations, we estimated that the Pattern CA-CA movement included distances that had been traveled within a 200-m radius per night, which is comparable to the homing behavior observed in *P. argus*.

The movement patterns CA-SA-CA and CA-SA both showed connectivity between the CA and SA. These patterns share the common characteristic of home-area relocation before and after the movement, suggesting a similar purpose related to shelter relocation. Shelter relocation, characterized as nomadic movement in which daily routines are re-established, is a feature observed in several lobster species (e.g., Jernakoff, 1987; Atkinson et al., 2005; Bertelsen, 2013; Giacalone et al., 2015). Although such movements are generally non-directional, our study showed a directional bias in lobster emigration from the CA to the SA, indicating possible reliance on cues such as olfactory signals (Nevitt et al., 2000; Derby et al., 2001) or magnetoreception (Boles and Lohmann, 2003) during shelter relocation. We also observed shifts in the lobsters' home areas even within the CA, indicating that shelter relocation does not necessarily occur exclusively between habitat patches, and that the distance associated with these movements can vary widely.

According to local lobster fishermen, catch per unit effort (CPUE) in a productive fishing ground tends to decline due to repeated fishing. However, if the area is left unfished for several weeks to months, the CPUE reportedly returns to its previous levels. This anecdotal knowledge suggests that the nomadic inter-habitat movements observed in this study may occur regularly, playing a key role in replenishing resources within fishing grounds. While our study focused exclusively on the closed season for lobster fishing, data during the fishing season are essential for gaining a deeper understanding of the interactions between the lobster movements and gillnet fishing.

Although migration has not been reported for *P. japonicus*, female *P. argus* is known to migrate from shallow waters to deeper areas during the reproductive season to release larvae (Warner et al., 1977; Kanciruk and Herrnkind, 1978; Bertelsen, 2013). We performed the present survey during the reproductive season of *P. japonicus*, but no significant differences were observed between the males and females or between the berried and non-berried females in terms of residency within the CA, home-area occupancy, or movement networks. Although only females were detected at the SA station (Stn. S8) located southwest of the CA, the timing of these movements did not align with the estimated timing of hatching events. However, variations in water temperature may cause shifts in the timing of hatching (Moss et al., 2004), making it difficult to definitively rule out a potential association. Thus, it would be worthwhile to investigate further the potential relationship between the arrival of females at Stn. S8 and hatching events.

4.3. Conclusion and implications for OWF development

The results of this study provide valuable pre-development data on habitat use and movements of *P. japonicus,* a commercially important species in an area where OWF development is planned. Palinurid lobsters are not only key components of benthic ecosystems globally but also economically significant species supporting coastal fisheries (Shears and Babcock, 2002; Phillips et al., 2013). Recently, these species have been recognized as valuable indicators for assessing marine pollution and ecosystem health (Loflen et al., 2018; Giraldes et al., 2021; Kampouris et al., 2023; Lopeztegui-Castillo, 2023). Thus, the data from this study form an essential foundation for predicting and evaluating the potential impacts of OWF installation on lobsters, local fisheries, and marine ecosystems.

Our findings indicate that although the Japanese spiny lobsters exhibit high site fidelity within the fishing ground (the CA), this single rocky habitat does not encompass their entire spatial range. This suggests that the behavior of *P. japonicus* is not confined to a single habitat patch as a fishing ground, highlighting the necessity of considering inter-patch movements when assessing the impact of OWF installation on the lobster fishing activities. Several previous studies have suggested that the artificial hard substrates of OWFs could serve as new habitats for crustaceans, including large decapods like *Homarus gammarus* (Thatcher et al., 2023), and benthic fish species (Reubens et al., 2014). If such OWF-related infrastructures provide new habitats for *P. japonicus*, the accessibility of OWF area could become a significant concern for fishermen. This highlights the importance of understanding how such developments affect the distribution and availability of lobster resource.

Currently, Japan lacks specific laws or guidelines regarding navigation within or around OWFs, and thus the access to these areas by fishermen is determined by OWF managers. The artificial reef effect of OWFs could create potential fishing opportunities if fishing within OWFs is permitted (Hooper and Austen, 2014; Stelzenmüller et al., 2021). Conversely, if fishing within OWFs is restricted, some areas may lose fishing opportunities (Hooper et al., 2015; Haggett et al., 2020). On the other hand, the exclusion of fishing activities within OWFs could enable these areas to function as marine protected areas (MPAs), contributing to ecosystem conservation and potentially benefiting adjacent areas through spillover and resource enhancement (Punt et al., 2009; Ashley et al., 2014).

Our investigation demonstrated that the lobster movement networks exhibited biases in connectivity and detected stations. Aquatic animals are not uniformly distributed; instead, their niche requirements are determined in relation to specific habitats or resources (Mittelbach, 1981; Rosenzweig, 1981). The creation of new habitats thus has the potential to alter the existing movement networks and the distribution of lobsters. Moreover, OWF construction and operation-related ecological disturbances, such as noise, vibration, and electromagnetic fields (EMF), could affect animal movement and habitat use (Bat et al., 2013). These disturbances might force lobsters to abandon familiar areas or render parts of their established movement network inaccessible. Such habitat loss and fragmentation may consequently lead to population declines through increased dispersal and intensified intraspecific competition (Fahrig, 1997; Bender et al., 1998). EMF generated by OWF submarine cables, in particular, could have considerable effects on animals that potentially use magnetic fields for navigation, such as lobsters (Lohmann et al., 1995; Hutchison et al., 2020). Evidence from other large crustaceans, such as European lobsters (*H. gammarus*) and brown crabs (*Cancer pagurus*), demonstrates significant impacts on early life stages, behavior, and physiology (Scott et al., 2018; Harsanyi et al., 2022). Robust baseline data, like those collected in this study, are essential for quantifying these potential changes. Comparative analyses of pre- and post-development data can yield deeper insights into how spatial distribution and habitat use of commercially important species change in response to OWF developments.

As OWF development in Japan is still in its early stages, considerable uncertainty surrounds its potential impacts on animals and coastal ecosystems. Addressing these uncertainties requires the application of adaptive management after development (Walters, 1986; Westgate et al., 2013). For example, future application of a before-and-after comparative approach using our baseline data could reveal shifts in lobster resources from traditional fishing grounds to newly created habitats within the OWF. If such shifts are detected, interventions such as installing guiding artificial reefs to facilitate lobster movement between the fishing grounds and the OWF, or establishing unrestricted fishing zones equipped with artificial reefs within the OWF, can be proposed (Berges et al., 2024).

In conclusion, the knowledge gained from our study on habitat use and movements of a commercially important species in an area designated for OWF development provides a basis for predicting and evaluating the impacts of such developments on fisheries and marine ecosystems. The combination of acoustic telemetry and a network analysis offers a visual representation of target species space use, and this approach can be recommended as a pre-assessment model for OWF development in cooperation with local fisheries as it supports discussions and consensus-building with non-academic stakeholders, including fishermen. Additionally, post-development monitoring is essential for evaluating the effects of habitat creation and ecological disturbances, to ensure the long-term sustainability of both fisheries and marine ecosystems.

Ethics approval

In Japan, ethical approval for animal experiments involving invertebrates is generally not required. However, the protocols and procedures used in this study were conducted with the utmost care to minimize any distress to the animals. For example, when the tags were attached to the lobsters, only the dorsal carapace was exposed above water while ensuring continuous water flow over the lobsters' gills to maintain proper respiration.

CRediT authorship contribution statement

Ikusei Sasaki: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Itsumi Nakamura:** Writing – review & editing, Investigation. **Ryo Kawabe:** Writing – review & editing, Supervision, Investigation, Funding acquisition. **Yoshiki Matsushita:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition. **Yuki Matsumoto:** Writing – review & editing, Formal analysis. **Munenari Takeda:** Writing – review & editing, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104037.

Data availability

Data will be made available on request.

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