

Onshore investigation of intertidal to subtidal mass benthic mortality assemblage: Preliminary assessment of the rocky reef coastline uplifted by the 2024 Noto Peninsula Earthquake (M7.6)

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Abstract: The sudden coastal uplift resulting from the 2024 Noto Peninsula earthquake exposed the previously subtidal and intertidal habitats, providing a unique opportunity to document the biotic community and immediate effects of geological disturbances on it. This study describes the characteristics of the benthic death assemblages around the Kaiso fishing port, which experienced approximately 3.6–3.9 m of uplift, with special attention to the vertical distribution of coastal benthos inhabiting Kaiso Reef. Our field surveys were initiated 66 days after the earthquake, integrating quadrat-based sampling with direct observation of emergent marine habitats. 92 molluscan and 5 echinoderm species were found in our quadrat investigation. The soft tissues of most molluscan individuals remained, indicating that their in situ life postures were undisturbed. Given this premise, species richness was estimated to have peaked between the pre-disaster middle to lower intertidal and uppermost subtidal zones, particularly in areas with reduced wave exposure. Additionally, the surveys identified several notable species at the Kaiso fishing port, including the Near-Threatened coral *Oulastrea crispata* and bivalve *Pinna bicolor*, both of which have their northernmost records in the Sea of Japan from the Noto area. The uplifted zone presents a rare opportunity to examine the subtidal fauna from terrestrial vantage points, yielding novel perspectives on marine biodiversity in the Sea of Japan. Also, these findings provide critical baseline data for monitoring post-uplift ecological succession against a backdrop of ongoing climate change.

Key words: Geological disturbances, Marine biodiversity, Noto Peninsula Earthquake, Sea of Japan, Threatened species

Introduction

On January 1, 2024, at 16:10 JST, a magnitude 7.6 earthquake with an epicenter at a depth of 16 km occurred beneath the northeastern edge of the Noto Peninsula located on the western side of central Japan facing the Sea of Japan (Japan Meteorological Agency 2024a). This event, categorized as a reverse-fault inland earthquake, resulted in a

rapid coastal uplift, with maximum vertical displacement of approximately 4.4 m at north-west coast of the Noto Peninsula (Fukushima et al. 2024). The extent of this onshore uplift exceeded that of major earthquakes recorded in Japan over the past century, including the Great East Japan Earthquake in 2011 (1.2 m subsidence of coastline at Oshika, Miyagi; Masaharu & Nagayama 2011) and Great Kanto Earthquake in 1923 (1.6 m uplift of the coastline at Tateyama, Chiba; Kunimi et al. 2001). It ranks as one of the world's most significant earthquake-induced coastal uplifts ever documented, because only a few larger dis-

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placements have been reported, such as the approximately 14 m uplift in the 1899 Yakutat Bay earthquakes, Alaska (Tarr & Martin 1912). Since May 2018, a series of earthquakes have been persistently occurring, with a substantial increase noted after December 2020 in the Noto Peninsula. This heightened seismic activity is attributed to compressive stress along the principal axis of N40–60°W (Ota et al. 1976) and the influence of underlying deep fluids (Umeda et al. 2024). On a geological timescale, at least three coastal terraces have been identified in the coastal area on the northwestern side of the Noto Peninsula, suggesting that this region has experienced similarly scaled uplifts resulting from major earthquake cycles of several thousand years (Shishikura et al. 2020). In the context of the recorded historical timescale, coastal uplift (up to 0.8 m) was estimated to have occurred due to a major earthquake with its epicenter off the northwestern Noto Peninsula in 1729 (Hamada et al. 2016).

Meanwhile, this massive earthquake comprises three major fault motions (Okuwaki et al. 2024) and therefore, a simulation study estimated that multiple tsunami waves struck the Sea of Japan coastline around the Noto Peninsula (Masuda et al. 2024). Comprehensive surveys on tsunami disaster found that tsunami height was dominant around north side of the Noto Peninsula with maximum height 5.57 m at Noto-cho (37°19'54.9" N, 137°15'45.6" E), while its west coast experienced relatively weak tsunami effects (Arita et al. 2024; Yuhi et al. 2024), presumably with relation to the coastal uplift. For instance, both studies reported that no significant tsunami trace was observed around Kaiso fishing port, which was highlighted in many news reports immediately after the earthquake as a symbolic site of the uplift. A simulation study of the tsunami height covering a broad area of the Noto Peninsula (Masuda et al. 2024) also estimated low heights near Kaiso fishing port. A qualitative reading of the color scale suggests values on the order of ~1.5 m at this locality (see their Fig. 2); this is consistent with minimized tsunami effects in areas that experienced significant uplift.

The marine biota of the Sea of Japan is distinct when compared to that of the opposite Pacific side of the Japanese archipelago due to the differences in tidal ranges and geohistorical contexts comprehensively reviewed by Nishimura (1965). The Sea of Japan is connected to adjacent seas through six shallow straits. For instance, the Tsushima Strait, situated at its western limit, features depths of 95 m and 130 m in the eastern and western channels, respectively (Yajima 1978b). This geographic setting leads to notable differences in the tidal range between the Sea of Japan and Pacific coast of Japan. The diurnal tidal range along the coast of the Sea of Japan is approximately 0.4 m, considerably smaller than the ~2 m range observed along the Pacific coast (Yajima 1978a, b). However, seasonal variation in the Sea of Japan is more pronounced than its diurnal variation. Therefore, the high-water line in spring can be positioned lower than the summer low-water

line along its coastlines [see Fig. 1 in Yajima (1978b) that shows sea-level variations at Wajima, Toyama, and Tokyo in 1976]. Furthermore, as an epeiric sea, the Sea of Japan was isolated from other seas during glacial periods (Oba et al. 1991). Recent studies have revealed that the genetic structures of various marine coastal organisms reflect the abovementioned characteristics of the Sea of Japan (amphipod; Takada et al. 2018, limpet; Teruya et al. 2024). These aspects suggest that the benthic assemblages specific to the Sea of Japan, primarily in the intertidal zone, were severely impacted by a sudden uplift of on the order of 4 m.

In this study, we examined the coastal mass benthic mortality assemblage around the Kaiso fishing port, which surfaced due to a 3.6–3.9 m uplift (Shishikura et al. 2024a, b) prior to the displacement of carcasses by rainfall. Our research objectives are: (1) to reconstruct the pre-earthquake intertidal to shallow subtidal benthic community of Sea of Japan by the detailed 'onshore' survey of the death assemblage exposed by the seismic uplift, and (2) to assess the biodiversity loss resulting from the uplift-induced habitat elimination, as to document the distinctive Sea of Japan benthic ecosystem and its abrupt disappearance. This assessment serves as fundamental data for long-term monitoring of potential ecosystem changes. Recent studies indicate that global warming substantially alters marine ecosystems (e.g. the northern limit of coral distribution in the Sea of Japan; Yamano et al. 2024). This underscores the need to consider the interplay between large-scale environmental changes and potential niche expansion in this region. Moreover, this study contributes to the reevaluation of marine diversity in the Sea of Japan. Notably, several new species have recently been identified in waters deeper than the subtidal zone (Henmi et al. 2022). The geological conditions of the study area allow for direct observation of subtidal fauna from land and provide a unique opportunity to explore marine diversity in the Sea of Japan.

Materials and Methods

Observations of landforms and walkover survey with hand collection of marine organisms were conducted at three sites arranged from north to south for seven occasions (March 7, 21, April 21, May 12, 19, July 11 2024; the first survey was 66 days after the disaster): Kaiso fishing port (37°17'37" N, 136°43'36" E), where a 3.6–3.9 m uplift was observed (Shishikura et al. 2024a, b); the adjacent rocky shore to the south (hereafter referred to as "Kaiso Reef"); and the Kuroshima Coast. The Kuroshima Coast is situated south of Kuroshima fishing port (37°16'57" N, 136°43'59" E), which is approximately 1.2 km south of Kaiso Reef.

Furthermore, the vertical distribution of coastal benthos inhabiting the pre-disaster intertidal to subtidal zones was investigated at the Kaiso Reef on April 21, 2024 (111 days following the earthquake-induced uplift). A prominent convex outcrop (37°17'31.98" N, 136°43'40.75" E) was

designated as a landmark point of the transect for this survey. Subsequently, we established our transect to the south (approximately 183°) in a direction nearly perpendicular to the coastline. We established 14 stations and placed 18 quadrats (each 30 × 50 cm) along the transect on alternating flat and vertical surfaces of the rocks while moving southward toward the shoreline. At four stations (Quadrats 5–8), we placed two adjacent quadrats (A and B) to capture microtopographic heterogeneity. Where sand partially covered a frame, we removed it and carefully picked all specimens. Quadrat 1 was located at the base of the landmark. The starting point (i.e., Quadrat 2; 37°17'31.06" N, 136°43'40.69" E) for continuous sampling was set at the location approximately 28.4 m south of the landmark point at the same elevation as Quadrat 1. Both quadrats were situated on the same wide, flat rocky bench, and were therefore at the same elevation. The topographic signature is illustrated by its natural step-like rocky benches and our southward, shore-perpendicular transect crossed these benches. The seaward margin was covered by beach sand. The positional relationship of each quadrat was measured using a laser measuring device (GLM150C, Bosch). The maximum tidal range recorded at Wajima, the closest monitoring point, was 11 cm, with high tide occurring at 13:23 JST (Japan Meteorological Agency 2024b) on the date of our survey. This indicates that our bottom quadrat (Quadrat 11) was positioned approximately <10 cm above the contemporaneous high-water line. Benthic organisms were collected from the quadrats and subsequently transported to the laboratory for species identification and counting of the number of individuals for each species, as all specimens were found to be deceased. Individuals were counted by categorizing them into three groups: (1) those with visible soft tissues and clearly alive at the time of the earthquake, (2) those lacking evident soft bodies but presumed to have been alive, because their hard tissues remained fresh, showing neither abrasions nor weathering, and (3) dead shells. Meanwhile, the algal cover within the quadrats had dried extensively and deteriorated, rendering individual counts infeasible. Consequently, we recorded the percentage algal cover in the field. The taxonomic nomenclature of the collected benthos was based on Okutani (2017) and the World Register of Marine Species (WoRMS, <http://www.marinespecies.org>, accessed April 5, 2025) for mollusks and Imahara (2023) for echinoderms, crustaceans, and algae. Additionally, we referred to the classification of corals by the Ishikawa Prefecture (2020).

Results

Observation of the coastal landscape and marine biota (Figs. 1, 2)

Kaiso fishing port (Fig. 1B, C): The sea bottom surface in the inner harbor was completely dried up due to the 3.6–3.9 m uplift (Fig. 1C). The harbor wall was covered

by hundreds of dead shells (*Saccostrea kegaki* Torigoe & Inaba 1981, and *Spondylus squamosus* Schreibers 1793) and calcareous tubes of serpulid polychaetes (Figs. 2A, B). In addition, some dead sessile bivalves [e.g. *Mytilisepta keenae* Nomura 1936, *Septifer bilocularis* (Linnaeus 1758), and *Cardita leana* Dunker 1860] were observed. Deceased specimens of several sessile bivalves, including *Saccostrea kegaki* *Pinctada fucata* (Gould 1850), and *Chama ambigua* Lischke 1870, were observed on the surfaces of dried-up boulders. Furthermore, numerous skeletons of *Oulastrea crispata* (Lamarck 1816), a Near-Threatened coral species (Ishikawa Prefecture 2020), were identified (Fig. 2C). Individuals found in this area were characterized by their blackish corallum, similar to those observed in Akasaki, an east-side locality of the Noto Peninsula that was reported by Yamashiro (2000). Meanwhile, shell remains of *Pecten* cf. *albicans* (Schröter 1802), *Laevicardium undatopictum* (Pilsbry 1904), *Heteromacoma irus* (Hanley 1845), *Semele zebuensis* (Hanley 1844), and *Venerupis aspera* (Quoy & Gaimard 1835) were identified from the sandy bottom. In addition, several dead individuals of *Pinna bicolor* Gmelin (1791) were observed dead in an in-situ life posture (Fig. 2D). This species is a Near-Threatened Japanese species, and its occurrence is considered to be the northern limit of the Sea of Japan (Ishikawa Prefecture 2020). As an exception, we found that *Patiria pectinifera* (Müller & Troschel 1842) were still active on the sandy bottom where seawater was present.

Kaiso Reef (Figs. 1D–F): A notable finding other than our quadrat investigation was that we found a small post-mortem corallum of *Culicia japonica tenuisepes* Ogawa et al. 1997 beneath the overhang (approximately at the same vertical level as Quadrat 9; Fig. 2E). This species is relatively rare on the western side of the Noto Peninsula (Ishikawa Prefecture 2020). The extensive rocky substratum at the “current” shoreline was found to be covered by hundreds of dead *Spondylus squamosus* while live green algae were observed at its base around and below the ‘current’ high water level (Fig. 1F). Conversely, living individuals of typical upper intertidal to supralittoral zone species in this locality, such as *Cellana toreuma* (Reeve 1854), *Patelloida saccharina* (Linnaeus 1758), and *Echinolittorina radiata* (Souleyet 1852), were not observed in this horizon. Between pre-disaster and current coastlines, reef surfaces were covered by whitened algae remains, and carcasses of some mollusks, crustaceans, and echinoderms were scattered, probably maintaining their in-situ life postures (Figs. 2F, G).

Kuroshima coast: The sandy beach extends on both sides around the mouth of the Yatsuga River south of the Kaiso fishing ports. After the earthquake, the sandy beach expanded horizontally seaward. Therefore, scattered basement rocks and boulders were exposed, and their dried-up dead biota were observed. A unique finding was that soft parts of deceased *Turbo sazae* Fukuda 2017 remained with dense adherence of dead *Sabia conica* (Schumacher 1817)



Fig. 1. A: The landscape around Kaisei fishing port (B, C) and our main study site, Kaisei Reef (D–F). (B) Exposed sea bottom surface due to uplift; (C) The uplifted harbor wall; (D) Kaisei Reef whose surface was covered with whitened algae remains. Note that the current sea surface was at the feet of the authors. (E) The presumed pre-disaster coastline coincides with the horizontal line between the blackish and whitish areas. (F) Green algae covering the current coastline. A was photographed on July 11, 2024. B, D, and E were taken on April 21, 2024. C was on March 21 and F was on March 27, 2024.

at the shell aperture (Fig. 2H).

Vertical distribution of coastal benthos remains in Kaisei Reef (Tables 1 and 2, Fig. 3)

We analyzed 18 quadrat samples collected at 14 positions (Quadrats 1–14); where two quadrats were taken at

a position, the number of individuals is averaged. As a result of our quadrat investigation, we identified 92 molluscan and 5 echinoderm species, as well as several arthropods and representatives of three major groups of macroalgae (Rhodophyta, Chlorophyta, and Phaeophyceae). We found 118 individuals of *Echinolittorina radiata* (Among

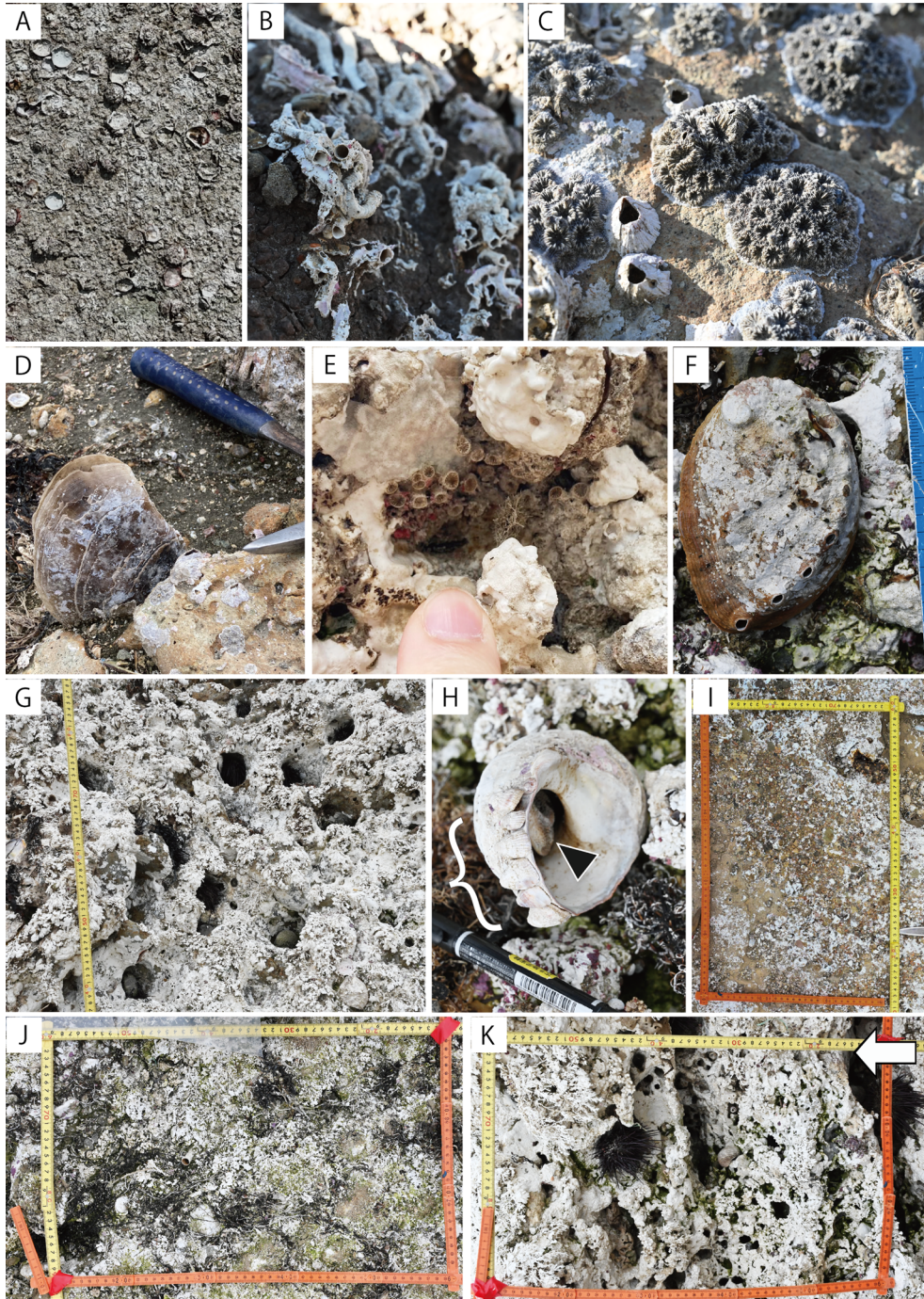


Fig. 2. Characteristic marine benthos in (A–D) Kaisei fishing port, (E–G) Kaisei Reef, along with (I–K) examples from our quadrat survey in Kaisei Reef, and (H) Kuroshima coast. (A) Sessile benthos attached to the harbor wall; (B) Calcareous tubes of annelids with diameters of ca. 1 mm; (C) Colonies of *Oulastrea crispata*. Corallites are ca. 5 mm in diameter; (D) *Pinna bicolor* in its life position; (E) *Culicia japonica tenuisepes*; (F) *Haliotis discus*; (G) Rock surface covered by whitened algae remains and an accumulation of *Heliocidaris crassispina* settled in boreholes; (H) *Turbo sazae* with its soft parts remaining (white arrowhead), and numerous *Sabia conica* attached around its shell aperture (white brace); (I) Quadrat 1; (J) Quadrat 7A; (K) Quadrat 10. A white arrow indicates a vertical upward direction. A, B and F were photographed on July 11, 2024. C was taken on March 7, 2024. D, and I–K was reported on April 21, 2024. E and H were photographed on May 12, 2024. G was on May 19.

the identified mollusks, *Siphonaria* sp. corresponds to the potentially undescribed species noted by Yokogawa et al. 2010.) in Quadrat 1, which was situated at the base of our landmark point. Quadrat 2, where 28.4 m south of

the landmark and 3.8 m above the sea surface, was covered by the sessile mollusk, *Saccostrea kegaki* and red algae, *Corallinaceae* spp. *Cellana toreuma* and *Patelloida saccharina* were abundant in Quadrats 2–4. *Acanthochi-*

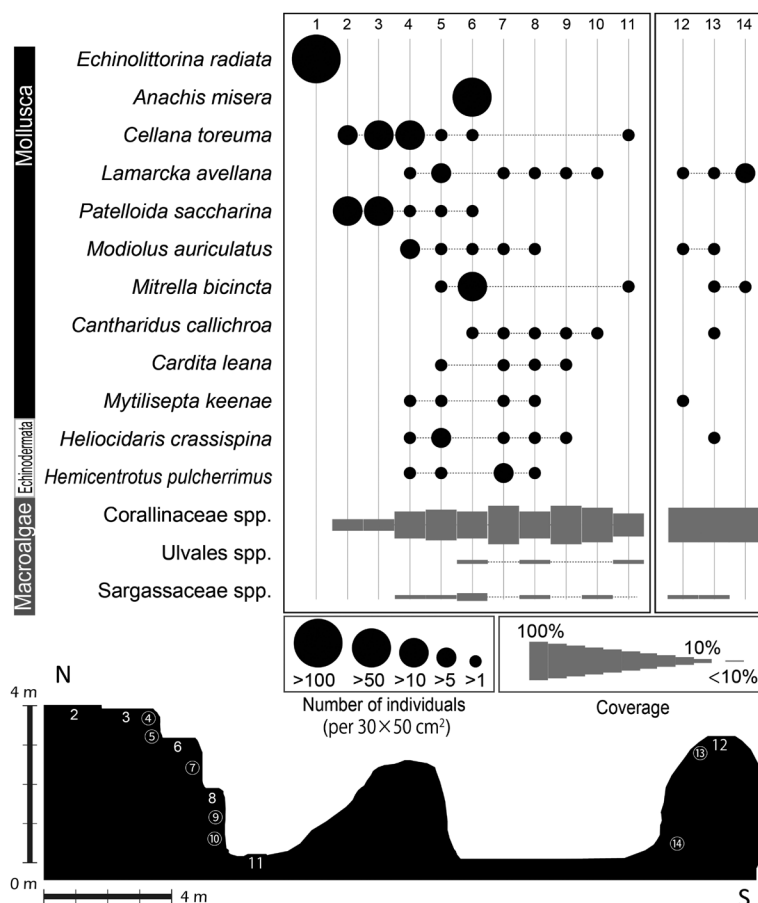


Fig. 3. The distribution of organisms and the profile of terrain. Quadrat 1 was not shown in the terrain profile diagram because it was located 28.4 m away from the continued quadrats, despite being at the same elevation as Quadrat 2. For Quadrats 5 to 8, which comprise two quadrats, the numbers of individuals were averaged. Values were rounded to the nearest integer. Quadrats located inclined or vertical surfaces are indicated by circled numbers. *Lamarcka avellana*, *Modiolus auriculatus*, *Cardita leana*, *Mytilisepta keenae* are sessile mollusks.

tona achates (Gould 1859) occurred in Quadrats 3–4. The vertical distance between Quadrats 2 and 4 was approximately 50 cm. Quadrats 5–6, which were located at lower elevations than the aforementioned areas (Quadrat 6: 3.0 m above the sea surface during the survey), were among the top five sections exhibiting the highest species richness identified in this study. Among the top 30 most abundant species, gastropods that inhabit algae (Okutani 2017)—including *Cantharidus japonicus* (Adams 1853), *Cantharidus callichroa* (Philippi 1850), *Euplica scripta* (Lamarck 1822), and *Anachis misera* (Sowerby 1844)—were observed below Quadrat 5. Crustaceans and echinoids were also relatively numerous in this zone. In addition, many rock-boring bivalves, including *Nettastomella japonica* (Yokoyama 1920) and *Irus mitis* (Deshayes 1854), were chiefly found at Quadrats near and below 5. Downslope along the transect, species diversity decreased slightly in Quadrats 7–9 and dropped markedly in Quadrats 10–11 (Quadrat 8: 1.8 m above the sea surface). In the wave-swept area between Quadrats 12 and 14, species diversity was highest in Quadrat 13, which had an elevation roughly equivalent to that of Quadrat 6 (Quadrat 12: 3.2 m above the sea surface).

Discussion

Assessment of the response to sudden geological disturbance and its resulting mortality

Catastrophic mortality of mollusks documented by our surveys conducted start from 66 days after the earthquake around Kaiso fishing port suggests that they died shortly after the event with retaining their pre-disaster distribution, as evidenced by the high proportion of individuals retaining soft tissues (Table 1), together with the tendency of mollusks to remain in place when emersed. For instance, gastropods, a group of motile mollusks, often exhibit taxon-specific defensive behaviors to mitigate desiccation rather than relocate, and consequently tend to remain in place when emersed (Vermeij 1971; Garrity 1984). Also, the homing behavior was reported in many limpets, including our observed *Patelloida saccharina* (e.g. Cook et al. 1969; Ohgushi 1954), strengthening our hypothesis. Haven (1972) similarly presumed most gastropods that died due to the uplift caused by 1964 Great Alaska earthquake stayed fixed. Although we cannot reject the possibility

Table 1. Molluscan species observed in the quadrat survey. Disarticulated bivalve shells were counted as 0.5 individuals each. All specimens were dead at the time of sampling. Counts are partitioned into three taphonomic categories: (1) Boldface = retaining soft tissues; (2) Regular numbers = scant remnants of soft tissue remaining or no visible soft tissue but unweather hard parts; (3) Numbers in parentheses = carcasses presumed to have died well before the earthquake. “Number of individuals” and “Occurrence” count only individuals excluding long-dead shells.

	Species	1	2	3	4	5A	5B	6A	6B	7A	7B	8A	8B	9	10	11	12	13	14	Number of individuals	Occurrence
	Nacellidae <i>Cellana toreuma</i> (Reeve 1854)	4+3	19	29	6	2+1	1+3					1	(2)	(1)		1+(2)		(1)		70	8
	Lottiidae <i>Patelloida saccharina</i> (Linnaeus 1758)	16+8	10+1	1	3			2	2											43	6
	<i>Lottia kogamogai</i> Sasaki & Okutani 1994			1	1			1												3	3
	<i>Patelloida signata</i> (Pilsbry 1901)				1				1								1			3	3
	<i>Lottia langfordi</i> (Habe 1944)									1								1		2	2
	<i>Nipponacmea gloriosa</i> (Habe 1944)																2			2	1
	Phasianellidae <i>Hilota variabilis</i> (Pease 1861)							1	1											2	2
	Trochidae <i>Cantharidus japonicus</i> (Adams 1853)	(1)			4			1+(1)	1+(2)											6	3
	<i>Cantharidus callichroa</i> (Philippi 1850)							6+(1)	2+(1)	2+3	1	5+1	1	1+2+(1)	1			1		26	9
	Calliostomatidae <i>Tristichotrochus unicus</i> (Dunker 1860)									(1)								1	1	2	2
	Trochidae <i>Trochus rota</i> Dunker 1860												1							1	1
	Turbinidae <i>Turbo sazae</i> Fukuda 2017						1			2			1+(1)	2	1		2	4	2	15	8
	<i>Astralium haematragum</i> (Menke 1829)													1+(1)			(1)	4+(1)	(1)	5	2
	Tegulidae <i>Tegula turbinata</i> (Adams 1853)				1			1+1	1	1		(1)								5	4
	<i>Tegula rusticus</i> (Gmelin 1791)									1		(1)	1							2	2
	Chilodontaidae <i>Herpetopoma lischkei</i> (Pilsbry 1904)								1											1	1
	Haliotidae <i>Haliotis discus</i> Reeve 1846									1							1			2	2
	<i>Haliotis diversicolor</i> Reeve 1846								1			2	2+1				1+1	1	(1)	9	5
	Fissurellidae <i>Tugali decussata</i> Adams 1852						1		1		1									3	3
	<i>Diodora sieboldii</i> (Reeve 1850)										1									1	1
	Cerithiidae <i>Cerithium dialaecum</i> Philippi 1849				1			5	7+(4)	(2)		1		2+(3)		1+2				19	6
	Batillariidae <i>Batillaria multiformis</i> (Lischke 1869)											1								1	1
	Littorinidae <i>Littorina brevicula</i> (Philippi 1844)								(1)											0	0
	<i>Echinolittorina radiata</i> (Souleyet in Eydoux & Souleyet 1852)																			118	1
	Hipponicidae <i>Sabia conica</i> (Schumacher 1817)								5				2		2				1	10	4
	<i>Antisabia foliacea</i> (Quoy & Gaimard 1835)						1			1			1							3	3
	Eulimidae <i>Melanella bovicornu</i> (Pilsbry 1905)				1															1	1
	Vermetidae <i>Thylacodes adamsii</i> (Mörch 1859)						1	(1)	(3)	1										2	2
	Cypraeidae <i>Purpuradusta gracilis</i> (Gaskoin 1849)				1	1				1										3	3
	<i>Naria helvola</i> (Linnaeus 1758)										1									1	1
	Eratoidea <i>Hesperato scabriuscula</i> (Gray 1832)					2														2	1
	Velutinidae <i>Lamellaria kiensis</i> Habe 1944				1															1	1
	Columbellidae <i>Euplia scripta</i> (Lamarck 1822)							2	2		2		2+1	1			1	1		12	7
	<i>Mitrella bicincta</i> (Gould 1860)				1+1			4+(1)	7+10+(4)	(1)			(1)			1		2+(1)	1+(1)	27	6
	<i>Mitrella martensi</i> (Lischke 1871)							1	1											2	2
	<i>Anachis misera</i> (Sowerby 1844)				1			39+21	30+9+(2)					(2)						100	3
	<i>Pardalinops testudinaria</i> (Link 1807)						(1)	1						1						2	2
	Nassariidae <i>Nassarius sufflatus</i> (Gould 1860)													(1)						0	0

		Species	1	2	3	4	5A	5B	6A	6B	7A	7B	8A	8B	9	10	11	12	13	14	Number of individuals	Occurrence	
Gastropoda		<i>Reticunassa fratercula</i> (Dunker 1860)								1+(1)											1	1	
	Buccinidae	<i>Engina menkeana</i> (Dunker 1860)													1						1	1	
	Muricidae	<i>Ergalatax contracta</i> (Reeve 1846)							(2)	1		3+1		1				(1)	1	2	11	6	
		<i>Reishia luteostoma</i> (Holten 1802)					1	2	1+2	3+2	2	2	(1)	1+(2)			1		1+(1)		18	9	
		<i>Bedequina birileffi</i> (Lischke 1871)																1			1	1	
	Costellariidae	<i>Vexillum inerme</i> (Reeve 1845)								1											1	1	
	Mangeliidae	<i>Hemicythara octangulata</i> (Dunker 1860)								1											1	1	
	Siphonariidae	<i>Siphonaria japonica</i> (Donovan 1824)								1+1	1										3	2	
		<i>Siphonaria sirius</i> Pilsbry 1894				2								1							3	2	
		<i>Siphonaria</i> sp.				1	2		1	2									1		7	5	
		<i>Siphonaria acmaeoides</i> Pilsbry 1894								1											1	1	
		<i>Williamia radiata</i> (Pease 1860)								1											1	1	
	Pyramidellidae	<i>Mormula philippiana</i> (Dunker 1860)									1											1	1
	Bivalvia	Arcidae	<i>Lamarcka avellana</i> (Lamarck 1819)				1+1	2+4	6	1+(1)		1+5	2+(1)	4	1+(0.5)	3	2	*(1)	4	3	5	45	13
			<i>Tetradarca boucardi</i> (Jousseaume 1894)					1+1							1							1	2
		<i>Barbatia stearnsi</i> (Pilsbry 1895)								2.5			(1)	0.5		1	*(0.5)				4	3	
Parallelodontidae		<i>Porterius dalli</i> (Smith 1885)																1			1	1	
Mytilidae		<i>Modiolus auriculatus</i> (Krauss 1848)				3+2.5	1+(0.5)	5	1	5	1	4+(0.5)	2	4			(1)	1	2+(0.5)		32.5	11	
		<i>Mytilisepta keenae</i> (Nomura 1936)				1	2+(3.5)	10+(1)	(0.5)		(2.5)	2	2+(2)	2	(1)			1	(1)		20	7	
		<i>Septifer bilocularis</i> (Linnaeus 1758)				2+4	1	4													11	3	
		<i>Leiosolenus lischkei</i> Huber 2010					1	1													2	2	
		<i>Gregariella coralliphaga</i> (Gmelin 1791)					1	1			1+(1)						(0.5)	1			4	4	
Ostreidae		<i>Magallana gigas</i> (Thunberg 1793)								1											1	1	
		<i>Saccostrea kegaki</i> Torigoe & Inaba 1981		3																0.5	3.5	2	
Limidae		<i>Ctenoides lischkei</i> (Lamy 1930)								(0.5)											0	0	
Pectinidae		<i>Laevichlamys cuneata</i> (Reeve 1853)					1		(0.5)						(0.5)		(0.5)		0.5		1.5	2	
Spondyliidae		<i>Spondylus squamosus</i> Schreibers 1793					1						2	1+(0.5)	1			3+1	1		10	6	
Anomiidae		<i>Anomia chinensis</i> Philippi 1849								1+1.5				1					0.5		4	3	
Carditidae		<i>Cardita leana</i> Dunker 1860					3+1			1+0.5+(0.5)	4+(1)	2.5+0.5	1+5	8	1+(1)			(1)	(1)		23.5	7	
Lucinidae		<i>Epicodakia delicatula</i> (Pilsbry 1904)															(0.5)		0.5		0.5		

Table 1. (Continued)

	Species	1	2	3	4	5A	5B	6A	6B	7A	7B	8A	8B	9	10	11	12	13	14	Number of individuals	Occurrence
Bivalvia	Tellinidae <i>Heteromacoma irus</i> (Hanley 1845)							(0.5)	0.5										(0.5)	0.5	1
	Semelidae <i>Ervilia bisculpta</i> Gould 1861							0.5	2											2.5	2
	Pholadidae <i>Penitella kamakurensis</i> (Yokoyama 1922)						2													2	1
	<i>Barnea manilensis</i> (Philippi 1847)						1													1	1
	<i>Nettastomella japonica</i> (Yokoyama 1920)				1+1		4+1			(1)										7	2
Polylaplacophora	Ischnochitonidae <i>Ischnochiton comptus</i> (Gould 1859)					2														2	1
	<i>Ischnochiton boninensis</i> Bergenhayn 1933					4	2	1												7	3
	<i>Lepidozona coreanica</i> (Reeve 1847)						1	2										2		5	3
	Chitonidae <i>Onithochiton hirasei</i> Pilsbry 1901				1	3				2									1	7	4
	<i>Rhyssoplax kurodai</i> (Taki & Taki 1929)					1				1		1		1						4	4
	<i>Rhyssoplax komaiana</i> (Taki & Taki 1929)					2														2	1
	Mopaliidae <i>Placiphorella stimpsoni</i> (Gould 1859)					1			1											2	2
	Acanthochitonidae <i>Acanthochitona achates</i> (Gould 1859)			1	1															2	2
	Number of species for each quadrat	1	3	3	15	30	20	26	32	19	12	12	17	12	5	4	16	20	8		

Table 2. Other benthic species observed in the quadrat survey. Occurrences of annelids are indicated by a plus sign. Algal cover values are percentages of quadrat area; the percent symbol is omitted in the table.

	Taxon	Species	1	2	3	4	5A	5B	6A	6B	7A	7B	8A	8B	9	10	11	12	13	14	Number of individual	Occurrence
Echinodermata	Asteroidea	Echinasteridae <i>Henricia</i> sp.							1												1	1
		Asterinidae <i>Patiria pectinifera</i> (Müller & Troschel 1842)							1												1	1
	Echinoidea	Echinometridae <i>Heliocidaris crassispina</i> (Agassiz 1864)				1	5	8		1	6	1		6	2				1		31	9
		Temnopleuridae <i>Temnopleurus toreumaticus</i> (Leske 1778)						1													1	1
		Strongylocentrotidae <i>Hemicentrotus pulcherrimus</i> (Agassiz 1864)				2	3					11		2							18	4
Arthropoda	Crustacea	Decapoda <i>Paguroidea</i> spp.						1	1		1		3		2		1	2			11	7
		Porcellanidae spp.					3	2		2					1						8	4
		Brachyura spp.				2		1		1	1										5	4
		<i>Pugettia</i> sp.						2				1	1	1							5	4
		<i>Hemigrapsus sanguineus</i> (De Haan 1835)													1						1	1
		Sessilia <i>Balanomorpha</i> spp.					1														1	1
	Annelida	Polychaeta spp.		+	+	+		+		+	+				+	+	+	+			—	10
Archaeplastida	Rhodophyta	Corallinaceae spp.		30	30	70	60	90	70	70	90	100	40	90	100	90	60	90	90	90	—	17
	Chlorophyta	Ulvaes spp.								10				10	10			10			—	4
Ochrophyta	Phaeophyceae	Sargassaceae spp.				10	10		20	30				10		10		10	10		—	8

that other benthic taxa, like arthropods, could have moved downward after the earthquake, our survey allows us to chronicle a mortality event while the spatial pattern of benthic fauna, especially mollusks, was still preserved.

Quantitative, fine-scale documentation of die-offs occurring soon after a seismic event is rare, highlighting the rich biodiversity of coastal benthic fauna on the Sea of Japan and its loss. Previous studies (Yajima 1978a, b) typically listed roughly around 10 taxa per locality on the Sea of Japan probably reflecting the specific objectives and coverage, but our dataset far exceeds these numbers. Studies fo-

cusing on recovery process of benthic fauna from the seismic disaster underlined that post-disaster faunal change continued for several years or more (Castilla 1988; Seike et al. 2013; Noda & Iwasaki 2017). Benthic fauna in the intertidal to uppermost subtidal zones around west side of Noto Peninsula will experience similar or even more significant biological succession, since approximately 3.6–3.9 m uplift at a maximum far exceeds the tidal range on the Sea of Japan.

Reconstructing the pre-disaster vertical distribution of benthic fauna

Clear patterns in the vertical distribution of benthic fauna allowed us to infer the pre-earthquake range of the intertidal zone. The co-occurrence at Quadrat 2 of sessile organisms *Saccostrea kegaki* and coralline algae suggests that the pre-disaster upper intertidal limit was just above this horizon. Quadrat 2 was located 3.8 m above the sea surface during our survey. This vertical interval was generally consistent with the range observed between sessile organism remains and the sea level at Kaiso fishing port in a previous survey (3.6–3.9 m in January 2024; Shishikura et al. 2024a, b). The vertical distance between Quadrats 2 and 4 was approximately 40 cm. The maximum width of the intertidal zone (i.e., between the summer high-water line and the spring low-water line) at Wajima in 2024 was approximately 60 cm, and the mean diurnal tidal range was approximately 40 cm (Japan Meteorological Agency 2024b). According to Yajima (1978a, b), who conducted a comprehensive survey of the coastal marine benthic biota around the Noto Peninsula, *Cellana toreuma* and *Patelloida saccharina*, *Echinolittorina radiata*, were primarily distributed in the upper intertidal to supratidal zone and exhibited vertical movement in response to seasonal tidal cycles. Also, Yajima (1978a, b) reported that *Echinolittorina radiata* appears supratidal zone, and *Acanthochitona achates* is typically found above the annual mean sea level (i.e., above the high-water line in spring and below the summer low-water line). Our observed vertical distribution of these species was consistent with that of both previous studies, if our assumption of intertidal zone.

The pre-disaster benthic biota in the Kaiso Reef exhibited the greatest diversity in the mid-lower intertidal to uppermost subtidal zone, particularly in the inner reef areas, where wave exposure was relatively reduced. The concentration below the presumptive uppermost subtidal zone (i.e. below Quadrat 5) of algal-associated gastropods, together with numerous crustaceans and echinoids suggest that a thriving biotic community, sheltered by macroalgae, flourished in this zone before the earthquake. In addition, many rock-boring bivalves were chiefly discovered within the presumed lower intertidal zone. The remaining organisms in this area are expected to be gradually washed away by rainfall; however, the shells of boring bivalves will likely remain as indicators of the pre-disaster intertidal zone. Further downstream, in Quadrats 7–9, the species diversity was slightly lower, and drastically diminished in Quadrats 10–11. This could be related to sand deposition and/or weak tsunami impact.

Comparison of the benthic fauna between adjoining sites

The Kaiso fishing port and its adjoining locality, Kaiso Reef, exhibited distinct biota, likely attributable to variations in substrate and wave exposure. Morino (2024), which investigated sessile organisms in Kaiso area using

a method similar to ours reported that benthic diversity on vertical harbor walls was lower than that on natural rocky reefs, and suggested that this difference was attributable to the surface irregularities formed by soft rock substrates in Kaiso Reef. These results call for a reassessment of the prevailing view that benthic diversity is comparatively low in the semi-enclosed Sea of Japan, and suggest that post-earthquake recovery process will be heterogeneous across microtopographic settings.

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