Estimates of mortality in sandy beach populations of Haustorioides japonicus (Amphipoda: Crustacea) and Excirolana chiltoni (Isopoda: Crustacea) during winter storm seasons

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Estimates of mortality in sandy beach populations of *Haustorioides japonicus* (Amphipoda: Crustacea) and *Excirolana chiltoni* (Isopoda: Crustacea) during winter storm seasons

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Abstract: Sandy beach habitats are mainly controlled by the physical environmental factors. This study investigated the effects of winter storms on populations of sandy beach infaunal peracarids. Two contrasting areas on the Japan Sea coast were selected: exposed sandy beaches in Niigata and protected sandy beaches in Sado. Regional differences in the mortality rate of two species of peracarids, *Haustorioides japonicus* and *Excirolana chiltoni*, were examined over two years, focusing on periods of high storm intensity (fall and winter) when sandy beach habitats are frequently disturbed. The results demonstrated that: (1) the mortality rate on the exposed beaches (Niigata) was significantly higher than that on the protected beaches (Sado); (2) the mortality rate in 2009–2010 was significantly higher than that in 2008–2009; and (3) the mortality rates were not significantly different between the two species. Sediment grain size, sorting coefficient, and beach slope were not different between the two study areas. Dominant waves during the stormy seasons were from the northwest, to which the beaches in Niigata were directly exposed. Moreover, mean wave height was higher in 2009–2010 than in 2008–2009. Therefore, the variations in wave disturbances were herein considered to be the major cause of the mortality variations in the two species. According to the predicted scenarios of climate changes, wave intensification will likely increase in the future, therefore increasing the mortality and the potential risk of local extinctions of these sandy beach infaunal animals.

Key words: disturbance, monsoon, population dynamics, sandy shore, survival, wave exposure

Introduction

Sandy beach habitats have unique characteristics that are predominantly controlled by physical environmental factors (McLachlan & Brown 2006). Because of the frequent disturbances caused by waves and wind on sandy beach substrates, organisms inhabiting these areas have

specific adaptations especially regarding their physiology, behavior, and life history traits (McLachlan & Brown 2006, Suda 2017). Larger impacts and higher frequencies of disturbances have been suggested to decrease performance of sandy beach organisms in relation to growth, survival, and reproduction (Defeo et al. 2003, Defeo & Martínez 2003). In addition, according to predictions of future global climate change (IPCC 2014), the frequency of extreme storms may increase, which may further induce habitat alternations, lower survival rates, and then poten-

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tially lead to local extinctions of sandy beach organisms. Several studies with field observations have reported that severe storms led to decreased abundances and altered assemblages of sandy beach animals (Alves & Pezzuto 2009, Lucrezi et al. 2010, Harris et al. 2011, Machado et al. 2016, Corte et al. 2017).

Around the Japan Sea area, the combined effects of sea level rise and frequent storms are predicted to accelerate degradation of sandy beach habitats (Yoshida et al. 2013), which is a potential risk for local benthic populations. On sandy beaches around the Sado and Niigata areas of the Japan Sea coast, two species of peracarid crustaceans are currently abundant (Takada et al. 2015, 2016): *Haustorioides japonicus* Kamihira, 1977 (Dogielinotidae: Amphipoda) and *Excirolana chiltoni* (Richardson, 1905) (Cirolanidae: Isopoda). Both species have a wide geographic distribution range in Japan, from Kyushu to Hokkaido (Bruce & Jones 1981, Kamihira 2000a). Individuals of these species usually burrow into the surface of sandy sediment of the swash zone (Kamihira 1979, 1992, Kaneko & Omori 2003). Females carry embryos in a brood pouch and juveniles develop directly without planktonic dispersal stages (Kamihira 1992, Kaneko & Omori 2005). Hence, because of the absence of migration between adjacent beaches, each sandy beach is considered to correspond to a single population of these peracarid species.

A demographic study of *H. japonicus* in Niigata demonstrated that the populations increased from spring to summer as a result of multiple events of recruitment of juveniles; then, from fall to winter, recruitment did not occur and the populations decreased (Suzuki et al. 2013). A similar seasonal life history was observed in *E. chiltoni* (Kaneko & Omori 2005): its recruitment occurred only in the warm season. Although these two species occur sympatrically on sandy beaches, *E. chiltoni* inhabits a wider vertical range of the intertidal zone and is mostly observed in the upper zone in comparison to *H. japonicus* (Takada et al. 2016). This is a consequence of *E. chiltoni*'s higher adaptation to the development of suction toward the upper zone of the sandy beach (Sassa et al. 2014, Yang et al. 2016); suction is negative pore water pressure relative to the atmospheric air pressure and governs sediment environment including hardness and moisture.

On the Japan Sea coast, fall and winter are the stormy seasons, when northern winds predominate and monsoon storms frequently change the profile of sandy beaches by erosion or deposition (Naganuma 2000). In order to adapt to these disturbances, sandy beach peracarids are known to change their position on the shore according to the geophysical environment changes, which are characterized by suction (Yang et al. 2016). Despite these species' adaptations, frequent disturbances increase their risk of being washed offshore, to the upper shore, or buried deeper into the sandy substrates, thereby preventing relocation to their suitable habitats. When they are displaced from their suitable habitats, predation by crabs, fishes, and birds, and
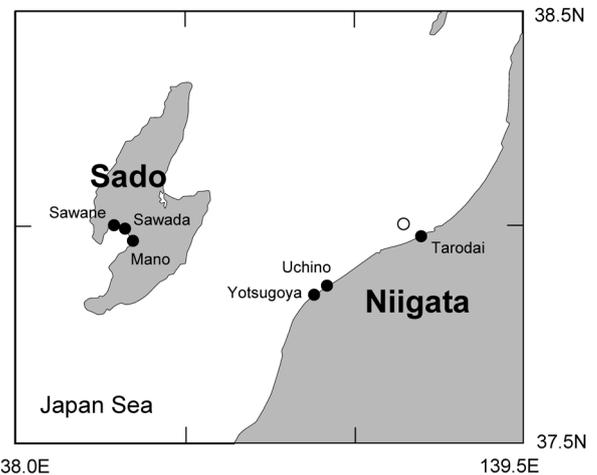
Fig. 1. Location of the sampling sites. The three sampling sites in Sado are protected in an inner bay and the three sites in Niigata are exposed to waves. Open circle indicates the wave observatory at the Off-Niigata station.

accumulation of physical and physiological damages increase the mortality rate of these sandy beach peracarids. Therefore, monsoon storms are considered a major factor of mortality of these peracarids during stormy seasons. Sandy beaches in Niigata face northwest, being therefore directly exposed to monsoon storms; in contrast, some beaches in Sado face southwest, are located in inner bay areas and are therefore largely protected from the direct effects of these storms (Fig. 1). A comparison of mortality rates of peracarids on these open and wave-protected sandy beaches provides a good opportunity to study the effects of winter storms on populations of sandy beach infauna.

Thus, the aim of the present study was to examine regional differences in the mortality rate of sandy beach infaunal peracarids during stormy seasons (fall and winter) when sandy beach habitats are frequently disturbed. Additionally, interspecific and annual variations in the mortality rates were also examined. The hypothesis herein tested was that the mortality of peracarid crustaceans was lower on the wave-protected beaches than on the open beaches.

Materials and Methods

Peracarid sampling

Field surveys were conducted on six sandy beach sites along the Japan Sea coast (Fig. 1). Three sites were in Sado (Sawane, Sawada, and Mano), located in the inner area of Mano Bay and largely protected from waves. The other three sites were in Niigata (Tarodai, Uchino, and Yotsugoya) and were the same study sites as in Suzuki et al. (2013); these sites were on open coasts facing the waves. In winter, harsh wind-driven waves frequently occur in this area; in contrast, generally calm weather and wave conditions occur in summer (Naganuma 2000). The mean spring tide is approximately 0.3 m. The study period was from

2008 to 2010, and 54 samplings were performed with ∼6–12- months intervals at the six sites. Coastal seawater temperatures in Niigata varied from 9.6 to 26.5℃ and 9.3 to 23.7℃ and temperatures in Sado were from 8.1 to 26.0℃ and 7.6 to 24.9℃ from September 2008 to March 2009 and September 2009 to March 2010, respectively (Niigata Prefectural Fisheries and Marine Research Institute 2009, 2010). Therefore, the variation between the two study periods and the two areas was similar.

At each study site, three transect lines were set perpendicularly to the shore line, while four lines were set in four sampling dates in 2010. Along the transect lines, samples of sediment columns (10 cm in diameter and 10 cm in depth) were collected using a cylindrical core sampler at 1-m intervals from the drift line to a point of 50 cm in depth. The number of stations where core samplings were performed ranged from 6 to 15 according to the beach slope. Using this sampling procedure, we covered the entire vertical distribution range of the two species (Takada et al. 2016) and estimated the abundance of the benthic macrofauna along the transect lines, which is equivalent to the abundance per strip transect (Brazeiro & Defeo 1996). We used this approach to avoid problems associated with fluctuations in density per unit area resulting from temporal changes in shore profiles between calm and rough conditions. All benthic macrofauna organisms were separated from the sediment by using a sieve (1-mm mesh) and preserved in a plastic bag with 70% ethanol. In the laboratory, *H. japonicus* and *E. chiltoni* were separated and counted.

Environmental factors

In order to estimate the median grain size ($\phi50$) and sorting coefficient (($\phi16$–$\phi84$)/2) of each beach, surface sediment up to 3 cm in depth were obtained in the swash zone during the samplings. The samples of wet sediment were sieved using a series of mesh sizes (2, 1, 0.5, 0.25, 0.125, and 0.063 mm). Phi-scale values of $\phi16$, $\phi50$, and $\phi84$ were obtained by interpolation with the best-fit sigmoid curves for the cumulative distribution of the sediment dry weight (Bale and Kenny 2005). Slope angle was measured along each transect with an inclinometer (Shinwa Rules, Sanjo). Because these environmental data were not measured in nine samplings in 2009, only data from 45 of the 54 samplings were used for nested analysis of variances (nested ANOVAs). The explanatory factors were: Season (January–March, April–June, July–September, and October–December), Area (Sado and Niigata), and Site within Area (Sawane, Sawada and Mano in Sado, and Tarodai, Uchino, and Yotsugoya in Niigata).

In order to compare annual variation in wave disturbance, data on significant wave height and wave direction at the Off-Niigata station (38°00′17″N, 139°07′34″E, Fig. 1) was obtained from the NOWPHAS (Nationwide Ocean Wave information network for Ports and Harbours) (Kawai et al. 2011). The wave data was compiled into 2-h intervals. Mean significant wave heights were estimated from the square-root transformed values because the data were right-tailed. The probability of occurrence of high wave events (significant wave height>5 m) was compared between two periods: from September to March in 2008–2009 and 2009–2010. Mean wave direction was estimated and Watson's Two-sample test was carried out to test whether the distribution of wind direction was common between the two periods. These analyses were performed using the circular package in R 3.3.3 (R Core Team 2017).

Mortality estimate

To estimate mortality rates, the abundance data of the two species during the two seasons without recruitment of juveniles, from August to March in 2008–2009 and 2009–2010 were used. Mortality rates were estimated from the temporal changes in the abundances using the exponential regression model and negative binomial distribution was applied to the observed abundance y with the rate parameter r:

$$mu_t = \exp(a - b \times t),$$
$$y \sim \text{Negative Binomial}\,(r/(r+mu), r),$$

where mu_t was the mean abundance of day t; a was the parameter of abundance at $t=0$; b was the daily mortality rate; and t was the number of days from the initial observation. To describe initial variations of abundances in species, year, and spatial hierarchy of sites within the two areas (Niigata and Sado), parameter a was calculated as the sum of two parameters:

$$a = a1(species, \; area, \; site \; in \; area) + a2(year, \; species),$$
$$a1 \sim \text{Normal}(c(species, \; area), \; sigma(species, \; area)).$$

Parameter $a1$ represented site variations within the area that were hierarchically defined based on area mean c and site random effects $sigma$. Moreover, to describe mortality variations in species, year, and the two areas, parameter b was the product of four parameters:

$$b = b1 \times b2(area) \times b3(year) \times b4(species).$$

Therefore, $a2=0$ indicates no variation in the initial abundances between the two years of observations, and $b2=1$, $b3=1$, and $b4=1$ indicates no variations in the mortality rates between area, year, and species, respectively. If the 95% credible interval (CI) of these parameters did not include the critical values (0 or 1), the parameters were considered to be significant.

The parameters of these models were estimated using Bayesian inference with a Markov Chain Monte Carlo (MCMC) simulation. All parameters were assigned conservative and weakly informative priors:

$$a2, \; c \sim \text{Normal}(0, \; 0.0001),$$
$$b1 \sim \text{Gamma}(1, \; 1),$$
$$b2, \; b3, \; b4 \sim \text{Normal}(1, \; 1),$$
$$r \sim \text{Exponential}(0.001),$$
$$sigma \sim \text{Gamma}(0.001, \; 0.001).$$
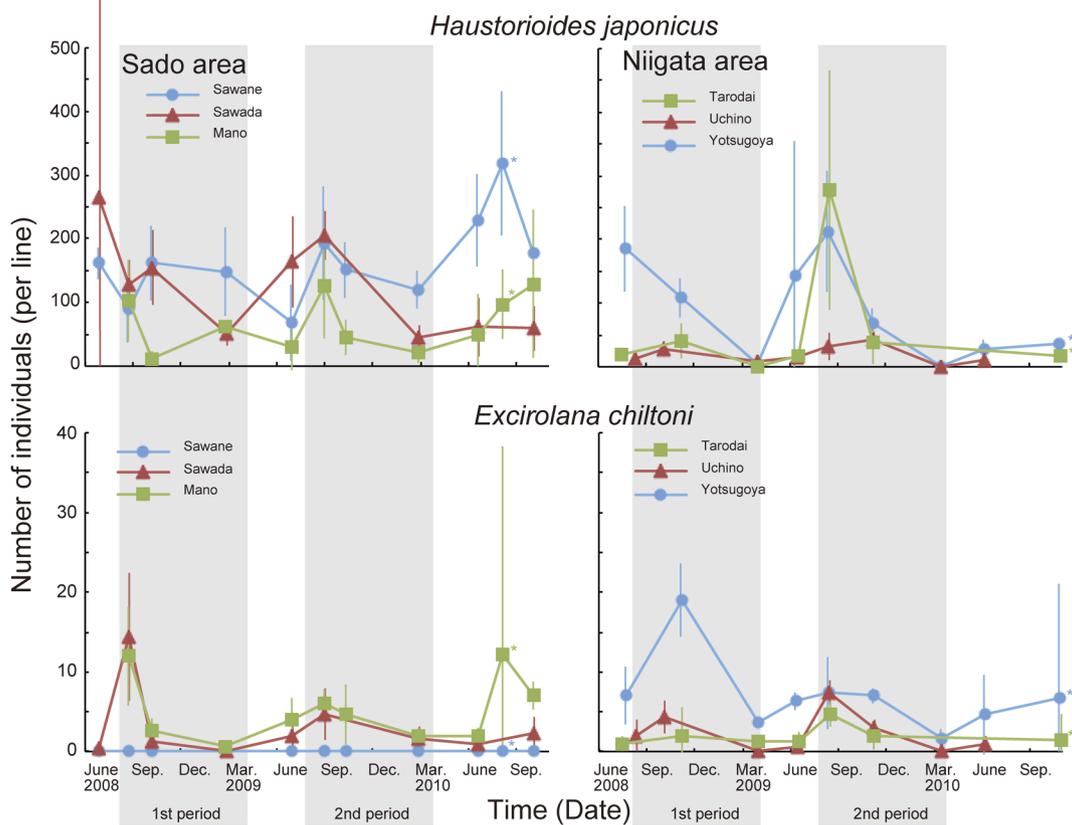
Fig. 2. Temporal changes in abundances of *Haustorioides japonicus* and *Excirolana chiltoni* in the three sites in Sado (Sawane, Sawada, and Mano) and the three sites in Niigata (Tarodai, Uchino, and Yotsugoya). Mean number of individuals captured per line (n=3, *n=4)±SD are shown. Shaded areas represent the periods of mortality estimates (1st and 2nd periods) with no recruitment of juveniles.

Five chains of MCMC simulations were performed for 51,000 steps. After discarding the first 1,000 steps as the burn-in period, we sampled at a 10-step interval. The convergence of the Markov chains was assessed using the Gelman–Rubin statistics; values under 1.05 were considered indicative of convergence, and convergence increased as the value became closer to 1. This assessment was performed using the rjags package in R and JAGS 4.3.0 (Plummer 2003).

In addition to the aforementioned full model, two reduced models were analyzed; the common mortality model with fixed $b2=1$, $b3=1$, $b4=1$ and the null model with only one intercept. To evaluate these models, verification using "leave-one-out cross-validation" (LOO) was also estimated with the loo package (Vehtari et al. 2017).

Results

Abundance of *H. japonicus* and *E. chiltoni* fluctuated temporally and spatially (Fig. 2). At each sampling occasion, *H. japonicus* was generally more abundant than *E. chiltoni*. Although the variations between transect lines were very large, the abundances of both species in summer were larger than those in winter, with a seasonal decreasing period from around August to March.

Bayesian inferences successfully estimated the mortality rates of the two species. Among the three models, the full model showed the lowest LOO values (251.6), followed by the common mortality model (260.5), and the null model was the highest (293.0). Therefore, the full model was chosen among the three tested models.

According to the posterior distributions of the parameters of the full model (Table 3), the mean values of parameter $b1$ showed that daily mortality rate of *H. japonicus* in Sado during the winter of 2008–2009 was 0.00506 (=1−exp(−0.00507)) (Table 1). Considering parameters $b2$ and $b3$, the mortality rate in Niigata was estimated as 2.2 times larger than that in Sado, and the mortality rate during the winter of 2009–2010 was 1.6 times larger than that of the winter of 2008–2009. Thus, the daily mortality rate in Niigata during the winter of 2009–2010 was 0.01772 (=1−exp(−0.00507×2.195×1.607). The CIs of parameters $b2$, $b3$, and $b4$ demonstrated that the mortality rates were significantly different between the areas (Sado<Niigata) and years (2008–2009<2009–2010) but not significantly different between the species (*H. japonicus* and *E. chiltoni*). The CIs of parameters c and the random effect parameters *sigma* showed that initial abundances varied considerably between species, areas, and sites. The CIs of the parameter $a2$ indicated that the initial abundances between the two

years were significantly different for *H. japonicus*, but not for *E. chiltoni*.

Median grain size (ϕ) ranged from 0.42 to 2.92 (0.13–

Table 1. Posterior distribution of parameters of the full exponential regression model to estimate mortality rates of the two species in the Sado and Niigata areas. Parameters with subscript Hj indicate *Haustorioides japonicus* and those with Ec indicate *Excirolana chiltoni*.

	Mean	SD	2.5%	97.5%
Mortality				
$b1$	0.00507	0.00097	0.00334	0.00713
$b2$ (area)	**2.195**	**0.431**	**1.472**	**3.155**
$b3$ (year)	**1.607**	**0.306**	**1.100**	**2.297**
$b4$ (species)	0.859	0.193	0.529	1.284
Abundance				
$c_{Hj, Sado}$	4.841	0.846	3.706	5.984
$c_{Hj, Niigata}$	4.242	0.538	3.526	4.926
$c_{Ec, Sado}$	−3.836	17.590	−44.960	17.480
$c_{Ec, Niigata}$	1.927	1.405	0.140	3.741
$sigma_{Hj, Sado}$	17.309	89.830	0.123	97.280
$sigma_{Hj, Niigata}$	141.7	353.2	0.452	1097.0
$sigma_{Ec, Sado}$	0.0583	0.1044	0.00009035	0.3546
$sigma_{Ec, Niigata}$	4.272	34.130	0.04958	16.510
$a2_{Hj}$	**0.616**	**0.229**	**0.174**	**1.066**
$a2_{Ec}$	0.216	0.254	−0.276	0.720
r	1.558	0.209	1.186	2.005

Bold numbers for the parameters indicate that the credible intervals do not include 1 (in $b2$, $b3$) or 0 (in $a2$); $a2$: initial abundance, $b1$–$b4$: mortality rates, cs: random effect parameters for the mean of the initial abundances within the areas, $sigma$s: random effect parameters for the variances of the initial abundances within the areas, r: rate parameter of the negative binomial distribution.

0.75 mm) and 1.45 to 3.07 (0.12–0.37 mm) in Sado and Niigata, respectively. The factors of Season and Area were not significant in the nested ANOVA (Tables 2 and 3), although Site within Area was significant. Sorting coefficient (ϕ) ranged from 0.29 to 1.77 and from 0.31 to 0.77 in Sado and Niigata, respectively. Although the mean values in Niigata tended to decrease in cold seasons (Table 2), seasonal and areal variations were not significant (Table 3). As in the median grain size, Site within Area was also significant for the sorting coefficient. Slope angle ranged from 2.0 to 9.7 and from 2.9 to 11.5 in Sado and Niigata, respectively. The mean slope angle in Niigata tended to decrease in cold seasons (Table 2), but the nested ANOVA did not detect any significance for Season and Area (Table 3).

The mean values of the significant wave height were 1.07 m ($=(1.033)^2$) and 1.24 m ($=(1.111)^2$) in 2008–2009 and 2009–2010, respectively (Table 4). A statistically significant difference in the mean values was detected between the two periods (Welch's t-test for square-rooted values, t=6.08, df=4229, p<0.005). Probability occurrences of high wave events (significant wave height>5 m) were 0.47% and 0.94% in 2008–2009 and in 2009–2010, respectively, and these values showed a marginally significant difference (Fisher's exact test p=0.066). Mean wave direction was from the northwest in both years (Table 4, Fig. 3). Watson's Two-sample test showed a statistically significant difference between the wind distributions of the two periods (test statistics 1.348, p<0.001).

Discussion

Local and temporal fluctuations in the populations

The quantitative field sampling of the present study indicated the existence of local and temporal fluctuations in

Table 2. Seasonal variations of median grain size, sorting coefficient, and slope angle (mean±SD) in the Sado and Niigata areas.

	Median grain size (ϕ)		Sorting coefficient (ϕ)		Slope angle (degree)		n	
	Sado	Niigata	Sado	Niigata	Sado	Niigata	Sado	Niigata
January–March	2.20±0.53	2.18±0.14	0.75±0.59	0.36±0.05	6.03±2.50	3.85±0.21	6	2
April–June	2.06±0.97	1.87±0.18	0.47±0.19	0.60±0.07	7.88±1.11	8.80±3.11	8	2
July–September	2.32±0.39	2.17±0.83	0.50±0.15	0.54±0.21	6.54±2.70	10.17±0.58	11	3
October–December	2.35±0.37	2.08±0.22	0.52±0.19	0.39±0.10	6.96±1.85	6.23±3.16	5	8

Table 3. Results of the nested analysis of variance for three environmental factors.

	df	Median grain size			Sorting coefficient			Slope angle		
		ssq	F	p	ssq	F	p	ssq	F	p
Season	3	0.416	1.097	0.363	0.234	1.462	0.241	33.80	1.982	0.134
Area	1	0.265	2.101	0.156	0.053	0.984	0.328	2.37	0.418	0.522
Site in Area	4	7.319	14.494	<0.001	0.828	3.883	0.010	40.93	1.800	0.150
Residual	36	4.545			1.919			204.62		

Table 4. Summary of the significant wave height and wave direction from September to March period at the Off-Niigata station. This data was obtained from the NOWPHAS database.

	1st period (2008–2009)	2nd period (2009–2010)
Significant wave height (Hs)		
Observed number	2541	1917
Number of high wave events (Hs>5 m)	12	18
Maximum (m)	5.53	5.94
Square-rooted mean ($\sqrt{Hs}$)±SD	1.033±0.437	1.111±0.415
Wave direction		
Mean (clockwise from north)	323.4°	326.2°
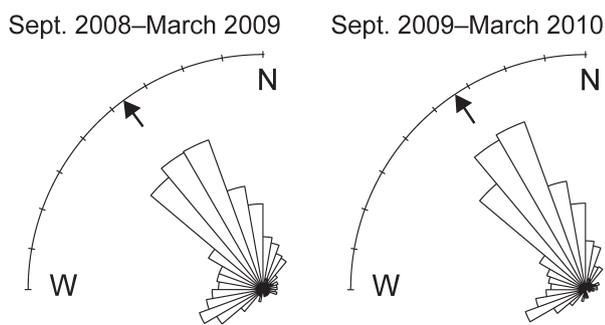
Fig. 3. Frequency histograms of wave direction from September to March in the 2008–2009 and 2009–2010 periods. Radius of each segment was proportional to the square root of the frequency. Arrows show the mean directions.

the abundance of the two peracarid species, *H. japonicus* and *E. chiltoni,* on the sandy beaches in the Sado and Niigata areas. Local variations in density of the two species have been recognized in previous studies on coasts of the Japan Sea (Hasegawa & Yajima 2000, Okumura et al. 2001, Suzuki et al. 2013, Takada et al. 2015, 2016) and Hokkaido (Kamihira 1992). Takada et al. (2015) showed that several environmental factors, including median grain size and sorting coefficient, affect the density of the two species; however, these results were based only on observations made during the summer, when these species' populations are increasing as a result of seasonal high recruitment. The present study focused on the decreasing phases of their populations.

The results of the present study clearly demonstrated the seasonal fluctuations in abundance of the two species both in the Sado and Niigata areas: abundance was high in summer and low in winter. Similar seasonal fluctuations were reported in previous studies on *H. japonicus* (Kamihira 1992, 2000b, Suzuki et al. 2013) and *E. chiltoni* (Kaneko & Omori 2005). One of the main differences in their life history is that *H. japonicus* has multiple generations per year (Kamihira 1992, 2000b, Suzuki et al. 2013), except in some populations in Hokkaido (northern Japan) (Kamihira 1992), whereas each generation of *E. chiltoni* lasts one year or more (Kaneko & Omori 2003). Moreover, it is known

that no recruitment occurs for both the species during winter (Kaneko & Omori 2005, Suzuki et al. 2013). Thus, the present study estimated the mortality of over-wintering individuals of both species during the stormy seasons (fall and winter).

Environmental factors

In this study, three beach characteristics—the median grain size, the sorting coefficient, and the slope angle—showed no statistically significant variations between Sado and Niigata areas. Regarding sediment characteristics, a part of the reason of this insignificance was the large variation between the sites within both areas. These beach characteristics are related to the classical morphodynamic beach types that govern the physical environment, and hence the ecological processes of sandy beaches (McLachlan & Brown 2006). In this context, dissipative beaches have a gentle slope, finer grain size, and diverse and abundant macrofauna, whereas reflective beaches have a steep slope, larger grain size, and less diverse and less abundant macrofauna (Defeo & McLachlan 2005, McLachlan & Brown 2006). The mortality rate of *E. braziliensis*, a congeneric species of *E. chiltoni*, has been shown to be higher on a reflective beach than on a dissipative beach (Defeo & Martínez 2003), and fecundity of *E. braziliensis* has been shown to be lower on a reflective beach (Caetano et al. 2006). In contrast, in the present study, local variations in mortality of the two peracarid species did not correspond to the variations in the three beach characteristics, indicating a lower importance of these factors and of the aforementioned morphodynamic classification.

Change of slope angle is a consequence of sediment reworking processes, i.e., erosion and sand deposition. Sediment reworking disturbs the habitats of burrowing animals on sandy beaches and increases their mortality risks because of increased predation and/or physiological damages. In the present study, although it was not statistically significant, slope angle showed a seasonal change in both areas: steep in summer and gentle in winter, corresponding to low waves and high waves, respectively (Takeda & Sunamura 1983). The large seasonal variation of slope angle in Niigata supports the hypothesis that there was a large amount of sediment reworking over the year. Yang et al. (2016) demonstrated short-term changes in the vertical distribution pattern of sandy beach infaunal peracarids as a result of storm-induced changes of beach profiles; they concluded that both *H. japonicus* and *E. chiltoni* are well adapted to short-term disturbances. Nevertheless, despite their short-term adaptations, frequent wave disturbances over the winter may lead to cumulative deleterious effects on their populations.

In this study, although the impact of storm waves and the resulting sediment reworking on the beaches were not directly observed, the data obtained from NOWPHAS on wave height and direction demonstrated the wave climate of the study area. During the winter (September–March),
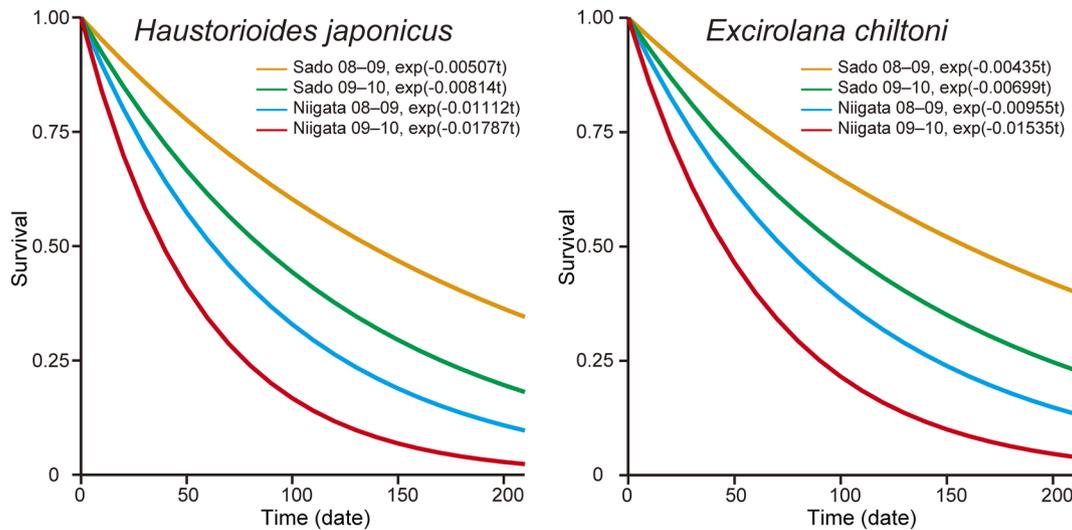
Fig. 4. Survival curves of *Haustorioides japonicus* and *Excirolana chiltoni* reconstructed by using the mean values of the posterior distribution of the parameters ($b1$, $b2$, $b3$, and $b4$, Table 1) of the full exponential regression model for 210 days corresponding to the observation period (September–March).

the sandy beaches in Niigata were directly exposed to waves from the northwest, while the beaches in Sado were largely protected because of the southwestwards opening of the bay (Fig. 1).

According to a sandy beach erosion model (Sunamura & Horikawa 1974, Takeda & Sunamura 1983) that including wave, beach slope, and grain size as variables, conditions of the high wave (significant high wave>5 m) and the average waves (Table 4) recorded in the present study can be categorized as "Bar formation"; this means that the dominant process is that sandy sediment on a beach is eroded and the sediment moves offshore forming a bar. Therefore, frequent severe storms with high waves in winter lead to increased erosive processes, which in turn increase the risk of being washed-out for the two peracarid species in the study areas.

Mortality rates

In the mortality rate estimates, all three models were converged in the MCMC simulations, indicating the validity of the assumptions of the models, which are the constant daily mortality rates during the winter periods and the negative binomial distribution of the observed abundance data. This also indicates that ambient temperature, which decreased during the study periods from fall to winter, have little effect on the regional differences of the mortality rates. Among the three models, the full model had the lowest LOO values. The posterior distribution of the parameters of the full model indicated that: (1) the mortality rate in Niigata was significantly higher than that in Sado; (2) the mortality rate in 2009–2010 was significantly higher than that in 2008–2009; and (3) the mortality rates were not significantly different between the two species. Survival curves were reconstructed by using the estimated parameters ($b1$, $b2$, $b3$, and $b4$) for 210 days, (i.e., each

7-month periods of the observation) (Fig. 4). The survival curves well illustrate the local, temporal, and interspecific variations in the mortality rates.

The present results support the hypothesis that the mortality rate on the wave-protected beaches (Sado) is lower than that on the open beaches (Niigata). Although this study did not evaluate the direct impact of high waves on sediment reworking on sandy beaches, it clearly supported the hypothesis that frequent disturbances resulting from the predominant waves from the northwest subsequently lead to the higher mortality in Niigata. The concordance between the annual variations in mortality and wave height also strengthened the hypothesis of the predominant effect of waves. The maximum and the mean significant wave heights, as well as the frequency of high waves events, were higher during the 2009–2010 period (Table 4), when the mortality rate was also higher.

The present study estimated the daily mortality of *H. japonicus* as 0.018 during the winter of 2009–2010 in Niigata, which is within Suzuki et al. (2013)'s estimate of 0.016–0.031. Kamihira (1992) reported average annual variations of 0.009 in the mortality rate of *H. japonicus* in Hakodate, Hokkaido, which is similar to the value of 0.005 herein presented for the winter of 2008–2009 in Sado. No significant differences in the estimated mortality of *H. japonicus* and *E. chiltoni* indicated that the factors caused almost the same impacts on the two species. Both species inhabit on the intertidal zone of sandy beaches, and the vertical distribution range of *E. chiltoni* is generally slightly higher than that of *H. japonicus* (Kaneko & Omori 2003, Takada et al. 2016). This difference is partly because of the *E. chiltoni*'s higher ability of burrowing into harder sediment that occurs on the upper intertidal zone (Sassa et al. 2014). This information may lead to a prediction that *E. chiltoni* would have a lower mortality than *H. japonicus*; however, in real-

ity, wave disturbances in winter may be high enough to override these differences in vertical distribution and burrowing ability.

Effects of increasing wave disturbances on sandy beach infauna

The survival of overwintering individuals is crucial for the persistence of the populations herein studied, because neither species has a planktonic dispersal stage and the burrowing behavior limits their migration to neighboring sandy beach habitats. A higher mortality rate during winter and a smaller population size on a beach increases the probability of local extinction. We hypothesize that this may have caused the absence of their populations on some sandy beaches within their geographic distribution ranges (Kamihira 1992, Takada et al. 2015, 2016).

According to the prediction of global climate change, the sea-level rise and wave intensification will decrease the width of sandy beaches and eventually induce disappearance of sandy beach habitats (Yoshida et al. 2013, Udo & Takeda 2017). The results of the present study indicate that, even before the loss of habitats, sandy beach peracarids may become extinct because of the increase in winter mortality caused by wave intensification. These peracarid species ecologically link the primary production and detrital organic matter that accumulates on sandy beaches (Kamihira 1992, Kaneko & Omori 2003) to upper trophic levels including fish and birds (Takahashi et al. 1999, Nuka et al. 2005). Therefore, local extinction of these peracarids will change the ecosystem functioning of the sandy beaches. To better manage sandy beach ecosystems and avoid problems related to predicted global climate changes, it is important to monitor population dynamics of sandy beach infauna in addition to their habitat environments.

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