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Small-scale spatial structure of two flatfish species, in Peter the Great Bay, Sea of Japan

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Density and spatial distributions on an intermediate scale of two flatfishes—marbled flounder *Pleuronectes yokohamae*, and the brown sole *Pleuronectes herzensteini* (Pisces: Pleuronectiformes) within large (10,000–100,000 m^2 patches of homogenous substratum (sand and silted sand)) were studied. Both species dominated in the demersal fish community. Densities of brown sole, were significantly higher in both types of habitat. Flatfish distribution was highly patchy and the mean fish densities in groups were as much as ten times higher than the mean fish densities in the area. More than 85% of all recorded flatfish were found within groups. Mixed groups with both species were most prevalent. The number of flatfish in one group ranged from 2 to 20. Brown sole was more abundant in the area and dominated in mixed groups. Levels of contacts between group members and densities within groups were inversely related to visibility condition. It is suggested that flatfish form a group and stay in the group, attracted by foraging movements of other flatfish and by plumes of upset particles caused by their bottom digging movements.

INTRODUCTION

Flatfish provide one of the most ecologically significant and industrially important fish species of the inshore zone of the Sea of Japan (Gavrilov et al., 1988; Takashi & Maeda, 1989). A demersal mode of life, relatively sluggish movements (Olla et al., 1969) and the peculiarity of their typical habitats, open areas of sea-floor make flatfish especially suitable for estimating spatial patterns and absolute density estimations using visual survey techniques. Knowledge about distribution at an intermediate scale (10–100 m; Hall et al., 1994) might be particularly important in areas where trawl fisheries are replaced with more environmentally friendly traps or seines. Conventional trawl or seine surveys can not obtain such data. Relative estimates, obtained during conventional surveys are important indices in fisheries studies, but they do not provide much information about spatial structure of the studied species in small and medium scales. Furthermore, visual surveys can be useful for gear (trawls and seines) calibration. Trawl surveys give 5–10 times lower flatfish density estimates, than visual diving surveys (Gavrilov et al., 1988; Gomelyuk & Shchetkov, 1993) because the fish are able to avoid the trawl (Vyscrebentcev, 1970; Wardle, 1986).

Most ecological studies of flatfish have been concerned with aspects of medium-scale and small-scale distribution in juveniles (age 0) within nursery areas (Gibson, 1973; Poxton & Nasir, 1985; Berghahn, 1986; van der Veer, 1986; Modin & Pihl, 1996).

This study is believed to be the first attempt to analyse the intermediate scale distribution and social structure of mature fish, not only in the marbled flounder *Pleuronectes yokohamae* Günter 1877, and the brown sole *P. herzensteini* (Jordan & Snyder, 1901), but in flatfish as a taxa.

Like many other Far Eastern flatfish *P. yokohamae* and *P. herzensteini* can be found in winter in dense aggregations offshore and at a depth range of 150–300 m (Moiseev, 1953; Fadeev, 1971; Tominaga et al., 1991). In early spring, aggregations of flatfish migrate to the shore, some travelling from 50 to 100 km. In the inshore zone, fish concentrate in small coves, bays and straits at depths of 5–10 m, where spawning eventually takes place in May (Fadeev, 1971). The eggs of *Pleuronectes yokohamae* are benthic and are laid on sand and gravel (Perceva-Ostroumova, 1961; Nikolsky, 1973; Lee & Kang, 1985), whereas *P. herzensteini* produce pelagic eggs. After spawning, flatfish begin feeding intensively (Moiseev, 1953; Fadeev, 1971). Grown flatfish with a standard length above 75–100 mm leave the shallow areas (5–10 m) in late June–early July as the water temperature in Peter the Great Bay increases to 12–15°C (Gomelyuk & Shchetkov, 1993). During the summer and early autumn, flatfish can be found gathering in the inshore waters at a depth ranging 15–70 m (Moiseev, 1953). The most dense concentration of flatfish are found at depths of 15–25 m (Gomelyuk & Shchetkov 1993). In October–November, flatfish return to deeper areas offshore (Moiseev, 1953; Fadeev, 1971).

Despite the commercial importance of these species of flatfish, little is known about their short-term movements, and distribution over their habitat. Information about intra- and interspecific interactions of flatfish within the habitats is very limited. *Pleuronectes yokohamae* and *P. herzensteini* are abundant in coastal areas, and at certain times of the year these species show a strong similarity in their habitat preferences, diet, and dial and

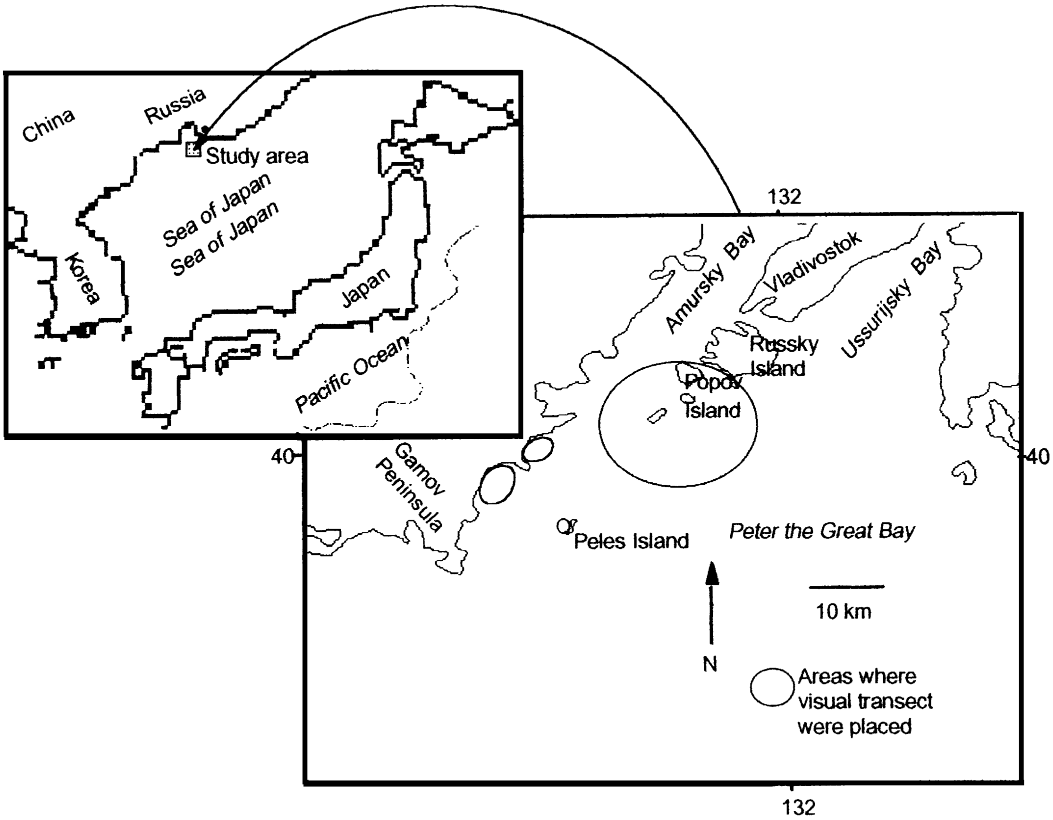

Figure 1. Location of study areas in Peter the Great Bay, Sea of Japan.

seasonal rhythms of feeding (Takahashi, 1987; Takahashi et al., 1987; Tominaga & Nashida, 1991). Some authors suggest that a potentially intense competition for food and habitat resources may exist between the species (Takahashi & Maeda, 1989). Feeding interrelation analysis has shown that intensive competitive interactions for food occur near the northwestern Honshu coast of Japan in April–May. However, since distinct habitat segregation was observed between *P. yokohamae* and *P. herzensteini* from July to December, it was concluded that such separation reduces the competition for food (Takahashi & Maeda, 1989). From April to October (the period flatfish spend in the inshore area), habitat segregation has not been noticed between these two species in Peter the Great Bay (Gomelyuk & Shchetkov, 1993).

The aim of this study was to determine if the small-scale pattern in the distribution of *P. yokohamae* and *P. herzensteini* indicates competition between species by determining, if the presence of one species affects the distribution of the other. We were also interested in assessing: (i) the type of spatial patterns (random, regular or clumped) of each species; (ii) whether flatfish is having a solitary or group mode of life; (iii) the type of groups (homogeneous or mixed) the flatfish form and the main features of these groups (size, composition and fish densities).

MATERIAL AND METHODS

Distribution and density in the habitats of 408 marbled flounder *Pleuronectes yokohamae*, and of 820 brown sole *P. herzensteini* recorded in areas around Popov Island, in Peter the Great Bay (Figure 1) were studied in July–September 1991.

From a variety of bottom compositions at depths available for SCUBA divers in the inshore zone, sand and silted sand were chosen. Together, these substrata represent more than 90% of the inshore zone of Peter the Great Bay (Krasnov, 1983) and *P. yokohamae* and *P. herzensteini* have shown highest densities in these habitats (Gomelyuk & Shchetkov, 1993).

A visual transect method was employed to estimate flatfish distribution and density. The surveys were carried out using SCUBA divers equipped with a special note pad, fitted with compass, timer, and flow-meter to measure transect length and distances between individuals and groups of fishes. Standard error of distance estimation was 4 m on 100 m. Distances shorter than 10 m were measured using a measuring tape and 1.5-m long fibreglass rod. The fish lengths were examined using a ruler attached to the fibreglass rod.

The locations for all surveys were chosen using sea-bottom geomorphologic maps with a scale of 1:2000 where areas of different sediment types were indicated. All transects were randomly laid through the central zones of large (10,000–100,000 m^2) areas of homogeneous sand or silted sand substrata. This approach provided important advantages. Firstly, within homogeneous habitat, the spatial structure and distribution of flatfish may be less affected by irregularities of the landscape. The spatial patterns inside such areas are more likely to depend upon interactions between individuals or follow

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patterns of distribution of prey organisms. Secondly, this approach allowed us to avoid the interference, the 'noise' related to environment heterogeneity (Ver Hoef & Cressie, 1993), particularly in ecotones (Hansen & di Castri, 1992; Kolasa & Zalewski, 1995) where organisms can be either extremely abundant or entirely absent.

Prior to setting up a transect, a diver using an underwater scooter, ensured that the habitat was homogeneous. Areas within depth ranging between 15–35 m, where visibility can vary from 0.5 to 10 m in the summer, were surveyed.

During our surveys the transect width was dependent on the visibility in the water. To avoid biased results, transect width was always 2 m less than the actual visible band of sea bottom to the left and to the right of the diver. If, for instance, the visibility was 2 m, the visible bandwidth was 4 m (2 m to the left+2 m to the right) and the transect width was 2 m.

During the surveys, the diver maintained a distance from the seabed that was approximately equal to a half of underwater visibility.

The sea bottom band, where flatfish were recorded was defined as the projection between two marks at a 1.5-m rod, extended at arm's length. Distances between these marks on the rod were pre-calculated for transect widths, corresponding to visibility conditions. After a flatfish was discovered, it was identified and the flow-meter reading was recorded. The distance between flatfish 'P' and the nearest conspecific neighbour 'Q' was measured as is recommended for T-square distance analysis (Diggle et al., 1976; Ludvig & Reynolds, 1988). The measurements were carried out separately for both species of flatfish in both types of habitat. The surveyor then descended close to the bottom and measured the total fish length with the ruler.

When a diver identified a group of flatfish clearly separated from other fish (>10 m distance), the number of fish in the group was recorded and the area occupied by the group was measured. Because the usual shape of groups was oval, the distance between the two most remote specimens in the group were measured and considered as a circle diameter, D.

From each visual transect, the following data were obtained: (i) the number of fish recorded within a transect of known length and width; (ii) the number of solitary flatfish and number of flatfish in the group, number of groups, the group composition (mixed or homogeneous), and the area occupied by each group; (iii) distances between flatfish for T-square analysis.

Flatfish do not fear divers. If the diver approached them slowly, avoiding abrupt movements and touching the fish, they could be watched and measured within a few centimetres distance. During the survey care was taken not to stir up sediments affecting the visibility of the water and the survey results as the flatfish were attracted to plumes of upset particles. If the bottom was disturbed, researchers sometimes found themselves surrounded by a large number of fish making further survey impossible.

STATISTICAL ANALYSIS

To evaluate pattern in the distribution of flatfish two approaches were used; analysis of indices of dispersion and T-square distance analysis.

Analysis of dispersal

During this analysis, each transect was divided into 10 m sections sampling units (SU). Sampling units were labelled as 1, 2, 3, etc. These labels were then randomly sampled using 'Random sampling' (analysis tool, Microsoft Excel 7.0). Numbers of flatfish in SU chosen were then counted and used in analysis. The null-hypothesis was that the distribution of flatfish follows a Poisson (random) distribution. Due to large samples size (>50 in all cases) a d-test statistic (Elliott, 1973) and Green's index GI (Green, 1966) were computed.

Along with these tests, observed frequencies of the number of flatfish in each SU were compared with Poisson (random pattern) and negative binomial (clumped pattern) distributions using χ^2 goodness-of-fit test (Snedecor & Cohran, 1967; Zar, 1974; Ludwig & Reynolds, 1988).

T-square distance analysis

During our surveys data on two distances were obtained, one from some arbitrary point to nearest flatfish (P), and the other from this flatfish to the nearest conspecific neighbour (Q). Two indices were calculated, the index of spatial patterns (C) (Diggle, 1983), and distance index of dispersion (I) (Johnson & Zimmer, 1985; Ludwig & Reynolds, 1988). Both indices were tested for the significance of any departure from randomness, comparing the calculated z-statistic with its critical value for a standard normal distribution (z=1.96 at P=0.05; Ludwig & Reynolds, 1988).

Interspecific association

To check for an association between *Pleuronectes yokohamae* and *P. herzensteini*, and, if present, to measure the extent of this association, we used data of presence or absence of species in SUs. A variance ratio, as an index of overall species associations (VR) and W statistic were computed (Schulter, 1984; Ludwig & Reynolds, 1988). Chi-squared statistics were also calculated to compare observed frequencies of occurrences of both species in one SU with expected ones. The significance of the χ^2 statistic was determined by comparing it to the χ^2 distribution critical value for df=1 at 5% probability (Zar, 1974).

To measure the degree of the association Ochiai, Dice and Jaccard indices (Hubalek, 1982; Greig-Smith, 1983; Schulter, 1984) were computed (Ludwig & Reynolds, 1988). Additionally, a covariation in species abundance in SU was assessed. We used Pearson's and Spearman's rank correlation coefficients (Snedecor & Cohran, 1973).

Other indices were compared using *t*-test for independent samples. When multiple comparison was required, we used one-way ANOVA and *post hoc* Tukey's HSD tests. Bartlett's test was used to check data for normality before applying ANOVA. Data was square and cube transformed if it was necessary to improve normality. SYSTAT 5.01 was used to calculate correlation and to perform the above tests.

RESULTS

Transect parameters

Due to more turbid water and notably lower visibility (*t*-test, t=9.28, P<0.001), transect widths on silted sand

Table 1. *Visual survey transect parameters (m) during flounder surveys on sand and silted sand habitats in July–September 1991 in Peter the Great Bay, Sea of Japan. Data are $\bar{x}$ and 95% CI. Sample sizes are given in parentheses.*

Parameters	Habitats Sand N=18	Silted sand N= 25	Significance
Visibility	3.63 ±0.12	5.75 ±0.43	$P<0.001$
Transect length	342.95 ±146.06	231.99 ±50.67	$P=0.07$
Transect width	4.56 ±1.10	2.58 ±0.36	$P=0.0019$
Mean depth	23.0 ±1.6	23.8 ±1.8	$P=0.25$
Minimal depth	16.5	14.5	
Maximal depth	25.5	30.0	

Table 2. *Demersal fish species ranked by their mean densities (ind 100 m^{-2}) and percentages of mean densities of all fish recorded in sand and silted sand habitats in July–September 1991 in Peter the Great Bay, Sea of Japan.*

Rank	Species names	Mean density (ind m^{-2})	%
1	*Pleuronectes herzensteini*	3.58	59.7
2	*Pleuronectes yokohamae*	1.78	29.8
3	*Limanda punctatissima*	0.19	3.3
4	*Hexagrammos stelleri*	0.09	1.7
5	*Cleistenes herzensteini*	0.07	1.3
6	*Eleginus gracilis*	0.06	1.1
7	*Myoxocephalus jaok*	0.059	1.0
8	*Liparis* sp.	0.053	0.9
9	*Myoxocephalus brandti*	0.052	0.9
10	*Myoxocephalus stelleri*	0.04	0.7
11	*Platichtys stelatus*	0.03	0.5
12	*Hemitripterus villosus*	0.02	0.4
13	*Gymnacanthus pistilliger*	0.01	0.2
14	*Novadon modestus*	<0.01	0.1

area were less than on sand (t=3.65, P=0.0019), while transect lengths and mean depth in both habitats were similar (t-test, t=1.53, P=0.07 and, t=0.66, P=0.25, respectively (Table 1).

Flatfish densities and distribution

Flounders *Pleuronectes yokohamae* and *P. herzensteini* were dominant components in the demersal fish community in the area. *Pleuronectes herzensteini* was approximately twice as numerous as *P. yokohamae* (Table 2). The majority of flatfish in the area were mature individuals, (length >100–150 mm. The mean length of *P. yokohamae* was greater than *P. herzensteini* in both habitats (Figures 2 & 3). *Pleuronectes yokohamae* inhabiting sand was significantly larger than those inhabiting silted sand: e.g. 272.4 75.4 mm compared to 249.9 62.9 mm, N=179 and N=203, respectively, t-test, t=3.14, P<0.001). The mean

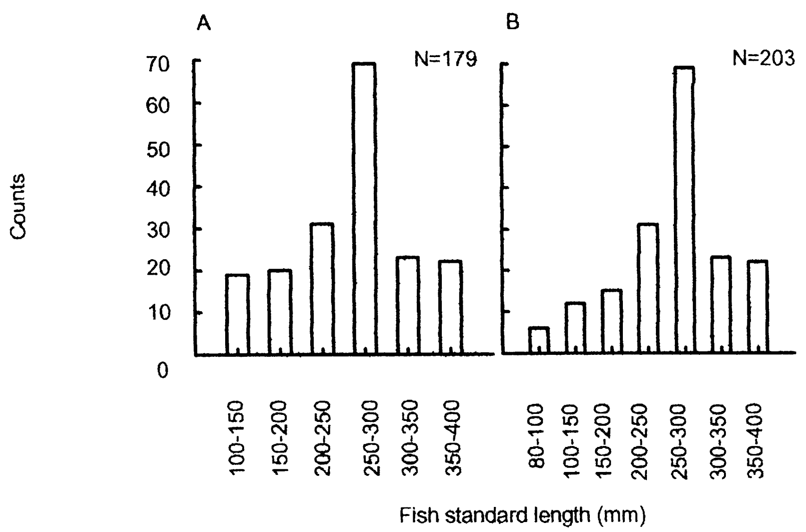

Figure 2. Size–frequencies distribution of *Pleuronectes yokohamae* recorded in (A) silted sand and (B) sand habitats.

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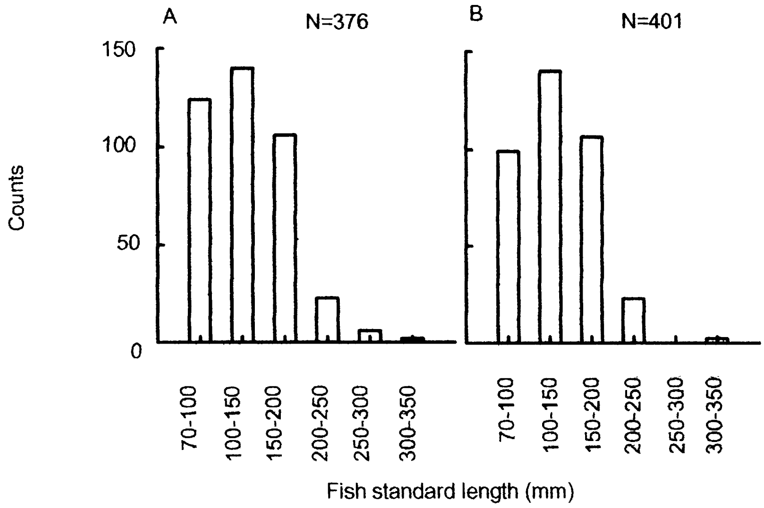

Figure 3. Size–frequency distributions of *Pleuronectes herzensteini* recorded in (A) silted sand and (B) sand habitats.

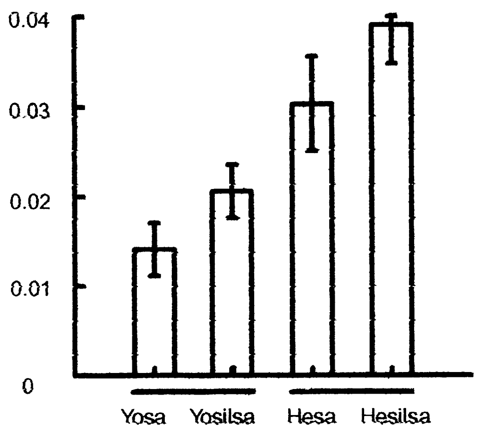

Figure 4. Mean flatfish densities (ind m^{-2}) in sand and silted sand habitats in July–September 1991 in Peter the Great Bay, Sea of Japan. Yosa, *Pleuronectes yokohamae* in sand habitat; Yosilsa, in silted sand habitat; Hesa, *P. herzensteini* in sand habitat; Hesilsa, in silted sand habitat. Underlined means are not significantly different by Tukey's HSD test ($P>0.05$). Other means are significantly different on $P<0.001$ probability level. Error bars are ±1SE.

lengths of *P. herzensteini* from both habitats was similar (142.6 47.3 mm and 145.4 49.7 mm, N=401, N=376, respectively, *t*-test, $t=-0.80$, $P=0.21$).

Densities of more abundant *P. herzensteini*, were significantly higher, than those of *P. yokohamae* in both types of habitat (one-way ANOVA, $F=7.90$, $P<0.001$, df=3). Differences in mean densities of *P. yokohamae* and *P. herzensteini* between sand and silted sand habitats were insignificant, *post hoc* Tukey's HSD test, $P=0.38$ and $P=69$, respectively (Figure 4).

More than 85% of the flatfish recorded in both habitats were gathering in groups. The percentage of solitary individuals in *P. yokohamae* was significantly higher on silted sand (one-way ANOVA $F=5.74$, $P=0.004$, df=5). *Pleuronectes herzensteini* showed a similar percentage of solitary individuals in both habitats (Figure 5).

Chi-square tests indicated that both *P. yokohamae* and *P. herzensteini* expressed a clear tendency to form aggregations (Tables 3 & 4). Various transect width results were checked and in all cases Green's index, GI was higher than 0 indicating a clumped distribution with a medium level of clumping (Green, 1966; Ludwig & Reynolds, 1988).

Chi-square test results shoved a strong agreement with a negative binomial distribution and confirmed aggregated patterns in both species' distributions. However, in the case of *P. yokohamae* within 3 m width transect (Table 3), the χ^2 statistic was less than its critical value for both Poisson and negative binomial distributions. This indicated that agreement either with random pattern or clumped pattern could be accepted.

T-square analysis showed that distances between fish within groups were notably smaller than distances between groups. The distribution index of dispersion, I, was always higher than 2, and index of spatial patterns C was always higher than 0.5. In all cases z-statistics for both indices were significant. This indicates clumped patterns (Johnson & Zimmer, 1985) in flatfish distribution (Table 5).

Group features

Relatively dense groups of flatfish were separated by rather large areas. Densities in groups were at least ten times higher than mean flatfish densities in habitat (Figures 4 & 6).

The group was not a stable formation. It could be formed and disintegrated within 5–15 min. Occasionally, this happened when some of the group members were attracted by other flatfish movements in an area nearby, at other times the reasons were not obvious.

The portions (percentage of flatfish recorded) of *P. herzensteini* found in silted sand habitats in homogeneous and mixed groups were similar (one-way

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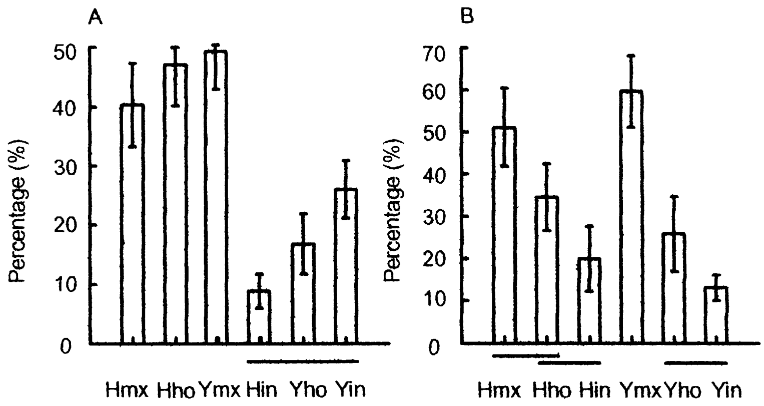

Figure 5. Percentage of flatfish found alone, in homogeneous, and in mixed groups recorded during visual diving surveys in (A) silted sand and (B) sand habitat in July–September 1991 in Peter the Great Bay, Sea of Japan. Hmx, *Pleuronectes herzensteini* in mixed groups; Hho, in homogeneous group; Hin, single fish recorded; Ymx, *Pleuronectes yokohamae* in mixed groups; Yho, in homogeneous groups; Yin, single fish recorded. Underlined means are not significantly different by Tukey's HSD test ($P > 0.05$). Other means are significantly different on $P < 0.001$ probability level. Error bars are $\pm$1SE.

Table 3. *Chi-square goodness-of-fit test, the observed frequency distribution of the number of marble flounders* Pleuronectes yokohamae *per sampling unit (SU=10 m×transect width) for transects of various widths vs expected frequency as given by Poisson (random distribution) and negative binomial (clumped distribution) probabilities.*

Transect Width (m)	Number of SU	d-statistic[a]	Green index, ID–1/n–1, GI	χ^2-test for agreement with a Poisson series, total χ^2 [b]	χ^2-test for agreement with a negative binomial distribution, total χ^2 [b]	Distribution patterns
Sand						
2	112	6.36, Clumped	0.02, Weak clumping	5.97, df=1, Rejected	1.28, df=1, Accepted	Clumped
3	96	5.36, Clumped	0.02, Weak clumping	14.53, df=2, Rejected	0.66, df=2, Accepted	Clumped
5	57	4.63, Clumped	0.02, Weak clumping	6.29, df=2, Rejected	0.34, df=1, Accepted	Clumped
8	102	13.11, Clumped	0.04, Weak clumping	32.14, df=1, Rejected	0.15, df=2, Accepted	Clumped
Silted sand						
1.5	90	5.28, Clumped	0.03, Weak clumping	5.78, df=1, Rejected	2.02, df=1, Accepted	Clumped
2	140	11.30, Clumped	0.02, Weak clumping	27.92, df=1, Rejected	2.45, df=2, Accepted	Clumped
3	132	4.81, Clumped	0.01, Weak clumping	6.44, df=3, Accepted	0.17, df=3, Accepted	Clumped? Random?
4	56	13.06, Clumped	0.25, Clumping	14.57, df=3, Rejected	0.90, df=2, Accepted	Clumped

[a], if $d < 1.96$, agreement with a Poisson series (a random dispersion) is accepted ($P > 0.005$), if $d > 1.96$, a clumped dispersion is likely (Elliott, 1973); [b], Poisson (random) distribution or a negative binomial distribution is accepted if χ^2 table value with the same degree of freedom at probability level ($P < 0.05$) is greater than test's value.

Table 4. *Chi-square goodness-of-fit test, the observed frequency distribution of the number of brown sole* Pleuronectes herzensteini *per sampling unit (SU=10 m×transect width) for transects of various widths vs expected frequency distributions as given by Poisson (random distribution) and negative binomial (clumped distribution) probabilities.*

Transect Width (m)	Number of SU	d-statistic[a]	Green index, ID–1/n–1, GI	χ^2-test for agreement with a Poisson series, total χ^2 [b]	χ^2-test for agreement with a negative binomial distribution, total χ^2 [b]	Distribution patterns
Sand						
2	103	3.67, Clumped	0.01, Weak clumping	14.61, df=1, Rejected	1.43, df=1, Accepted	Clumped
3	96	17.54, Clumped	0.03, Weak clumping	124.33, df=2, Rejected	4.53, df=2, Accepted	Clumped
5	57	12.60, Clumped	0.03, Weak clumping	71.35, df=3, Rejected	0.07, df=1, Accepted	Clumped
8	99	17.92, Clumped	0.04, Weak clumping	86.10, df=2, Rejected	0.36, df=1, Accepted	Clumped
Silted sand						
1.5	90	8.45, Clumped	0.02, Weak clumping	15.48, df=1, Rejected	0.11, df=1, Accepted	Clumped
2	139	17.22, Clumped	0.02, Weak clumping	61.42, df=2, Rejected	0.83, df=2, Accepted	Clumped
3	132	17.20, Clumped	0.01, Weak clumping	139.40, df=3, Rejected	4.22, df=2, Accepted	Clumped
4	56	14.96, Clumped	0.08, Weak clumping	60.62, df=2, Rejected	1.38, df=1, Accepted	Clumped

[a], if $d < 1.96$, agreement with a Poisson series (a random dispersion) is accepted ($P > 0.05$), if $d > 1.96$, a clumped dispersion is likely (Elliott, 1973); [b], Poisson (random) distribution or a negative binomial distribution is accepted if χ^2 table value with the same degree of freedom at probability level ($P < 0.05$) is greater than test's value.

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Table 5. *Point-to-individual and individual-to-nearest neighbour distances statistics. Sample number is given in parentheses.*

Habitats	Species	Mean 'point-to-nearest individual distance' (m)	Mean 'individual-to-nearest neighbour distance' (m)	T-square index of spatial patterns, C	z-statistic and probability of obtaining z by chance[a]	Johnson & Zimmer index of dispersion, I	z-statistic and probability of obtaining z by chance[b]	Distribution patterns
Sand								
	P. yokohamae (73)	66.10	1.52	1.00	11.16; $P<0.001$	14.95	44.98; $P<0.001$	Clumped
	P. herzensteini (92)	44.53	1.25	1.00	13.19; $P<0.001$	6.01	16.17; $P<0.001$	Clumped
Silted sand								
	P. yokohamae (129)	46.89	2.10	0.99	8.21; $P<0.001$	7.48	14.90; $P<0.001$	Clumped
	P. herzensteini (212)	47.71	0.62	1.00	10.63; $P<0.001$	7.77	19.21; $P<0.001$	Clumped

[a, b], z-value was compared to a table critical values for the standard normal distribution.

ANOVA, $F=8.5$, $P=0.054$, df=5). The portion of *P. yokohamae* found in mixed aggregations was significantly higher than in homogeneous aggregations in both sand and silted sand habitats (one-way ANOVA, $F=5.74$, $P=0.001$, df=5; $F=8.5$, $P=0.001$, df=5, respectively; Figure 5).

In both habitats, the mean number of *P. herzensteini* in the group was higher than the number of *P. yokohamae* (one-way ANOVA, $F=20.15$, $P<0.001$, df=3; Figure 6). The mean areas occupied by flatfish groups were 21.86 ± 1.81 m^2 in sand habitat and only 5.80 ± 0.24 m^2 in silted sand habitats. The differences were highly significant (*t*-test, $t=10.16$, $P<0.001$). The mean number of *P. herzensteini* in groups in sand habitat was significantly higher than in silted sand habitat, post hoc Tukey's HSD test, $P=0.04$. The mean number of *P. yokohamae* in groups was close to two in both habitats, *post hoc* Tukey's HSD test, $P=0.99$ (Figure 6).

The number of *P. herzensteini* in groups was related to visibility in water. The better the visibility, the greater the number of fish within a group. However, the number of *P. yokohamae* did not vary a lot in different visibility conditions (Figure 7).

In both species, and particularly in *P. herzensteini*, the group density was higher on silted sand than on sand, one-way ANOVA, $F=29.79$, $P=0.001$, df=3 (Figure 6). Group density reflects the level of spatial and behavioural contacts within groups and the higher the group density, the higher the level of contacts. This index in both species was inversely related to visibility in the water (Figure 8).

The mean number of *P. herzensteini* in groups was greater than that of *P. yokohamae* (one-way ANOVA, $F=12.92$, $P<0.05$, df=3; Figure 9). More homogeneous than mixed groups were observed within sand habitats (57 and 35, respectively, χ^2 goodness-of-fit test, $P=0.02$, df=1). On silted sand these numbers were very close to each other (72 and 57, respectively, χ^2 goodness-of-fit test, $P=0.18$, df=1). The mean number of *P. yokohamae* individuals in homogenous and mixed groups did not differ significantly in sand and silted sand habitats, *post hoc* Tukey's HSD test, $P=0.74$ and $P=0.99$, respectively. Similar results were obtained for *P. herzensteini* in sand and silted sand, *post hoc* Tukey's HSD test, $P=0.91$ and $P=0.99$, respectively. Generally, flatfish number within groups in silted sand habitat was higher, than in sand habitat (Figure 9).

In silted sand habitat the mean densities of *P. yokohamae* in mixed and homogeneous groups were close (Figure 10). Differences between the densities within homogeneous groups and mixed groups of *P. herzensteini* were small, but statistically significant, one-way ANOVA, $F=3.20$, $P<0.01$, df=3. In sand habitat fish densities in homogeneous groups were higher than in mixed in both *Pleuronectes yokohamae* and *P. herzensteini post hoc* Tukey's HSD test, $P<0.001$, $P<0.001$, respectively (Figure 10).

Flatfish interspecific association

In most cases in sand habitats values of the W-test statistic for the index of overall association (VR) were within a critical limit. Values of Ochiai, Dice and Jaccard

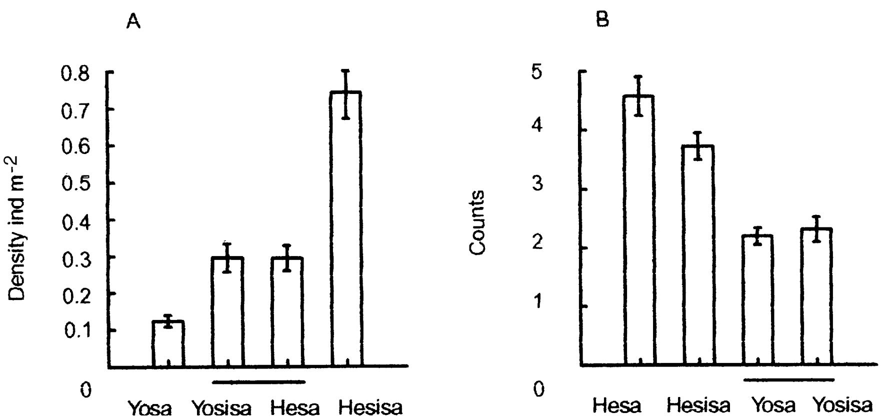

Figure 6. (A) Mean density of fish in groups (ind m^{-2}) and (B) number of fish in groups of flatfish in sand and silted sand habitats. Yosa, *Pleuronectes yokohamae* in sand habitat; Yosisa, in silted sand habitat; Hesa, *Pleuronectes herzensteini* in sand habitat; Hesisa, in silted sand habitat. Underlined means are not significantly different by Tukey's HSD test ($P>0.05$). Error bars are ±1SE.

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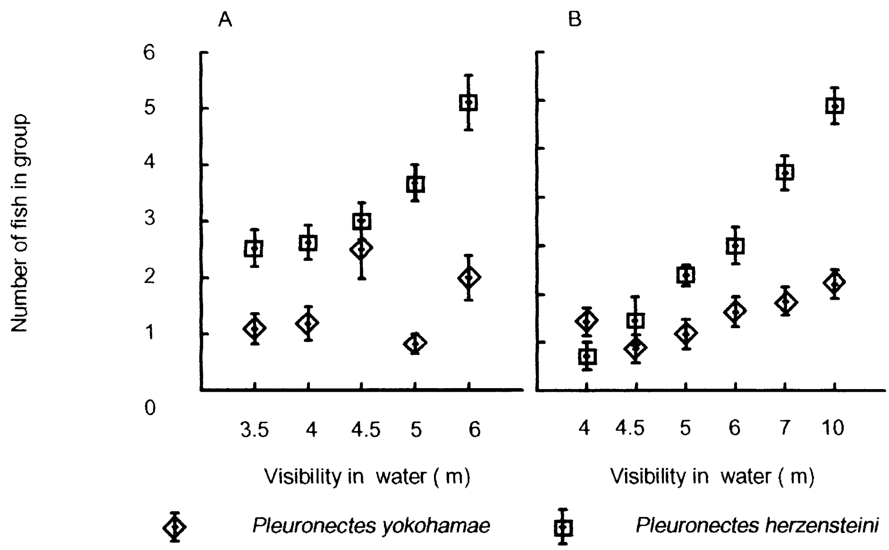

Figure 7. Mean number of flatfish in groups in (A) silted sand and (B) sand habitat in different visibility conditions. Error bars are ±1SE.

indices and χ^2 statistic were very low, indicating no association between *P. yokohamae* and *P. herzensteini*. Only data from transects of width 3 m indicated positive association at a very high probability level, and association indices show a medium level of species association.

In the silted sand habitat a positive association was found in all cases (Table 6).

Flatfish species association was higher in lower visibility conditions and *vice versa*. Pearson and Spearman correlation analysis, based on data of abundance of both

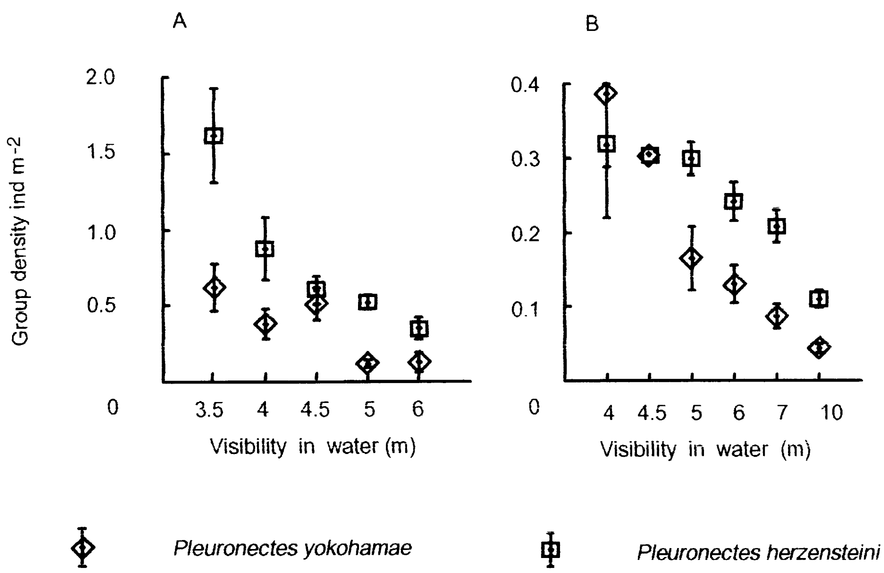

Figure 8. Mean densities of flatfish in groups (ind m^{-2}) in the (A) silted sand and (B) sand habitats in different visibility conditions. Error bars are ±1SE.

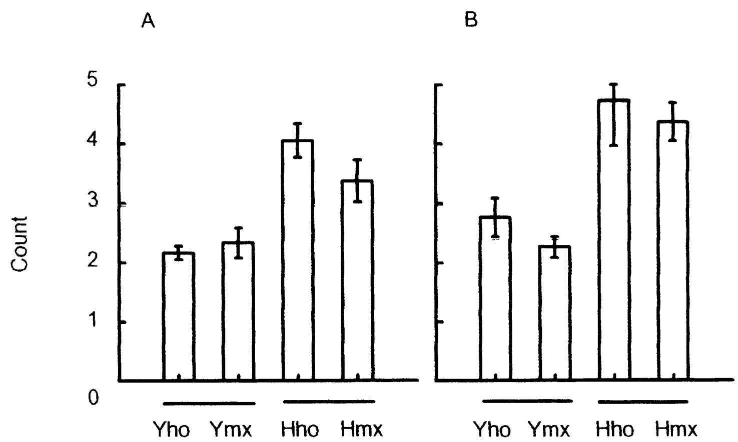

Figure 9. Mean number of flatfish recorded during visual diving surveys in homogeneous and mixed groups, in (A) silted sand and (B) sand habitats in Peter the Great Bay in July–September 1991. Hmx, *Pleuronectes herzensteini* in mixed groups; Hho, in homogeneous groups; Ymx, *Pleuronectes yokohamae* in mixed groups; Yho, in homogeneous groups. Underlined means are not significantly different by Tukey's HSD test ($P > 0.05$). Other means are significantly different at $P < 0.001$ probability level. Error bars are ±1SE.

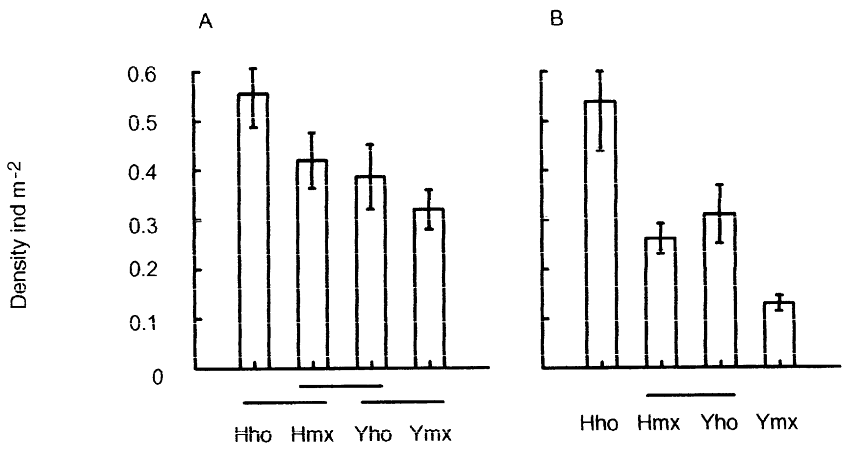

Figure 10. Mean densities of flatfish (ind m^{-2}) recorded during visual diving surveys in homogenous and mixed groups in (A) silted sand and (B) sand habitats, in Peter the Great Bay in July–September 1991. Hmx, *Pleuronectes herzensteini* in mixed groups; Hho, in homogeneous groups; Ymx, *P. yokohamae* in mixed groups; Yho, in homogeneous groups. Underlined means are not significantly different by Tukey's HSD test ($P>0.05$). Other means are significantly different at $P<0.001$ probability level. Error bars are ±1SE.

Table 6. *Some interspecific association indexes for* Pleuronectes yokohamae *and* P. herzensteini *based on data of the number of flounders in 10 m samplings units.*

Transect width (m)	Number of sampling units, N	Index of overall association, VR	Test statistic,[a] W	Type of association	Significance[a]	$\chi^{2\,b}$	Ochiai Index	Dice Index	Jaccard Index
Sand									
2	107	1.119	119.74	No association	ns	0.79	0.30	0.30	0.17
3	96	1.439	141.06	+	$0.001<P<0.01$	16.67	0.57	0.56	0.39
5	61	0.992	57.55	No association	ns	0.29	0.25	0.25	0.14
8	99	1.079	106.85	No association	ns	0.21	0.23	0.22	0.12
Silted sand									
1.5	91	1.278	116.36	+	$0.01<P<0.05$	5.74	0.45	0.44	0.28
2	141	1.474	207.95	+	$P<0.001$	32.08	0.68	0.57	0.40
3	133	1.50	200.35	+	$P<0.001$	29.95	0.60	0.59	0.42
4	57	1.279	115.18	+	$0.01<P<0.05$	2.73	0.38	0.35	0.21

[a], W-test statistic critical values lie between χ^2 0.05, $N<W<\chi^2 0.95,N$, (Schulter, 1984); [b], critical value for this statistic is 3.84 (χ^2 value for df=1 at 5% probability; Zar, 1974); ns, not significant.

Table 7. *Relationship between two flatfish,* Pleuronectes yokohamae *and* P. herzensteini *based on their co-occurrence in 10 m sampling units over sand and silted sand habitats.*

Transect width (m)	Number of observations, N	Pearson correlation coefficient	Probability	Spearman's rank correlation coefficient
Sand				
2	99	0.64, modest	$P<0.001$	0.75
3	57	0.46, modest	$P<0.001$	0.54
5	96	0.36, weak	$P<0.001$	0.48
8	55	0.10, ns	0.435, ns	0.07
Silted sand				
1.5	90	0.46, modest	$P<0.001$	0.51
2	132	0.48, modest	$P<0.001$	0.50
3	139	0.37, weak	$P<0.001$	0.32
4	56	0.24, ns	0.068, ns	0.30

ns, not significant.

species in sampling units, revealed relationships from weak to modest levels. In this test, *P. yokohamae* and *P. herzensteini* association was also higher in poor visibility conditions, compared to good visibility conditions (Table 7).

DISCUSSION

The data obtained in our study showed that both *Pleuronectes yokohamae* and *P. herzensteini* for the period they spend in the inshore zone, expressed a clear clumped

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pattern in their distribution. They formed small to medium sized groups in homogeneous habitats where random distribution usually was expected (Pemberton & Frey, 1984). The level of spatial (and behavioural) contacts within such groups is likely to be quite high.

Fish could enter a certain area and form a group attracted by presence of conspecific or congeric individuals (Radakov, 1972). Aggregations could also appear in situations when animals were attracted to some resource, concentrated in a certain area (Radakov, 1972; Krebs et al., 1972; Lazarus, 1979). Factors, underlying origination of groups remains unclear, but we suggest that flatfish form and maintain groups through visual contact between specimens. Field studies confirmed by laboratory experiments have demonstrated that flatfish from *Pleuronectes* and *Limanda* genera are typical sight feeders (de Groot, 1971), active during the day and passive during the night (Olla et al., 1969, 1972; Girsa 1981; Girsa et al., 1981; Mochek, 1981).

We suggest that the relationship between visibility in water and the fish group's size and densities within the groups (Figures 7 & 8) is a solid confirmation of our suggestion on the role of visual contacts between flatfish. While the mean flatfish densities (and abundance) in sand and silted sand habitats were similar (Figure 4), density in groups was higher on silted sand, in poorer visibility conditions (Figures 6 & 8). At the same time, in better visibility conditions the mean number of *P. herzensteini* in a group was higher than in a poorer one (Figure 7). We suppose that a lack of such dependence in *P. yokohamae* (as well as bias result for *P. yokohamae* distribution patterns; Table 3) can be related to poor abundance in the area compared to *P. herzensteini* (Table 1).

We argue, that flatfish form groups, attracted by the presence and behaviour (digging movements) of other flatfish, as well as by the results of such movements, e.g. plumes of sediments which arise during digging. In better visibility conditions, more flatfish can be attracted, and fish can be attracted from greater distances. Since in higher visibility fish can maintain contacts while staying further from each other, groups in a sand habitat are looser. While differences in densities of both species of flatfish between habitats were insignificant (Figure 4), flatfish densities within groups in silted sand habitat were higher, e.g. in poor visibility conditions flatfish tend to aggregate closely and groups are more compact, than in the sand habitat, (Figure 10), so in poorer visibility conditions the group sizes were smaller (Figure 7). Accordingly, distances between fish within groups in good visibility conditions were greater, than in poorer visibility. The groups contained more members and covered larger areas in good visibility, than in poorer visibility conditions.

Fish numbers and fish densities in mixed and homogeneous groups were similar (Figures 9 & 10). Mixed groups predominated, that indicate that flatfish generally do not discriminate while joining or staying in groups. However, in the sand habitat, where the mean visibility was almost twice as good as in silted sand habitat (Table 1), mean flatfish densities in mixed groups were half of that of homogeneous groups (Figure 10). This may be evidence that flatfish are able to distinguish between individuals of their own and other flatfish species and probably prefer conspecific individuals. The fact that affinity between these two species existed, but was expressed rather weakly (Tables 6 & 7), may also support this argument. Both *P. yokohamae* and *P. herzensteini* are attracted by the presence of any other flatfish and their movements. In limited visibility and in situations when conspecific fish were absent, groups with other species can be formed. While *P. herzensteini*, being abundant in the area, had a very similar proportion of fish in mixed and homogeneous groups, the majority of more rare *P. yokohamae* are found in groups with *P. herzensteini* (Figure 5).

There is still some possibility that group formation in flatfish was related to patchy food distribution within habitat or variable prey availability on a micro-scale (1–10 m). This can happen because of local substrata wash-out by turbulent bottom currents occurring during storms, as it was shown for shallow habitats (Hall et al., 1994, Bock & Miller, 1995). Vertical migrations of benthic organisms within substrata can also make prey more available for flatfish. During these surveys vast areas of sea bottom with more than 200 groups of flatfish were checked and 2–3 fish feeding within groups were rarely viewed. In most cases, fish were grouped together, which suggested that other factors influence aggregation rather than food presence.

It appears that *P. yokohamae* and *P. herzensteini* have very similar habitat and food preferences, thus, their niches widely overlap. However, we can not find any obvious evidence of the proposed existence of any form of competition for resources between *P. yokohamae* and *P. herzensteini*. A regular distribution quite often results from negative interactions between individuals, such as various forms of competition for food or space (Pembertone & Frey, 1984). We found no indication of such patterns (Tables 3–5). The association between the two species was in all cases positive (Table 6). Moreover, flatfish, a dominant component of the demersal fish community, have relatively low mean densities (5.5 ind 100 m^{-2}) in both types of habitats. At the same time, the benthic invertebrates in sand habitats in Peter the Great Bay have very high indices of animal density. Polychaeta and Phoronida, important parts of the flatfish diet (Moiseev, 1953; Klimova & Ivankova, 1977; Dou & Jiming, 1993) have a biomass from 10 to 40 g m^{-2} in sand habitats (Tarasov, 1981). In silted sand habitats these groups of animals are particularly abundant (805–7420 ind m^{-2}) and their biomass was high (43–210 g m^{-2}).

Therefore, it is highly unlikely that significant competition between studied species of flatfish takes place in Peter the Great Bay. No competition for food or other resources was reported for any of the intensively studied species of flatfish in Peter the Great Bay so far (Ivankova, 1975, 1988; Klimova & Ivankova, 1977; Tihonov, 1984; Strelcov et al., 1985; Gavrilov et al., 1988). Spatial interactions between two studied species analysed in this study show no evidence of such competition.

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REFERENCES

Berghahn, R., 1986. Determining abundance, distribution and mortality of 0-group plaice (*Pleuronectes platessa* L.) in the Wadden Sea. *Journal of Applied Ichthyology*, **2**, 11–22.

Bock, M.J. & Miller, D.C., 1995. Storm effects on particulate food sources on an intertidal sand flat. *Journal of Experimental Marine Biology and Ecology*, **187**, 81–101.

Diggle, P.J., 1983. *Statistical analysis of spatial point patterns*. New York: Academic Press.

Diggle, P.J., Besag, J. & Gleavs, J.T., 1976. Statistical analysis of spatial points patterns by means of distance methods. *Biometrics*, **32**, 659–667.

Dou, S. & Jiming, Y., 1993. Feeding habit and seasonal variation of stomach contents of sand dab *Pseudopleuronectes yokohamae*, in the south Bohai Sea. *Acta Oceanologica Sinica*, **12**, 629–635.

Elliott, J.M., 1973. *Some methods for the statistical analysis of sample of benthic invertebrates*. Ambleside: Freshwater Biological Association. [Scientific Publication no. 25.]

Fadeev, N.S., 1971. *Biology and fisheries of Pacific flounders*. Vladivostok: Dalizdat.

Gavrilov, G.M., Pushkareva, N.F. & Strelcov, M.C., 1988. Composition and biomass of demersal fishes of the exclusive zone of the USSR in the Sea of Japan. In *Variability of ichthyophauna composition, yield year classes and forecasting techniques of fishes in the western Pacific* (ed. N.S. Fadeev), pp. 37–55. Vladivostok: TINRO.

Gibson, R.N., 1973. The intertidal movements and the distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *Journal of Experimental Marine Biology and Ecology*, **12**, 79–102.

Girsa, I.I., 1981. *Light and fish behaviour*. Moscow: Nauka.

Girsa, I.I., Gorin, A.N. & Krishans, K., 1981. Tidal currents and light influence on distribution and some aspects of behaviour of inshore fish species in White Sea. In *Fish behaviour* (ed. D.C. Pavlov), pp. 5–27. Moscow: IEMEA.

Gomelyuk, V.E. & Shchetkov, S.Y., 1993. Distribution of fish in coastal biotopes of Peter the Great Bay, Sea of Japan, in summer. *Russian Journal of Marine Biology*, **18**, 80–84.

Green, R.H., 1966. Measurement of non-randomness in spatial distributions. *Researches in Population Ecology*, **8**, 1–7.

Greig-Smith, P., 1983. *Quantitative plant ecology*, 3rd ed. Berkeley, CA: University of California Press.

Groot, S.J. de, 1971. On the interrelationship between morphology of the alimentary tract food and feeding behaviour in flatfishes (Pisces, Pleuronectiformes). *Netherlands Journal of Sea Research*, **5**, 121–196.

Hall, S.J., Raffaelli, D. & Thrush, S.F., 1994. Patchiness and disturbance in shallow water benthic assemblages. In *Aquatic ecology: scale, pattern and process* (ed. P.S. Giller et al.), pp. 333–375. London: Blackwell Scientific Publications.

Hansen, A.J. & Castri, F. di, 1992. *Landscape boundaries*. New York: Springer.

Hubalek, Z., 1982. Coefficient of association and similarity based on binary (presence–absence) data: an evaluation. *Biological Reviews*, **57**, 669–689.

Ivankova, Z.G., 1975. Changes in population structure of flatfish in Peter the Great Bay during regulated fisheries. *Proceedings of Far-Eastern Institute of Fisheries and Oceanography*, **96**, 149–160.

Ivankova, Z.G., 1988. Stock assessment and prospect of catch of flat-fishes in Peter the Great Bay. In *Variability of ichthyophauna composition, yield year classes and forecasting techniques of fishes in the western Pacific* (ed. N.S. Fadeev), pp. 56–63. Vladivostok: TINRO.

Johnson, R.B. & Zimmer, W.J., 1985. A more powerful test for dispersion using distance measurements. *Ecology*, **66**, 1084–1085.

Klimova, V.L. & Ivankova, Z.G., 1977. Changes in bottom population and its influence on feeding and growth rate of some flatfish species in Peter the Great Bay. *Russian Journal of Oceanology*, **17**, 896–900.

Kolasa, J. & Zalewski, M., 1995. Notes on ecotone attributes and functions. *Hydrobiologia*, **303**, 1–7.

Krasnov, E.V., 1983. Geology and geomorphology of south-western zone of Peter the Great Bay. In *Peter the Great Bay* (ed. V.S Levin), pp. 18–34. Vladivostok: Academy of Science Publishing.

Krebs, J.R., McRoberts, M. & Cullen, J.M., 1972. Flocking and feeding in the great tit *Parus major*—an experimental study. *Ibis*, **114**, 507–530.

Lazarus, J., 1979. Flock size and behaviour in captive red-billed weaverbird (*Quelea quelea*): implications for social facilitation and the functions of flocking. *Behaviour*, **71**, 121–145.

Lee, T.Y. & Kang, Y.J., 1985. Reproduction and population dynamics of marbled sole *Limanda yokohamae*. 1. Reproduction. *Bulletin of the Korean Fisheries Society*, **18**, 253–261.

Ludvig, J.A. & Reynolds, J.F., 1988. *Statistical ecology: a primer on methods and computing*. New York: Wiley-Interscience Publications.

Mochek, A.D., 1981. Some aspects of fish behaviour in inshore zone of White Sea. In *Fish behaviour* (ed. D.C. Pavlov), pp. 29–45. Moscow: IEMEA.

Modin, J. & Pihl, L., 1996. Small scale distribution of juvenile plaice and a flounder in relation to predatory shrimp in a shallow Swedish bay. *Journal of Fish Biology*, **49**, 1070–1085.

Moiseev, P.A., 1953. Far-eastern cod and flatfish. *Proceedings of Far-Eastern Institute of Fisheries and Oceanography*, **40**, 119–287.

Nikolsky, G.V., 1973. *Systematic ichthyology*. Moscow: High School Publishing.

Olla, B.L., Samet, C.E. & Studholme, A.L., 1972. Activity and feeding behavior of the summer flounder (*Paralichthys dentatus*) under controlled laboratory conditions. *Fisheries Bulletin, National Oceanic and Atmospheric Administration, Washington, DC*, **70**, 1127–1136.

Olla, B.L., Wicklund, R. & Wilk, S., 1969. Behavior of winter flounder in a natural habitat. *Transactions of American Fisheries Association*, **4**, 717–720.

Pemberton, S.G. & Frey R.W., 1984. Quantitative methods in ichnology: spatial distribution among populations. *Lethaia*, **17**, 33–49.

Perceva-Ostroumova, T.A., 1961. *Reproduction and development of Far-Eastern flounders*. Moscow: Academy of Science Publishing.

Poxton, M.G. & Nasir, N.A., 1985. The distribution and population dynamic of 0-group plaice (*Pleuronectes platessa* L.) on nursery grounds. *Estuarine, Coastal and Shelf Science*, **21**, 845–857.

Radakov, D.V., 1972. *Schools in fishes and their ecological significance*. Moscow: Nauka.

Schulter, D., 1984. A variance test for detecting species associations, with some example applications. *Ecology*, **65**, 998–1005.

Snedecor, G.W. & Cohran, W.G., 1973. *Statistical methods*. Ames, Iowa: Iowa State University Press.

Strelcov, M.S., Vdovin, A.N. & Ivankova Z.G., 1985. Quantitative estimations of demersal ichthyophauna in the Peter the Great Bay. In *Investigation and rational exploitation of biological resources of far-eastern and north seas of the USSR* (ed. N.P. Novikov), pp. 66–67. Vladivostok: TINRO.

Takahashi, T., 1987. Intraspecific relationship for food in right eye flounders *Limanda herzensteini* and *L. yokohamae* in Mutsu Bay. *Bulletin of the Japanese Society of Scientific Fisheries*, **53**, 189–194.

Takahashi, T., Maeda, T., Tsuchiya, Y. & Nakatani, T., 1987. Distribution and food habits of right eye flounders *Limanda herzensteini* and *L. yokohamae*. *Bulletin of the Japanese Society of Scientific Fisheries*, **53**, 177–187.

Takahashi, T. & Maeda, T., 1989. Feeding interrelation between two species of *Pleuronectes* in Mutsu Bay Aomori Prefecture. *Bulletin of the Japanese Society of Scientific Fisheries*, **55**, 1727–1739.

Tarasov, V.G., 1981. Respiration of the soft-bottom communities in Vostok Bay (Sea of Japan) as related to the environmental factors and density of macrobenthos. *Russian Journal of Marine Biology*, **2**, 32–39.

Tihonov, V.I., 1984. The yield year-classes of the flounder *Limanda aspera* (Pallas) (Pleuronectidae). *Russian Journal of Ichthyology*, **24**, 66–67.

Tominaga, O. & Nashida K., 1991. Interspecific relationships between brown sole *Pleuronectes herzensteini* and other demersal fishes in the coastal waters of the northern Niigata Prefecture. *Bulletin of the Japan Sea Fisheries Research Institute*, **41**, 11–26.

Tominaga, O., Nashida, K., Maeda, T., Takahasi, T. & Kato K., 1991. Annual life cycle and distribution of adult right eye flounder *Pleuronectes herzensteini* in the coastal waters of northern Niigata Prefecture. *Bulletin of the Japanese Society of Scientific Fisheries*, **57**, 2023–2031.

Veer, H.W. van der, 1986. Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Marine Ecology Progress Series*, **29**, 223–236.

Ver Hoef, J.M. & Cressie, N., 1993. Spatial statistics: analysis of field experiments. In *Design and analysis of ecological experiments* (ed. S.M. Scheiner and J. Gurevitch), pp. 319–341. New York: Chapman & Hall.

Vyscrebentcev, B.V., 1970. Fish behaviour in the zone of trawling. In *Biological bases of fish behaviour management* (ed. B.P. Manteufel), pp. 267–301. Moscow: Nauka.

Wardle, C.S., 1986. Fish behaviour and fishing gears. In *Behaviour of teleost fishes* (ed. T.J. Pitcher), pp. 609–641. London: Chapman & Hall.

Zalewski, M., Thorpe, J.E. & Gaudin, P., 1991. *Fish and land/inland water ecotones*. University of Lodz: UNESCO.

Zar, J.H., 1974. *Biostatistical analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.

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