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Ichthyofaunistic Biogeography of the East Sea : Comparison between Benthic and Pelagic Zonalities

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Abstract : An ichthyofauna analysis of the East Sea using quantitative investigation procedures for latitudinal variations of the species richness and clustering of the species list is presented to illustrate the application of the adopted geographical scaling (less than 1:10,000,000) which provides a principal opportunity for common benthic and pelagic biogeographical zonation. The distribution of both pelagic and benthic marine fish biota at a scale of biosphere (or its major sections) was highly influenced by spatial nonuniformity of hydrological structure associated with the various water circulations and frontal zones. Following zoogeographical zonations were established for the East Sea: Osaka, East Korea, Primorye, North Primorye, Northern East Sea, Uetsu, Tsugaru, Soya and West Sakhalin.

Key words : Biogeography, East Sea (Japan Sea), Ichthyofauna, Benthic fish, Pelagic fish.

1. Introduction

Since Zimmermann (1783) and Buffon (1802), biogeographical science has been witnessing the presence of the intricate relationship between geography and biology. In the early studies, specific features in animal and plant distribution were predominantly explained from zonal-geographical (temperature-belting) distribution of all natural phenomena (Humboldt 1817, 1845). This particular trend was, for instance, shared by the founders of marine biogeography e.g., Forbes (1844, 1851, 1856, 1859) and Dana (1846, 1852-1853, 1853a,b, 1854-1855), and became a leading approach in modern marine biogeography (e.g., Blaxter and Southward 1997). And then, one of the latest geographic approach to biogeographic research is the development of zonal-biogeographic (bio-climatic and bio-oceanographic) zonation charts. Since this approach started with the distribution analyse of the corresponding water masses where the organismic distribution is subsequently correlated can be attributed to biological oceanography.

The biological aspect in biogeographic researches for explaining spatial differentiation in biota and communities is primarily based on those features which characterize living organism and related environment including capability of organisms to reproduce, distribution and effect of the biogeographic barriers, tolerance to environmental impacts, competition and food web, etc. The starting point of biology in biogeographical study is the classification of distribution ranges in taxa, faunas and floras. The final goal is faunistic or floristic zonation which is specified by physical and geographic (oceanographic) data. Thus, the biological aspect of biogeographic studies represents an independent division of life sciences. In other words, biological oceanography starts from identifying geographical areas with similar inhabitancy conditions before investigating inhabitants of those areas. In turn, faunistic (floristic) biogeography begins with identifying areas

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with similar population and proceeds with the comparison between the areas and environmental factors.

Spatially discrete (for the assumed zonation scale) areas for biodiversity are distinguished by local maxima and minima in species richness index, serving as a boundary for basic biogeographical units. In zoogeography, the concentrations of species ranges are termed synperates (Greek *syn* - together, *peratos* - occuring) (Kuznetsov 1936), and in phytogeography they are termed *chorion* (Turrill 1958). Etimological sections of local minima of species richness may be logically named *asynperates*. Watery areas located between the adjacent synperates and/or asynperates are also forming basic biogeographic units. Subsequent qualitative analyse of species composition make it possible to identify biotic relationship between separate units and obtain a faunistic or floristic zonation scheme. Thus, the basic operating procedure in faunistic (floristic) biogeography is the distribution analysis of species richness (Kafanov 1991). In this case natural boundaries between the adjacent biogeographic units can be delineated regardless of possible existence of physical geographic barriers identified from organismic distribution patterns.

Statistical analyse of the distribution between the minima and maxima of the species richness of fishes and cyclostomates has permitted us to outline a system of ichthyofaunistic zonation in the East Sea (Kafanov *et al.* 2000). An earlier attempt of ichthyofaunistic zonation of the Gulf of Mexico (Sauskan 1979; see also: Kuronuma 1942 for flatfishes of the Japanese Islands) was made using a range boundary of "condensation"procedure for a large-scale sampling. Their analysis was based on bottom fishes only, and our analysis is based on whole ichthyofauna without classifying the ichthyofauna into different ecological groups. Such an approch may cause certain suspicion since the ecological conditions in pelagic and benthic zones are substantially different, and marine biodiversity is known to be higher in the benthic zone than in the pelagic zone (Ray and Grassle 1991; Angel 1993; Lambshead 1993; Gray 1997). However, it is common to use separate zonation for benthic and pelagic realms in marine biogeography (e.g. Briggs 1974).

With respect to fishes and cephalopod molluscs, studies were attempted for making common benthic and pelagic zonation systems (Nesis 1982; Parin and Nesis 1986). Thus far, such attempts were based on assumptions rather than supported by rigorous quantitative analyse.

Based on the previous quantitative procedures (Kafanov *et al.* 2000), the present study tried to make an assessment of a possibility of forming a common system for benthic and pelagic biogeographic zonation by way of a case analysis of well known ichthyofauna of the East Sea.

2. Materials and methods

The materials used for this study were taken from the species list of fishes and cyclostomates from the west and east coasts of the East Sea, compiled for each latitudinal degree. The list was based on comprehensive reports on the ichthyofauna of the East Sea (Honma 1952; Mori 1952; Lindberg and Legeza 1959, 1965; Lindberg and Krasyukova 1969, 1975, 1987; Chyung 1977; Masuda *et al.* 1984; Matsuura and Arai 1984, 1986; Lindberg and Fedorov 1993) supplemented by the current ichthyological literature and original evidences by D.L.Pitruk. The borders of biogeographic units in the open sea are approximated on allocation of isotherms and currents (see: Kafanov *et al.* 2000)

Unfortunately, accurate biotic (benthic or pelagic) identification, more or less, who made of 379 species only, accounting for no more than 33.5% of the total ichthyofauna of the East Sea. Of 379 species, 145 species are referred to be typically palagic and 234 species as benthic (i.e. demersal and intertidal). In the east coast of which is subjected to direct impact of the Tsusima cur-

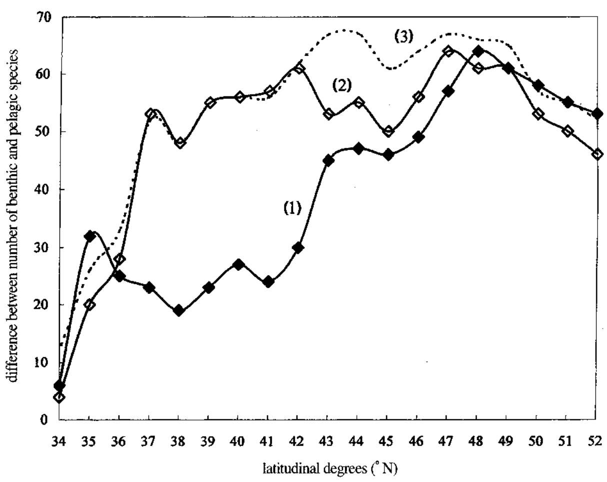

Fig. 1. Latitudinal variations in the difference between the species richness of benthic and pelagic fishes near the west (1) and east (2) coast and for the whole of the East Sea (3).

rent the latitudinal variations in the species richness of benthic and pelagic fishes are to a larger degree dictated by ichthyofaunistic composition (Fig.1).

As previously reported (Kafanov *et al.* 2000), the identification of local non-uniformities in the distribution of the species richness of benthic and pelagic ichthyofauna was based on an analysis of residuals in polynomial trends and arithmetic differences in a number of fish species at *i*-th and *i*+1-st latitudes.

Analysis of residuals in polynomial trends.

The first part of this procedure depends on obtaining a latitudinal trend of the species richness, i.e. some smooth curves describe a general decreasing tendency in the species number in the south-north direction ignoring local (particularly, random) changes in the species richness. For this purpose, polynomial approximation was used. The order of polynomial expression was determined by stepwise regression procedure; the polynomial function was increased till the determination coefficient proceeded to increase and the residual dispersion decreased while all the regression coefficients remained significantly different from zero. The following expressions have been obtained for benthic and pelagic ichthyofauna of the west and east coasts:

$$S_{WP} = 33201.4 - 3016.53 \cdot L + 102.619 \cdot L^2 - 1.54651 \cdot L^3 + 0.00870463 \cdot L^4,$$

$$S_{EP} = 708.783 - 25.7075 \cdot L + 0.238316 \cdot L^2,$$

$$S_{WB} = 6899.57 - 468.742 \cdot L + 10.6512 \cdot L^2 - 0.0801045 \cdot L^3,$$

$$S_{EB} = 8.44922 \cdot L - 0.140052 \cdot L^2,$$

where L is geographical latitude, °N, S is the number of species (subscripts W and E denote the west and east coasts, respectively, P and B - pelagic and benthic ichthyofauna, respectively).

The second part of the procedure depends on finding the residuals; substracting the trend from the initial data to obtain the local gradient pattern of the species richness which is undistorted by the general trend of the latter. As shown earlier (Kafanov *et al.* 2000), the positions of maxima and minima of those residuals were practically always coinciding with the boundaries of elementary biogeographical units.

Analysis of differences in a number of fish species at *i*-th and *i*-1-st latitudes.

In addition to the arithmetic differences in a number of fish species at *i*-th and *i*-1[st] latitudes (an elementary index requiring no explanations), $D = (\sqrt{n_i} - \sqrt{n_{i-1}})^2$, was used where n_i was the number of species at a given latitudinal degree, n_{i-1} was the number of species at a preceding latitudinal degree (variations in the species richness are being considered in the south-north direction). This measure accepts only non-negative values, the greater the value the more expressed the local variations in the species richness. Similarly, the arithmetic difference in the species number, measure D is free from any hypotheses or regression model of latitudinal trend of the species richness. Local maxima of D identify the position of the beginning of the units.

Clustering of species lists.

This procedure was used only as a supplementary work. Since the clustering results are heavily dependent on the adopted measures of distance and operational algorithms, and there are no objective criteria for judging whether the obtained results are correct or incorrect. Besides, the result of zonation of a region under study in biogeographical investigations is basically determined by selected dimensions and boundaries of the units (e.g. Lobanov *et al.* 1995). Therefore, clustering of species lists for biogeographical zonation will be meaningful only for the cases of; 1) the data analysis for basic faunas (at the adopted scale of biogeigraphical zonation they constitute the fauna of one latitudinal degree), and 2) the comparison between species lists for the units identified independently, e.g. according to the variations in the species richness. In the first case, the authors preferably used Ward' s method (1963) for clustering the species lists. The difference of this method from numerous other methods lies in the fact that it uses a dispersion analysis for evaluating the distance between the clusters, minimizing the intraclass scatter between the objects of clustering.

3. Results

Latitudinal variations in the species richness in benthic and pelagic zones.

The qualitative assessment of latitudinal variations in the species richness (Figs. 1 and 2) is already sufficient for identifying certain influencing factors.

1. The species richness is higher near the bottom than in pelagic zones. This conclusion basically supports the

above cited publications stating that marine biodiversity is higher in the benthic system rather than in the pelagic one. The difference between the number of bottom and pelagic species is the smallest in the south, becoming larger in the northward direction along both coasts of the East Sea.

2. The species richness near the east coast is higher than that of the west. The difference between the number of species living in the east and west increases in the southward direction, and the beginning from 36-37° N shows a sharp decrease in both bottom (especially a heavy decrease) and pelagic zones. The difference may be sufficiently explained by the impact of the Tsusima current.

3. The species richness at the bottom and pelagic zones near the east and west coasts tends to decline from south toward north. This decline is more rapid near the west than the east coast and in pelagic than bottom zones.

4. The pattern of all these changes is neither smooth nor uniform. However on the background of general reduction in the species richness in the south-north direction, a set of local maxima and minima is always observed.

Of 234 benthic species, 78% occur near both coasts, while 22% occur near one of the coasts of the East Sea (18% only near the east coast and 4% only near the west coast). Of 145 pelagic species, 88% occur near both coasts and only 12% occur near one of the coasts(Table 1). This supports the idea that the Tsusima current is leading influence on the formation of the composition of both pelagic and benthic ichthyofaunas of the East Sea.

The differences in the species richness of ichthyofauna of the opposite coasts are proportional to the distance between the coasts (Fig. 3A). Similarly, the increase this distance gives rise to a number of species occurring only near one of the coasts (Fig. 3B). The distance between the coasts produces greater effect on the distribution of benthic ichthyofauna than to that of pelagic fishes. These differences might be associated with greater capability of pelagic ichthyofauna to settle and overcome biogeographical barriers albeit the settlement of a major part of benthic ichthyofauna occurs through pelagic juvenile stages.

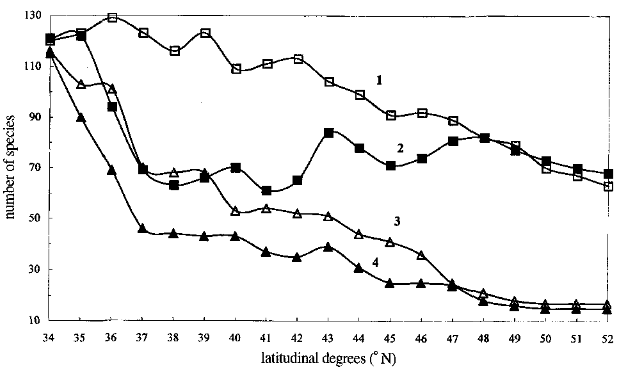

Fig. 2. Latitudinal variations in the species richness of benthic (1, 2) and pelagic (3, 4) ichthyofauna near the west (2, 4) and east (1, 3) coasts of the East Sea.

Identification of biogeographical units for benthic and pelagic zones.

Clustering of species lists of benthic and pelagic fishes compiled for each degree of the west and east coasts (Fig. 4) indicated that the comparison between the obtained dendrograms and those based on complete species lists (Kafanov *et al.* 2000) showed, but negligible, changes in the position and extension of the zones of similar ichthyofauna. As a rule, the differences in the unit boundary locations did not exceed one latitudinal degree, and for the east coast practically complete coincidence in the unit boundaries was observed. The analysis of latitudinal variations in the species richness (Figs. 5 and 6; Tables 2-4) gave the same results.

The species richness of pelagic ichthyofauna in the south-north direction (Fig. 6B) showed a very smooth decrease pattern near the east coast while near the west coast it changed rather sharply near 37-38° N where the Polar front was located. Its influence was even more pronounced in the distribution of benthic ichthyofauna (Fig. 5B) which showed minimum species richness at 37-42° N near the west coast. These latitudes located in the cyclonic circulation path of cold waters (North Korean current) which is separated, year round, from the surrounding water area by the Polar front (Yurasov and Yarichin 1991).

The intercomparison between various proven methods (Figs. 5 and 6; Tables 2-4) may have permited to make unequivocal identifications of biogeographical units. For further convenience, the units were given symbolic indices according to the following scheme; the initial letter *W* or *E* denoted the west and east coast respectively; the subsequent letter *P* or *B* stood for pelagic or benthic zone, respectively; the ultimate figure was the ordinal number of a unit in the south-north direction. Thus, WP_1 denoted the southernmost unit for

Table 1. Distance between the coasts and differences between ichthyofauna of the opposite coasts at various latitudes of the East Sea

Latitude, °N	Distance between the east and west coast, km	Absolute difference in the species number between the coasts		Number of species occuring only near one of the coasts*		Number of species common for the west and east coast*	
		pelagic	benthic	pelagic	benthic	pelagic	benthic
52	20	2	-5	2 (12%)	7 (10%)	15 (88%)	62 (90%)
51	111	2	-3	2 (12%)	7 (10%)	15 (88%)	65 (90%)
50	121	2	-3	2 (12%)	5 (7%)	15 (88%)	69 (93%)
49	121	2	2	2 (11%)	10 (12%)	16 (89%)	73 (88%)
48	200	3	0	3 (14%)	10 (11%)	18 (86%)	77 (89%)
47	271	1	8	9 (31%)	22 (23%)	20 (69%)	74 (77%)
46	328	11	18	17 (44%)	40 (39%)	22 (56%)	63 (61%)
45	400	16	20	22 (50%)	48 (46%)	22 (50%)	57 (54%)
44	500	13	21	21 (44%)	53 (46%)	27 (56%)	62 (54%)
43	534	12	20	22 (39%)	58 (47%)	34 (61%)	65 (53%)
42	837	17	48	27 (47%)	60 (50%)	30 (53%)	59 (50%)
41	914	17	50	27 (46%)	58 (50%)	32 (54%)	57 (50%)
40	1028	10	39	20 (34%)	49 (43%)	38 (66%)	65 (57%)
39	1077	25	57	35 (48%)	67 (52%)	38 (52%)	61 (48%)
38	946	24	53	34 (47%)	63 (52%)	39 (53%)	58 (48%)
37	751	24	54	36 (47%)	64 (50%)	40 (53%)	64 (50%)
36	706	32	35	38 (37%)	51 (37%)	66 (63%)	86 (63%)
35	341	13	1	23 (21%)	23 (17%)	85 (79%)	111 (83%)
34	152	1	-1	3 (3%)	17 (13%)	114 (97%)	112 (87%)
Over all latitudes		17	31	17 (12%)	51 (22%)	128 (88%)	183 (78%)
Near west coast only				0 (0%)	10 (4%)		
Near east coast only				17 (12%)	41 (18%)		

Note : *In all the rows of these columns, except the three ultimate ones, the absolute number of species is accompanied by a fraction of all the species number, pelagic and benthic respectively, inhabiting this particular latitude and shown in brackets. The three ultimate rows present fractions of the total number of species (of the relevant groups) inhabiting all the latitudes. In this and subsequent tables the species with indefinite ecological origin are not accounted for.

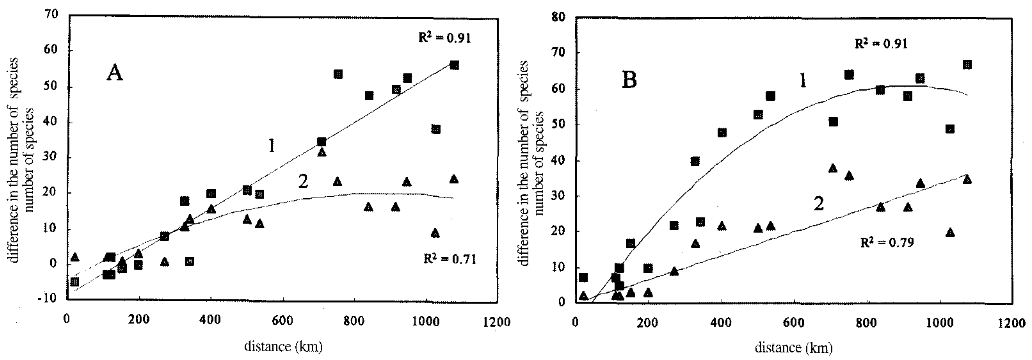

Fig. 3. The relationship between the difference in the species richness of the coasts (A), the number of species occurring near one of the coasts only (B) and the distance between the east and west coasts for benthic (1) and pelagic (2) ichthyofauna of the East Sea. R^2 - determination coefficient.

pelagic zone of the west coast. The alternatives formed by non-coincidence of the zonation schemes were additionally marked by letter indices a,b,c inaccordance with the figures.

The pelagic zone near both coasts between 34 and 35° N was evidently the boundary northward of which the pelagic ichthyofauna of the East Sea was located. To its south, there were very small units WP_1 and EP_1 of only one latitudinal degree in extension. They were followed by two other symmetric units WP_2 and EP_2 along two latitudinal degrees. The most important changes in the species richness were taking place near both coasts. This was where the symmetry finished and the next units in the west and east were different in dimensions and relative positions.

Near the west coast between 37 and 40° N the unit WP_3 was well identified by all the methods. It was succeeded by unit WP_4 in the water area between 41 and 43 ° N. The boundary between the latter unit and northward lying areas was marked by a very substantial change in the species composition. The subsequent four

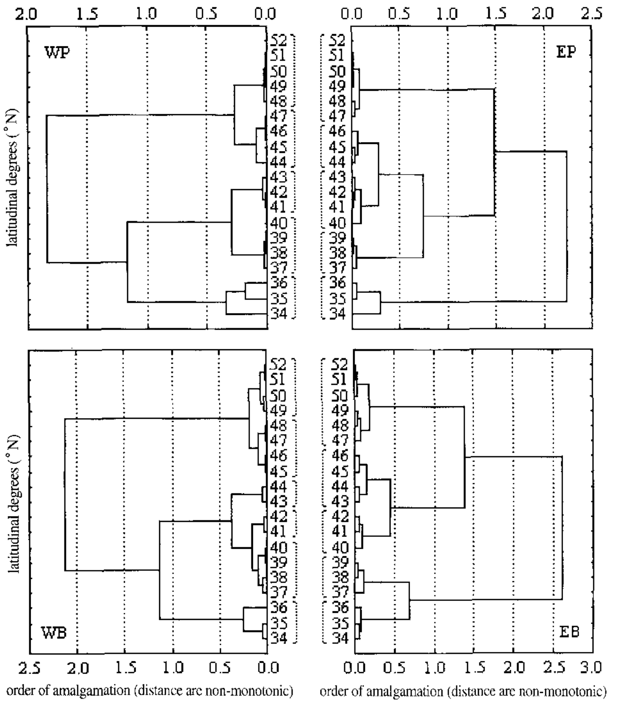

Fig. 4. Dendrograms (Ward's method) of similarity between the species lists of pelagic (upside) and benthic (downside) fishes of the west (left) and east (right) coasts of the East Sea. Latitudinal degrees with similar composition of ichthyofauna are bracketed in the centre (an attempt to observe one of possible zonation alternatives).

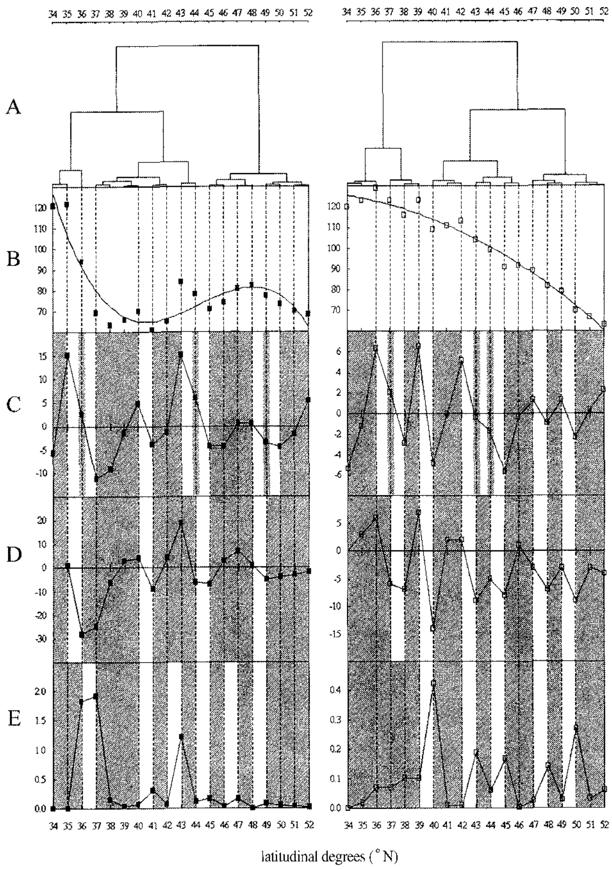

Fig. 5. Mutual correspondence between the species composition, variation in species composition and zonation results by various methods of distribution analysis of benthic ichthyofauna of the west (left) and east (right) coasts of the East Sea. Methods: A - clustering of the species lists per each degree, B -latitudinal trend of species richness, C - distribution of residuals of polynomial trends, D - distribution between minimal and maximal difference in species number at adjacent latitudes, E - distribution of peak values of measure D. The alternatives of the units found by each of the methods are cross-hatched.

latitudinal degrees of unit WP_5 within which, judging from a polynomial trend residuals method (not contradicting to the clustering results), there who a boundary between 44 and 45° N. This unit incorporated two unequal portions WP_{5a} and WP_{5b}. The species richness of WP_{5a} was noticeably different from the species richness of the remaining portion of the unit. In the north, the west coast is terminated by one large-sized unit WP_6 stretching between 48 and 52° N.

Near the east coast, at 37-40° N, unit EP_3 was equally identified by all the methods. Unit EP_4 located at 40-43 ° N was unequally identified by the two latter methods due to irregularity at 42° N (this irregularity was caused by a negligible increase in a number of species at 41° N).

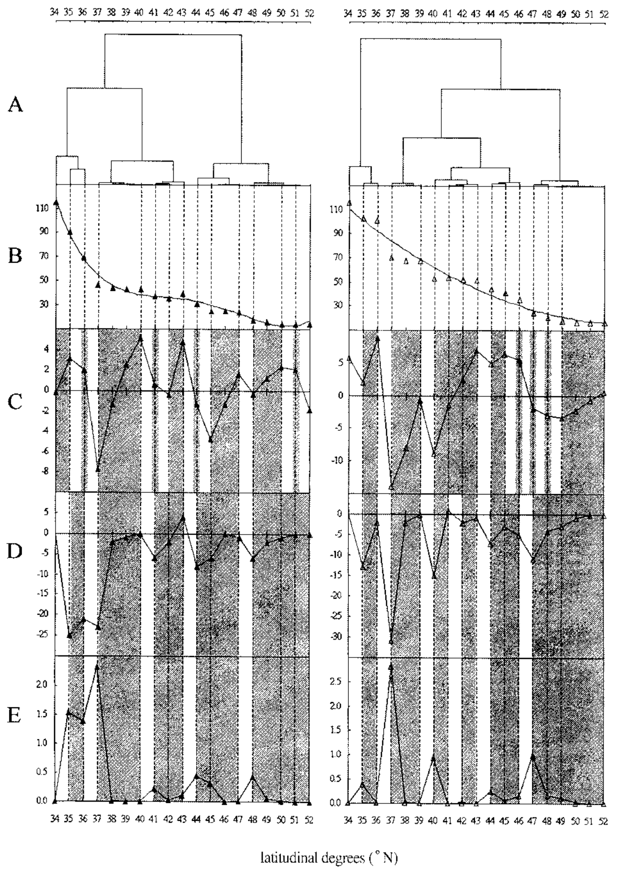

Fig. 6. Mutual correspondence between the species composition, variation in species composition and zonation results by various methods of distribution analysis of pelagic ichthyofauna of the west (left) and east (right) coasts of the East Sea. Methods: A - clustering of the species lists per each degree, B - latitudinal trend of species richness, C - residuals distribution of polynomial trends, D - distribution between minimal and maximal difference in the number of species at adjacent latitudes, E - distribution of peak values measure D. The alternatives of the units found by each of the methods are cross-hatched.

Within each of the units, the species richness showed but a faint variation. Within the bounds of next unit EP_5, the number of species was conspicuously decreased, and the unit was subdivided into EP_{5a} (44-45 ° N) and EP_{5b} (46° N). This subdivision was suggested by a polynomial trend residuals procedure. Between 46 and 47° N, the species composition characteristic of the middle portion of the sea was changed by a conspicuously differing set of species of the northern part of the sea. The northern unit EP_6 was composed of two short sections EP_{6a} (47° N) and EP_{6b} (48° N) where the species richness fell further down, and a relatively extended EP_{6c} (49-52° N) where it reached its minimum, subsequently remained unchanged.

In the benthic zone near the west coast the southernmost unit WB_1 was also non-uniform in the species richness. At its first portion WB_{1a} (34-35° N), the number of species was somewhat increased while at the second WB_{1b} (36° N), it was sharply reduced. As in the pelagic zone, in the north of 36° N, the maximum variation in the species number was observed accompanied by replacement of the species composition. The next unit WB_2 (37-40° N) was distinguished by initial falling and subsequent rising of the species richness, however, by all the methods involved, it was identified as a unique total. The units WB_3 (41-42° N) and WB_4 (43-44° N) can be identified only by using measure *D*. However, these units could not be combined since unit WB_3 was similar in the species composition to the previous and not subsequent unit. Moreover, the species richness of the two units was different; that of the first unit was comparatively low tending to rise in the northward direction while the species richness of the second unit was high and tended to decrease. Most substantial variation in the species composition of benthic ichthyofauna was reported between 44 and 45° N. According to the changes in measure *D* and clustering results, the next unit WB_5 could be subdivided into two equal portions WB_{5a} (45-46 ° N) and WB_{5b} (47-48° N), though each of the portions showed a uniform rise in the species richness. The concluding northernmost unit WB_6 extended between 49 and 52° N. The species richness of this unit tended to decrease uniformly in the northward direction.

In the east, for the bottom zone, a large-sized unit EB_1, was separated out, northward of which a dramatic change was observed in the species composition. The unit itself was composed of three portions, EB_{1a} (34-36 ° N), EB_{1b} (37° N) and EB_{1c}(38-39° N). The first portion was characterised by the rise in the species richness, the second one by its decrease while the third by a new rise. The next unit EB_2 (40-42° N) is the ultimate one where an important rise was observed in the northward direction. The unit EB_3 was located at 43-44° N. To the north of this unit, the ichthyofauna of the next three latitudinal degrees was identified in terms of various species composition as belonging to a common unit, though, according to clustering results of the species lists two different units [EB_4 (45-46° N) and EB_5 (47° N)] should be distinguished.

Between 46 and 47° N, a substantial change in the species composition of benthic ichthyofauna took place.

Table 2. Comparison between the actual values and polynomial trends of the species richness.

Latitude, °N	Number of species at the west coast						Number of species at the east coast					
	Pelagic			Benthic			Pelagic			Benthic		
	actual	trend	residual	actual	trend	residual	actual	trend	residual	actual	trend	residual
52	15	16.85	-1.85	68	62.50	5.50	17	16.40	0.60	63	60.66	2.34
51	15	12.86	2.14	70	71.56	-1.56	17	17.56	-0.56	67	66.63	0.37
50	15	12.59	2.41	73	77.41	-4.41	17	19.20	-2.20	70	72.33	-2.33
49	16	14.75	1.25	77	80.53	-3.53	18	21.31	-3.31	79	77.75	1.25
48	18	18.30	-0.30	82	81.40	0.60	21	23.90	-2.90	82	82.88	-0.88
47	24	22.37	1.63	81	80.51	0.49	25	26.97	-1.97	89	87.74	1.26
46	25	26.32	-1.32	74	78.33	-4.33	36	30.51	5.49	92	92.31	-0.31
45	25	29.72	-4.72	71	75.34	-4.34	41	34.54	6.46	91	96.61	-5.61
44	31	32.35	-1.35	78	72.02	5.98	44	39.03	4.97	99	100.63	-1.63
43	39	34.17	4.83	84	68.86	15.14	51	44.01	6.99	104	104.36	-0.36
42	35	35.39	-0.39	65	66.34	-1.34	52	49.46	2.54	113	107.82	5.18
41	37	36.40	0.60	61	64.93	-3.93	54	55.38	-1.38	111	110.99	0.01
40	43	37.81	5.19	70	65.12	4.88	53	61.79	-8.79	109	113.89	-4.89
39	43	40.45	2.55	66	67.39	-1.39	68	68.67	-0.67	123	116.50	6.50
38	44	45.34	-1.34	63	72.21	-9.21	68	76.03	-8.03	116	118.84	-2.84
37	46	53.71	-7.71	69	80.08	-11.08	70	83.86	-13.86	123	120.89	2.11
36	69	67.01	1.99	94	91.46	2.54	101	92.17	8.83	129	122.66	6.34
35	90	86.89	3.11	122	106.84	15.16	103	100.96	2.04	123	124.16	-1.16
34	115	115.23	-0.23	121	126.70	-5.70	116	110.22	5.78	120	125.37	-5.37

Note : Local minima of the residuals are designated by single underlining, local maxima by double underlining.

Table 3. Comparison between the species richness of ichthyofauna at the adjacent latitudes.

Latitude, °N	West coast				East coast			
	Pelagic		Benthic		Pelagic		Benthic	
	number of species at this latitude (n_i)	difference in the number of species at this and previous latitude (n_i-n_{i-1})	number of species at this latitude (n_i)	difference in the number of species at this and previous latitude (n_i-n_{i-1})	number of species at this latitude (n_i)	Difference in the number of species at this and previous latitude (n_i-n_{i-1})	number of species at this latitude (n_i)	difference in the number of species at this and previous latitude (n_i-n_{i-1})
52	15	0	68	-2	17	0	63	-4
51	15	0	70	-3	17	0	67	-3
50	15	-1	73	-4	17	-1	70	-9
49	16	-2	77	-5	18	-3	79	-3
48	18	-6	82	1	21	-4	82	-7
47	24	-1	81	7	25	-11	89	-3
46	25	0	74	3	36	-5	92	1
45	25	-6	71	-7	41	-3	91	-8
44	31	-8	78	-6	44	-7	99	-5
43	39	4	84	19	51	-1	104	-9
42	35	-2	65	4	52	-2	113	2
41	37	-6	61	-9	54	1	111	2
40	43	0	70	4	53	-15	109	-14
39	43	-1	66	3	68	0	123	7
38	44	-2	63	-6	68	-2	116	-7
37	46	-23	69	-25	70	-31	123	-6
36	69	-21	94	-28	101	-2	129	6
35	90	-25	122	1	103	-13	123	3
34	115		121		116		120	

Note : Local minima of differences are underlined.

Table 4. Latitudinal variations in the actual species richness (n_i)and measure *D*.

Latitude, °N	West coast				East coast			
	Pelagic		Benthic		Pelagic		Benthic	
i	n_i	$\left(\sqrt{n_i}-\sqrt{n_{i-1}}\right)^2$	n_i	$\left(\sqrt{n_i}-\sqrt{n_{i-1}}\right)^2$	n_i	$\left(\sqrt{n_i}-\sqrt{n_{i-1}}\right)^2$	n_i	$\left(\sqrt{n_i}-\sqrt{n_{i-1}}\right)^2$
52	15	0.000	68	0.014	17	0.000	63	0.062
51	15	0.000	70	0.031	17	0.000	67	0.033
50	15	0.016	73	0.053	17	0.014	70	0.272
49	16	0.059	77	0.079	18	0.116	79	0.028
48	18	0.431	82	0.003	21	0.174	82	0.143
47	24	0.010	81	0.158	25	1.000	89	0.025
46	25	0.000	74	0.031	36	0.163	92	0.003
45	25	0.322	71	0.165	41	0.053	91	0.168
44	31	0.459	78	0.111	44	0.258	99	0.062
43	39	0.108	84	1.216	51	0.005	104	0.187
42	35	0.028	65	0.064	52	0.019	113	0.009
41	37	0.225	61	0.310	54	0.005	111	0.009
40	43	0.000	70	0.059	53	0.933	109	0.423
39	43	0.006	66	0.035	68	0.000	123	0.103
38	44	0.022	63	0.136	68	0.014	116	0.103
37	46	2.323	69	1.929	70	2.833	123	0.071
36	69	1.393	94	1.823	101	0.010	129	0.071
35	90	1.530	122	0.002	103	0.386	123	0.019
34	115		121		116		120	

Note : Local maxima of measure *D* are underlined.

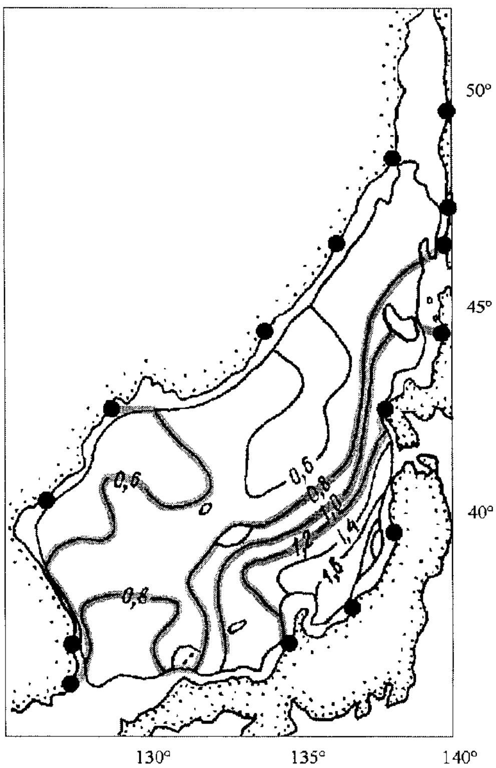

Fig. 7. Location of boundaries of benthic faunistic units (black circles) due to temperature distribution at 300m depth (from: Yurasov and Yarichin 1991). Grey lines along isotherms denote probable course of the boundaries of faunistic units.

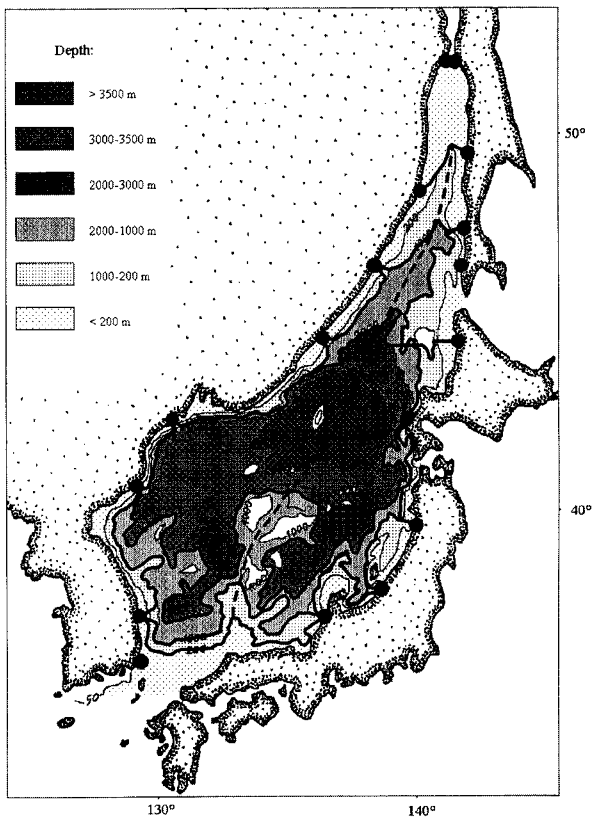

Fig. 8. Location of boundaries of benthic faunistic units (black circles) due to distribution of depths in the East Sea (from: Dobrovolsky and Zalogin 1982).

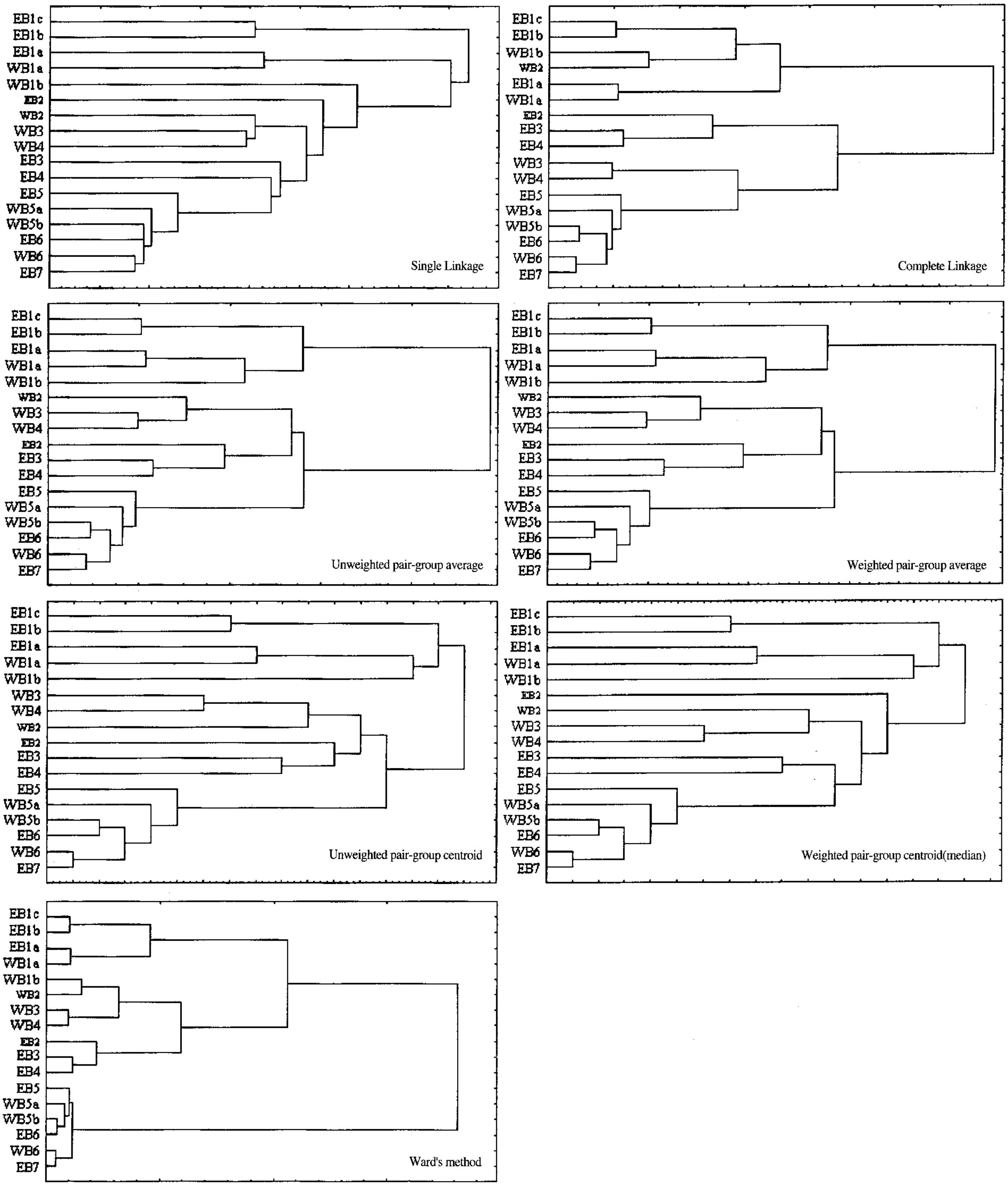

Fig. 9. Similarity dendrograms between species composition of the units determined by various clustering procedures for benthic ichthyofauna of the East Sea.

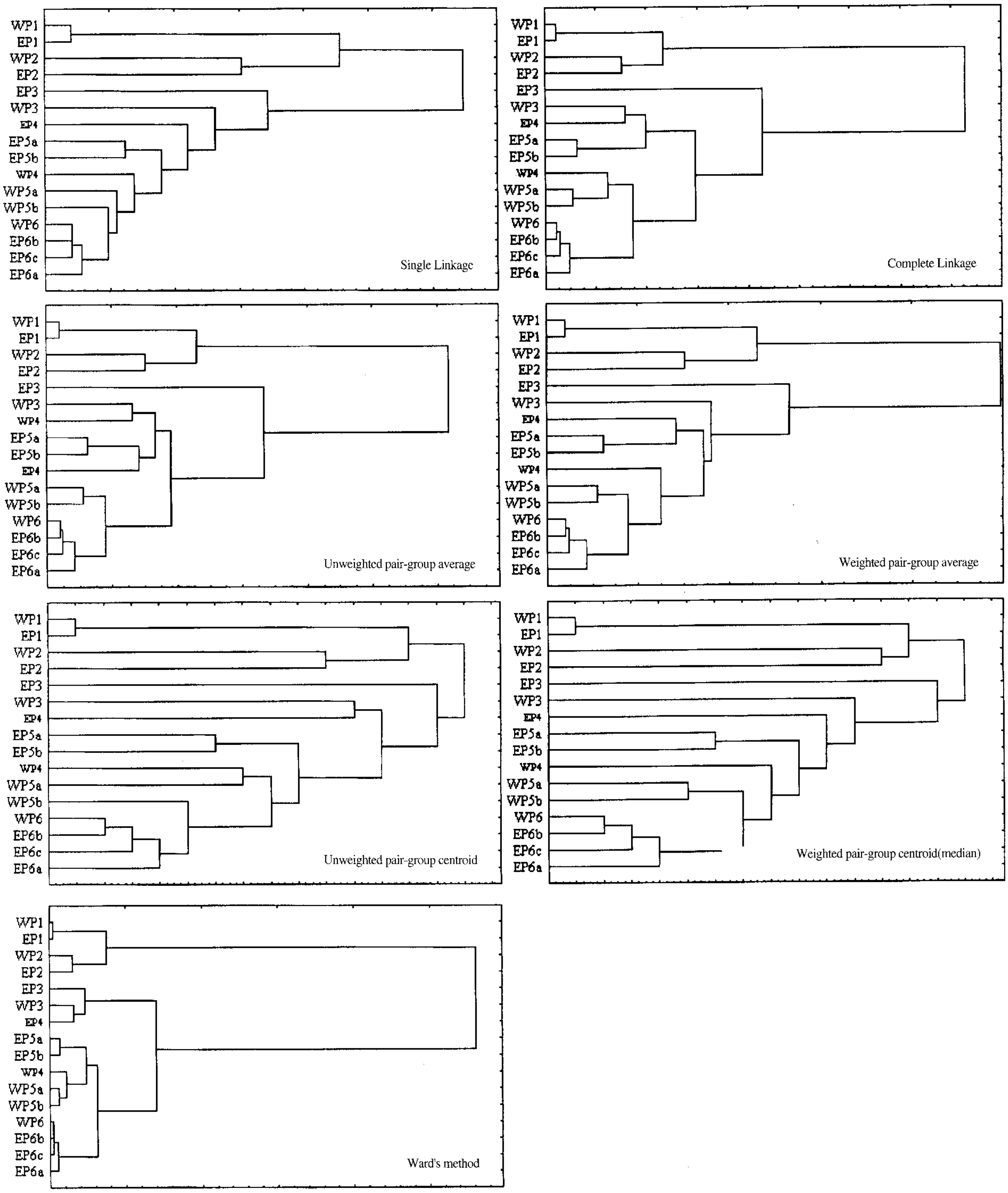

Fig. 10. Similarity dendrograms of between species composition of the units determined by various clustering procedures for pelagic ichthyofauna of the East Sea

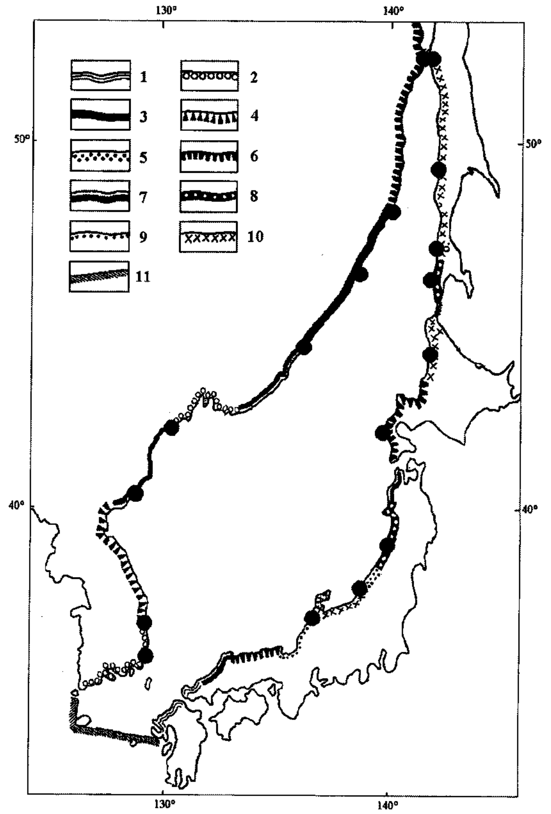

Fig. 11. Location of boundaries of benthic faunistic units (black circles) due to distribution of coastal geomorphological types of the East Sea (from: Dobrovolsky and Zalogin 1982). Coastal types shores formed by subaeral and tectonic processes: 1-bight, 2-rias, 3-plaited, 4-fault; shores formed by predominantly non-wave processes: 5-coasts of alluvial flatness; shores formed by predominantly wave processes: 6-abrasion-bight, 7-bight abrasion-accumulative, 8-levelled abrasion-accumulative, 9-levelled accumulative, 10-levelled accumulative with modern marine terrase; 11-south limit of the East Sea.

All the methods reported a similarly distinct identification of the two northernmost units, *EB₆* (48-49° N) and *EB₇* (50-52° N). Mutual relationship between benthic and pelagic faunistic units is shown in Table 5.

Table 5. Mutual correspondence between benthic and pelagic units.

<table>
<tr><th rowspan="2">Latitude, °N</th><th colspan="2">West coast</th><th colspan="2">East coast</th></tr>
<tr><th>benthic</th><th colspan="2">Pelagic</th><th>benthic</th></tr>
<tr><td>52</td><td rowspan="4">WB_6</td><td rowspan="5">WP_6</td><td rowspan="4">EP_{6c}</td><td rowspan="3">EB_7</td></tr>
<tr><td>51</td></tr>
<tr><td>50</td></tr>
<tr><td>49</td><td rowspan="2">EB_6</td></tr>
<tr><td>48</td><td rowspan="2">WB_{5b}</td><td>EP_{6b}</td></tr>
<tr><td>47</td><td rowspan="3">WP_{5b}</td><td>EP_{6a}</td><td>EB_5</td></tr>
<tr><td>46</td><td rowspan="2">WB_{5a}</td><td>EP_{5b}</td><td rowspan="2">EB_4</td></tr>
<tr><td>45</td><td rowspan="2">EP_{5a}</td></tr>
<tr><td>44</td><td rowspan="2">WB_4</td><td>WP_{5a}</td><td rowspan="2">EB_3</td></tr>
<tr><td>43</td><td rowspan="3">WP_4</td><td rowspan="4">EP_4</td></tr>
<tr><td>42</td><td rowspan="2">WB_3</td><td rowspan="3">EB_2</td></tr>
<tr><td>41</td></tr>
<tr><td>40</td><td rowspan="4">WB_2</td><td rowspan="4">WP_3</td></tr>
<tr><td>39</td><td rowspan="3">EP_3</td><td rowspan="2">EB_{1c}</td></tr>
<tr><td>38</td></tr>
<tr><td>37</td><td>EB_{1b}</td></tr>
<tr><td>36</td><td>WB_{1b}</td><td rowspan="2">WP_2</td><td rowspan="2">EP_2</td><td rowspan="3">EB_{1a}</td></tr>
<tr><td>35</td><td rowspan="2">WB_{1a}</td></tr>
<tr><td>34</td><td>WP_1</td><td>EP_1</td></tr>
</table>

4. Discussion

It is evident that the living conditions of benthic and pelagic ichthyofauna are basically different and the local abiotic factors greatly affect the distribution of, for instance, bottom and near-bottom fishes. This is evidenced by a definite correlation in the boundary position of benthic faunistic units according to the distribution of the bottom temperature (Fig. 11), bottom relief (Fig. 8) or geomorphological type of coast (Fig. 9). However, the distribution of marine biota within the bounds of biosphere (or its major sections) is much more influenced by spatial non-uniformity of hydrological structures associated with interchanges in diversely directed circulations of waters and frontal zones.

Large-scale gyres extending from coast to coast encompass primary water masses supporting primary oceanic communities. The effect of these gyres (even in the form of depth anti-gyres) is traced down to sea bottom (Defant 1961). A large number of benthic fishes have pelagic eggs and/or larvae stages. Therefore, spacing of benthic and pelagic fishes (and other marine organisms) should basically conform one another.

The results of biogeographical zonation made with respect to the ichthyofauna of the East Sea as a whole, without its subdivision into separate ecological groups (benthic and pelagic) have permitted us (Kafanov *et al.* 2000) to conclude that at the west coast of the East Sea, the elementary faunistic units are confined to 34-36 (unit W_1), 37-40 (W_2), 41-44 (W_3), 45-47 (W_4), 48-49 (W_5) and 50-52° N (W_6) and at the east coast to 34-36 (E_1), 37-39 (E_2), 40-43 (E_3), 44-46 (E_4) and 47-52° N (E_5). The com-

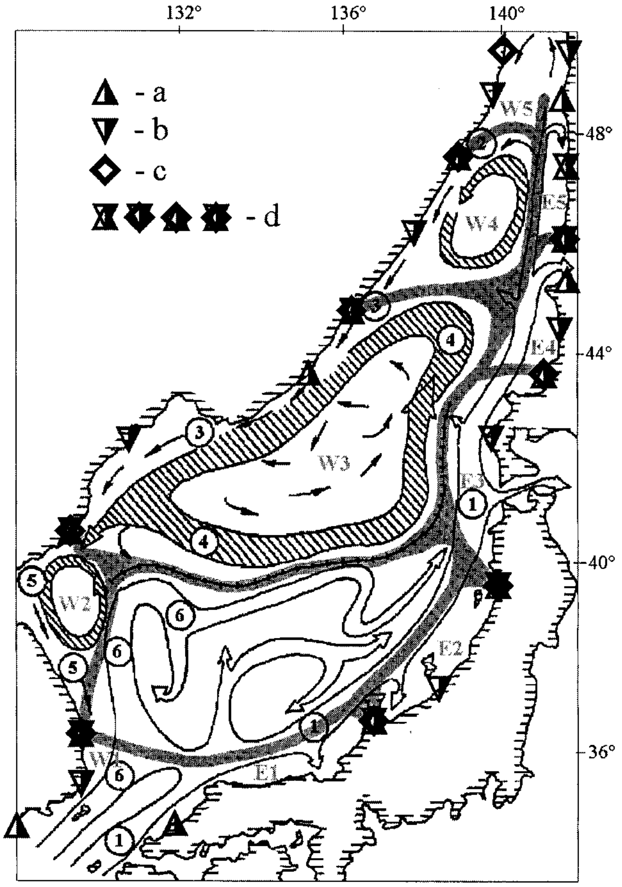

Fig. 12. Common biogeographical zonation chart of the East Sea for benthic and pelagic ichthyofauna. Provinces: W1+E1 Osaka (Tanaka 1921; for east coast may be also used as Middle Honshu (Jordan 1901)), W2-East Korea (Kafanov 1991), W3-Primorye (Golikov 1963), W4-North Primorye (proposed herein), W5-Northern East Sea (Ushakov 1953), E2-Uetsu (Nomura and Hatai 1936), E3-Tsugaru (Kafanov 1991), E4-Soya (Kussakin *et al.* 1975), E5-West Sakhalin (proposed herein). A wide transitional zone places to the south from Polar Front, in zone of East Korea Current. Generalization of water circulation scheme is made from Uda (1952), Yarichin (1980), Yurasov and Yarichin (1991), and evidence of researchers from the Pacific Research and Fisheries Centre (Shuntov, in press). Light arrows: warm currents; dark arrows: cold currents. Currents (designated by white circles): 1-Tsushima, 2-Liman, 3-Primorye, 4-South Primorye, 5-North Korea, 6-East Korea. Polar Front is designated by a line with points in the sea centre between South Primorye and East Korea currents. The symbols a-c indicate positions of biogeographical boundaries established by miscellaneous methods of analysis (see Figs. 5, 6), symbols d-coincidence of all these results.

parison between the boundaries of these units with those separately identified for benthic and pelagic ichthyofauna (Table 5) as well as with the results of various species list clustering procedures for each unit (Figs. 9 and 10) indicates that the coincidence is observed in 73% of the cases. Certain cases of non-coincidence do not exceed 1°N. Thus, with the use of the adopted geographical scale (below 1:10,000,000) (see: Kafanov and Kudrayshov 2000), a unique biogeographical zonation for benthic and pelagic ichthyofauna can be used in practice. (Fig. 12).

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This paper is dedicated to the memory of Academician Alexey V. Zhirmunsky (1921-2000), founder and first director of the Institute of Marine Biology, Far East Branch, Russian Academy of Sciences.

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