Zonal distribution and community structure of euphausiid on the coastal shelf off central Oregon, during 1970-1972: A multivariate approach

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ABSTRACT: Community structure and inshore-offshore zonal distribution of euphausiids off the central Oregon, USA (Newport Hydrographic line, 44° 40'N) was examined from oceanographic surveys from January 1970 through July 1972. The community variables were related to monthly changes in temperature, salinity, Bakun upwelling index (BUI), and regional ocean circulation. Multivariate analysis was done to identify strongest environmental gradients that influence the temporal and spatial changes in the euphausiid community structure. Fourteen euphausiid species were found associated to this upwelling ecosystem with a β-diversity of 7.3 and a Gamma diversity of 14. The main reproductive area where egg and nauplii were mainly distributed was nearshore (< 10 nautical miles from the coast during summer). The euphausiid community assemblage in the Oregon upwelling region is separated in two groups: neritic and oceanic assemblages by strong longitudinal gradient indicated by the distance from the coast (the coastal zone limit is about 25 nautical miles offshore). Positive Bakun upwelling index (upwelling) 5 days before sampling was associated to *T. spinifera*, while negative BUI were associated to the presence of the oceanic species in the NH-line during October to November each year. Other variables like time of sampling (D/N) and sea surface temperature were secondary variables to separate these two assemblages. The dominant species *Euphausia pacifica* and *Thysanoessa spinifera* have a strong life-stage segregation within the Oregon upwelling region where early larvae stages inhabits in different environmental conditions than juvenile and adults stages. High densities of larvae and juveniles of *T. spinifera* also were found nearshore but older stages were mainly recorded offshore (10 to 60 nm from the coast). *Euphausia pacifica* was found relatively homogeneously distributed in shelf and offshore waters but were recorded chiefly inshore in mid-summer and offshore the rest of the year. Four species can be considered as good indicator species for offshore environment of the Oregon upwelling region: *Tessarabrachion oculatus, Thysanoessa longipes, T. gregaria, Nematoscelis atlantica, N. difficilis*, and *Euphausia pacifica* featured by temperatures larger than 10°C. Our data support the hypothesis there are strong inshore-offshore segregation in species distributions suggesting active maintenance strategies of these euphausiids within this upwelling region.

Table 1. Average and relative abundance (ind 1000 m^3) of eggs, larvae (NI to furcilae stages) and juveniles and adults of the euphausiids along the Newport Hydrographic line during 1970 to 1972 period. Abundance was divided in coastal stations (NH1-NH10) and shelf break and oceanic waters (NH15 to NH60). Number of station analyzed are shown in parenthesis.

Species	Coastal stations (NH1 to NH10) 1970 (n=41)	1971 (n=48)	1972 (n=30)	% 1970-1972	Oceanic stations (NH20-NH60) 1971 (n=102)	1972 (n=42)	% 1970-1972
Eggs							
Euphausia pacifica	13475	117	1141	23.2	2140	1809	85.7
Thysanoessa spinifera	28420	19493	877	76.8	495	156	14.1
Thysanoessa longipes	0	0	0	0.001	9	0	0.2
Total	**41895**	**19610**	**2019.1**		**2644**	**1966**	
Larvae (nauplii, metanauplii, calyptrope, and furciliae)							
Euphausia pacifica	3700	10	148	29.3	831	835	58.6
Thysanoessa spinifera	5139	3045	1114	70.5	505	483	34.7
Nematobrachion flexipes	0	0	0	0.0	0	0	0.0
Nematoscelis atlantica	0	0	0	0.0	0	1	0.02
Nematoscelis difficilis	1	2	0	0.02	7	10	0.6
Stylocheiron abbreviatum	0	0	0	0.0	0	0	0.0
Stylocheiron affine	0	0	0	0.0	0	0	0.02
Stylocheiron longicorne	0	0	0	0.0	0	0	0.0
Stylocheiron maximum	0	0	0	0.0	0	0	0.0
Thysanoessa longipes	0	0	4	0.03	25	61	3.0
Thysanoessa gregaria	0	0	1	0.004	17	44	2.2
Thysanoessa inermis	0	20	0	0.15	1	0	0.05
Thysanoessa inspinata	0	0	0	0.0	3	0	0.1
Tessarabrachion oculatus	0	0	0	0.001	4	15	0.7
Total	**8840**	**3077**	**1265.5**		**1393**	**1449**	
Juvenile and adults							
Euphausia pacifica	18.2	136.2	34.9	9.2	662.1	751.8	65.8
Thysanoessa spinifera	41.2	1585.4	249.4	90.7	120.9	449.6	26.5
Nematobrachion flexipes	0.0	1.0	0.0	0.05	2.4	1.1	0.2
Nematoscelis atlantica	0.0	0.0	0.0	0.0	0.0	26.8	1.2
Nematoscelis difficilis	0.4	0.0	0.0	0.04	13.3	2.3	0.7
Stylocheiron abbreviatum	0.0	0.2	0.0	0.01	0.0	0.0	0.0
Stylocheiron affine	0.0	0.0	0.0	0.0	0.1	1.0	0.1
Stylocheiron longicorne	0.0	0.0	0.0	0.0	0.0	0.4	0.02
Stylocheiron maximum	0.0	0.0	0.0	0.0	0.6	0.0	0.03
Thysanoessa longipes	0.2	1.2	0.0	0.1	59.8	3.8	3.0
Thysanoessa gregaria	0.0	0.0	0.5	0.03	15.6	18.0	1.6
Thysanoessa inermis	0.0	0.0	0.0	0.0	0.3	0.0	0.01
Thysanoessa inspinata	0.0	0.0	0.0	0.0	1.8	0.0	0.09
Tessarabrachion oculatus	0.1	0.0	0.0	0.01	12.1	5.1	0.8
Total	**60**	**1724**	**284.9**		**889**	**1260**	

Data reduction and statistical methods. All analyses were conducted using the computer software PC-ORD v 4.36 beta

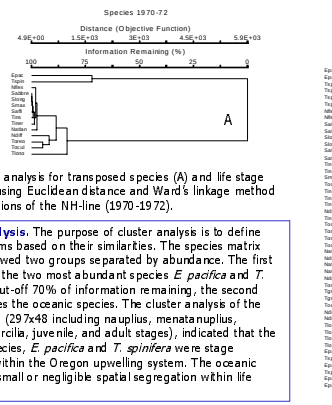

Fig. 3 Cluster analysis for transposed species (A) and life stage (B) matrices using Euclidean distance and Ward's linkage method for all the stations of the NH-line (1970-1972).

Cluster analysis. The purpose of cluster analysis is to define groups of items based on their similarities. The species matrix (297x14) showed two groups separated by abundance. The first one included the two most abundant species *E. pacifica* and *T. spinifera* at cut-off 70% of information remaining, the second group includes the oceanic species. The cluster analysis of the stages matrix (297x48 including nauplius, menatanauplius, calyptopis, furcilia, juvenile, and adult stages), indicated that the dominant species, *E. pacifica* and *T. spinifera* were stage segregated within the Oregon upwelling system. The oceanic species had small or negligible spatial segregation within life stages.

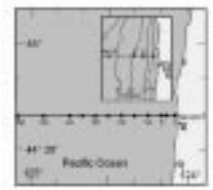

Fig. 1. **Area of study.** The Newport hydrographic line (NH) located at 44° 40'N, Oregon, USA has 12 stations from NH1 to NH60 (the number indicates the distance from the coast in nautical miles).

***Euphausia pacifica* Hansen**

***Thysanoessa spinifera* Holmes**

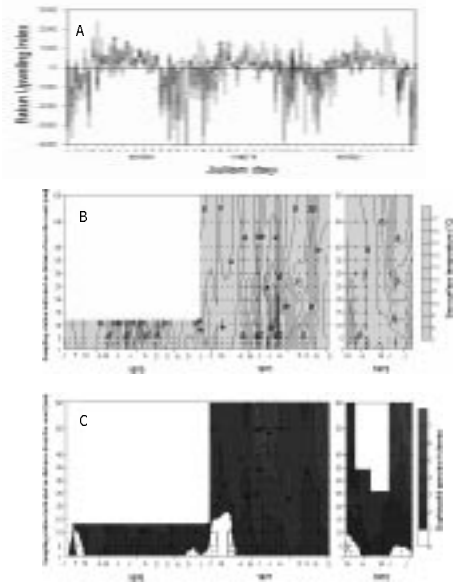

Fig 2. Daily Bakun upwelling index $m^3 s^{-1} 100 m^{-1}$ (red line) and sampling days (blue circles) (A), temporal and inshore-offshore distribution of sea surface temperature (B), and euphausiid species richness (C) along the NH-line during 1970-1972. Maximum alpha diversity was 7 species. White area indicates not data available.

The community structure of the euphausiid in the Oregon upwelling region during 1970-1972 included 14 species (see Table 1). *Euphausia pacifica* and *Thysanoessa spinifera* dominate the euphausiid abundance and biomass in this region. The coastal zone (NH1-NH10) is virtually inhabited by these two species during the three years. The species richness increased from the station NH25 to NH60 mainly during summer time when temperature increases offshore (see Figure 2). High diversity of euphausiid community offshore is associated to high temperature (>10°C) and downwelling conditions within the Oregon upwelling region.

Multiresponse Permutation Procedure (MRPP) is a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities. MRPP has the advantage of not requiring assumptions (such as multivariate normality and homogeneity of variances) that are seldom met with ecological community data. We tested seven null hypothesis (H_0) using data for the species matrix (287x14) for all the NH-line. The same hypotheses were tested for the coastal (NH1-NH15) and oceanic (NH20-NH60) environment data sets. There were significant differences in abundance of the euphausiid at Day/Night sampling time, inshore-offshore distribution pattern, and between upwelling and downwelling conditions (indicated by Bakun upwelling index and < 10°C SST). Community structure associated to Upwelling index five days before date sampling was significantly different in the coastal and oceanic environment.

Table 2. Multiresponse permutation Procedure (MRPP) results for the comparison of environmental conditions in the Newport Hydrographic line during 1970-1972 period. All MRPP analyses were done using Sorensen (Bray-Curtis) distance measure, the weighing of groups was [n/sum(n)], and the distance matrix was rank transformed. Environmental data were categorized according to the correspondance null hypotheses showed in group tested column.

Groups tested and hypothesis	Matrix used	Delta	A	p-value
Day (n=249) vs Night (n=48) samples all the NH-line using the twilight criteria	Species (267x14)	-19.1620	0.0317	**0.0000**
Day (n=163) vs Night (n=4) coastal stations (1970, 1971, 1972)	Species (167x7)	-0.0001	0.0244	0.4336
Day (n=84) vs Night (n=44) oceanic stations (1971 vs 1972)	Species (128x13)	-9.1231	0.0305	**0.0000**
Inshore (NH1-NH15, n=171) vs Offshore (NH20-NH60, n=126) all the NH-line	Species (267x14)	-26.1657	0.0430	**0.0000**
Years 1970 (n=75), 1971 (n=154), 1972 (n=68) all the NH-line	Species (267x14)	-6.3267	0.0148	**0.0001**
Years 1970 (n=75), 1971 (n=64), and 1972 (n=28) coastal stations (NH1-NH15)	Species (167x7)	-0.9296	0.0048	0.1573
Years 1971 (n=88) and 1972 (n=40) oceanic stations (NH20-NH60)	Species (128x13)	-1.5552	0.0052	0.0791
Sea surface temperature <10°C (n=197) vs >10°C (100) all the NH-line	Species (267x14)	-2.5322	0.0042	**0.0271**
Sea surface temperature <10°C (n=133) vs >10°C (64) coasta stations (1970, 1971, 1972)	Species (167x7)	-0.4587	0.0017	0.2332
Sea surface temperature <10°C (n=39) vs >10°C (80) oceanic stations (1971 vs 1972)	Species (128x13)	-4.3238	0.0145	**0.0029**
Sea surface salinity <30 ppm (n=41) vs >30 ppm (n=256) all the NH-line	Species (267x14)	-0.3110	0.0005	0.2865
Bakun upwelling index during sampling day, upwelling (+, n=91) vs downwelling (-, n=206) all the NH-line	Species (267x14)	-4.0215	0.0066	**0.0052**
BUI during sampling day in coastal region, upwelling (n=54) vs downwelling (n=113)	Species (167x7)	-4.9419	0.0181	**0.0026**
BUI during sampling day in oceanic region, upwelling (n=37) vs downwelling (n=91)	Species (128x13)	-0.6539	0.0022	0.2002
Bakun upwelling index 5 days before day sampling, upwelling (n=96) vs downwelling (n=201) all the NH-line	Species (267x14)	-10.5714	0.0174	**0.0000**
BUI during 5 days before sampling in coastal region, upwelling (n=54) vs downwelling (n=113)	Species (167x7)	-19.5884	0.0717	**0.0000**
BUI during 5 days before sampling in oceanic region, upwelling (n=37) vs downwelling (n=91)	Species (128x13)	-3.7254	0.0125	**0.0000**

A max = 1 when all items are identical within groups (delta=0), A = 0 when heterogeneity within groups equal expectations by chance, and A < 0 with more heterogeneity within groups than expected by chance.

The **Indicator Species Analysis (ISA)** method combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group. It produces indicator values for each species in each group. These are tested for statistical significance using a Monte Carlo technique.

Table 3. Indicator Species Analysis results for euphausiid species in the Oregon upwelling region during 1970-1972 according to the grouping criteria used in the MRPP analysis. Only the species with significant probability and higher indicator values are shown. The indicator value is expressed as percentage of perfect indication (average abundance of a given species in a given group of oceanographic stations over the average abundance of that species in all stations). Species matrix (297 x 14) was transformed by log (x+1) and general relativized by species total.

Groups tested	Species	Group	Relative	p-value
Upwelling waters (<10°C vs. >10°C)	*T. oculatus*	<10°C	91	0
Salinity < 30 indicating Columbia river influence	*T. oculatus*	< 30	68	0.034
	T. gregaria	< 30	69	0.037
	N. atlantica	<30	84	0.024
Upwelling (+) vs. downwelling (-)	None			> 0.061
Upwelling vs. downwelling five days before sampling date	*T. spinifera*	Upwelling	59	0.000
On-shelf (NH1 to NH15) vs. Off-shelf (NH20 to NH60)	*T. spinifera*	On-shelf	58	0.000
	E. pacifica	Off-shelf	57	0.004
	N. atlantica	Off-shelf	100	0.019
	N. difficilis	Off-shelf	74	0.002
	T. longipes	Off-shelf	90	0.000
	T. gregaria	Off-shelf	97	0.000
	T. oculatus	Off-shelf	94	0.000

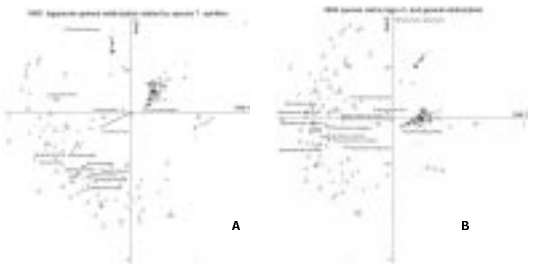

Fig. 4 Non-metric Multidimensional Scaling (NMS) for the species matrix using Sorensen (Bray-Curtis) distance measurement, 2 axes solution, 20 runs, and stability criterion of 0.0001 for all the NH-line data set (1970-1972). Data was transformed by log(x+1) and general relativization by species columns. The size of the triangle indicates the station, the smallest triangle is NH1 and the largest triangle is NH60. Ordination was rotated by the neritic species *T. spinifera* (A) and to maximize the distance from the coast vector (B).

Non-metric Multidimensional Scaling (NMS) is an ordination method that is well suited to data that are nonnormal or are on arbitrary, discontinuous, or otherwise questionable scales. An advantage of NMS is that, being based on ranked distances, it tends to linearize the relation between environmental distance and sociological distance, relieving the "zero-truncation problem". The NMS ordination by species showed that the stations on and off the continental shelf occupied distinct places in the species space demonstrating there were distinct differences in euphausiid community structure. The Monte Carlo analysis gave a probability of 0.0343 that the final stress level could have been obtained by chance. The first axis (52% of the variance) is correlated with upwelling/downwelling 5-days before sampling (r=0.156). The NMS analysis shows that *E. pacifica* (r=-0.308) was negatively and *T. spinifera* (r=0.289) positively associated with UI-5 conditions and most of the species (*N. difficilis*, *S. abbreviatum*, *S. affine*, *T. longipes*, *T. inermis*, and *T. inspinata*) were associated with downwelling conditions (r=-0.028 to –0.143). The second axis (25% of the variance) is negatively correlated to distance from the coast (r=-0.529), other variables like SST (r=-316) and Day/Night (r=-0.404) also are associated with this axis because SST also increase as a function of distance from the coast and because most of the night samples were taken offshore. The first two axes of the NMS explained the 78% of total variance.