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Regional variation in springtime ichthyoplankton assemblages in the northeast Pacific Ocean

Miriam J. Doyle [a,*], Kathryn L. Mier [b], Morgan S. Busby [b], Richard D. Brodeur [b,c]

[a] *Joint Institute for the Study of Atmosphere and Oceans, University of Washington, Seattle, WA 98195, USA*
[b] *Alaska Fisheries Science Center, Seattle, WA 98 115-0070, USA*
[c] *Present address: Northwest Fisheries Science Center, Newport, OR 97365-5296, USA*

Abstract

The coastal regions of the northeast Pacific support large, economically valuable fishery resources and provide nursery areas for many fish species. Over the last few decades, there have been dramatic shifts in species abundance and composition in this area. In this paper, we examine the springtime spatial patterns in the ichthyoplankton of three oceanographically different regions, the Southeast Bering Sea, the Gulf of Alaska and the U.S. West Coast. The data examined are a subset of a larger database (comprising data from cruises conducted from 1972 to 1997) that is being used to investigate spatial, seasonal and interannual patterns in ichthyoplankton of the northeast Pacific in relation to environmental conditions. Ichthyoplankton were collected during seven cruises using 60-cm bongo nets. Spatial patterns of ichthyoplankton were examined using both classification and ordination techniques. Relative Bray-Curtis dissimilarity coefficients calculated from the $\log_{10}$ (n+1) of abundance data were used as input to the numerical classification of species and stations. Nonmetric multidimensional scaling was also applied to the abundance data to examine geometric patterns in the data. The numerical analyses of the species abundance data sets for each cruise revealed spatial patterns in the ichthyoplankton that suggest the occurrence of geographically distinct assemblages of fish larvae in each region. For all three sampling regions, the assemblage structure is primarily related to bathymetry, and Shelf, Slope, and Deep-Water assemblages are described. This shallow to deep-water gradient in species occurrence and abundance reflects the habitat preference and spawning location of the adult fish. Another degree of complexity is superimposed on this primary assemblage structure in each region and seems to be related to local topography and the prevailing current patterns. The patterns in ichthyoplankton assemblages of the three regions in the northeast Pacific Ocean described here form the basis for future investigations of spatial and temporal patterns in the ichthyoplankton of the subarctic Pacific.

Regional Index Terms: Northeast Pacific Ocean, Southeast Bering Sea, Gulf of Alaska, U.S. West Coast. © 2002 Published by Elsevier Science Ltd.

Keywords: ichthyoplankton; assemblages; spatial patterns; habitat; topography; current patterns

* Corresponding author. Tel.: +1-206-526-4318; fax: +1-206-526-6723.
E-mail address: miriam.doyle@noaa.gov (M.J. Doyle).

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Contents

1. Introduction

Ichthyoplankton surveys have been carried out in many large marine ecosystems as a way of generating fishery-independent stock assessment and as a result have played a key role in understanding how marine ecosystems function (Moser & Smith, 1993a). For certain regions it is hypothesized that spawning strategies among marine fish populations have evolved in synchrony with prevailing oceanographic conditions to give rise to persistent multi-species assemblages of fish larvae (Parrish, Nelson & Bakun, 1981; Frank & Leggett, 1983; Doyle, Morse & Kendall, 1993). Distinct assemblages of larvae have been recognized in diverse marine ecosystems and their occurrences reflect temporal and spatial patterns in the oceanographic environment (Moser, Smith & Eber, 1987; Olivar, 1987; Sabates, 1990; Moser & Smith, 1993b; Doyle, 1992; Doyle, Morse & Kendall, 1993; Raynie & Shaw, 1994; Thorrold & Williams, 1996; Witting, Able & Fahay, 1999).

The present paper reviews an ongoing study of ichthyoplankton and environmental conditions in the northeast Pacific, begun in 1980, during several past and current research programs of the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS). Initially (1980-1984), ichthyoplankton surveys and environmental data collection were conducted by the Recruitment Processes Task of the Northwest and Alaska Fisheries Center (NWAFC). During the period 1980-87, several cooperative research cruises were conducted between NWAFC and Russian scientists aboard Russian vessels. In 1984, the Fisheries Oceanography Coordinated Investigations (FOCI) research program was initiated as a long-term cooperative effort by NOAA scientists at the Pacific Marine Environmental Laboratory (PMEL) and the Alaska Fisheries Science Center (AFSC) in Seattle. The goal of the program is to understand processes leading to recruitment variability of commercially valuable fish and shellfish stocks of the northeast Pacific Ocean (Kendall & Picquelle, 1990; Schumacher & Kendall, 1991; Kendall, Schumacher & Kim, 1996). While most of the effort has been concentrated on walleye pollock (*Theragra chalcogramma*) springtime distribution in the western Gulf of Alaska, ancillary information has been gathered on the distribution and abundance patterns of eggs and larvae of other fish species that spawn in the coastal zone and adjacent deep water of the northeast Pacific Ocean and Bering Sea. This information can contribute significantly to an understanding of the biology and ecology of fish populations in this region and the relationships between their life history strategies and the marine environment. Beginning in 1998, AFSC and PMEL scientists initiated research on ecosystems of the North Pacific Ocean sponsored by the Global Ocean Ecosystems Dynamics (GLOBEC) program. In this paper, we identify the numerically dominant species and species assemblages in the ichthyoplankton of the Gulf of Alaska (GOA), eastern Bering Sea (EBS), and U.S. West Coast (WC). We describe geographic distributions of these assemblages, and relate them to the prevailing oceanographic conditions in the three regions. Future studies will address temporal patterns in the ichthyoplankton of these regions.

2. Materials and Methods

2.1. Study Regions

The three geographic regions examined in this study differ significantly in terms of their topography, and physical and biological oceanography. We provide brief descriptions of these differences to aid interpretation of the results that follow.

The EBS is characterized by an exceptionally broad (>500 km) continental shelf region, with a narrow continental slope adjoining the extensive Aleutian Basin (Fig. 1). Circulation in the basin is cyclonic and is fed by inflow from the Alaska Stream through the Aleutian Islands (Schumacher & Stabeno, 1998). Flow is greatest in the Bering Slope Current, which transports nutrients onto the outer shelf. Flow over the shelf itself is generally weak and large eddies are a common feature. Ice covers a substantial portion of the EBS each winter and spring, although there is considerable interannual variation in the duration and extent of coverage (Wyllie-Echeverria & Ohtani, 1999). There are three recognized biophysical domains on the shelf, separated by frontal boundaries approximating to the 50 m, 100 m and 200 m isobaths, which

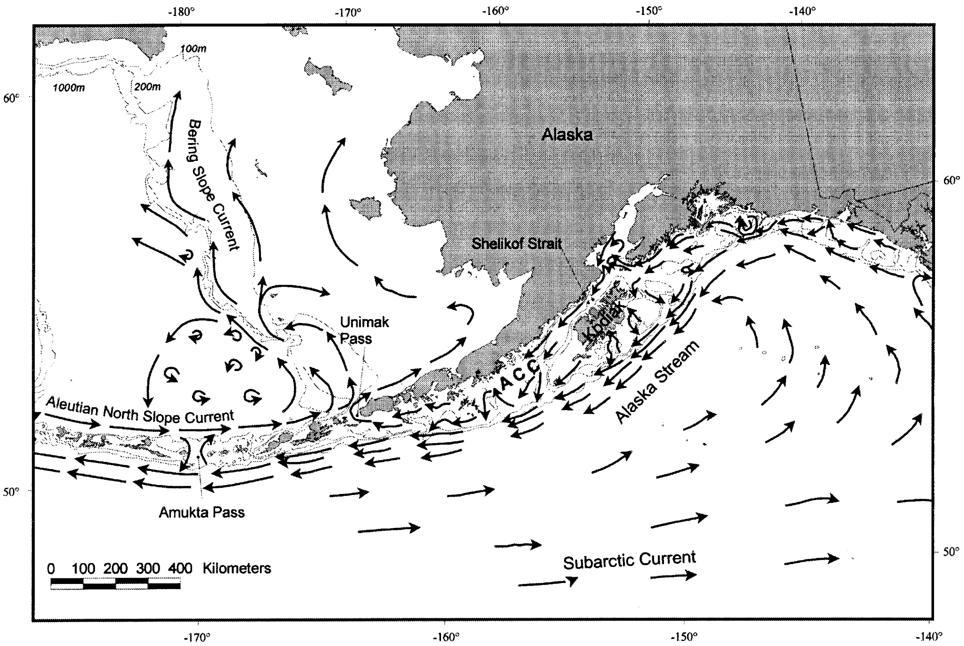

Fig. 1. Map of sampling area and schematic of prevailing pattern of circulation in the Southeast Bering Sea and Gulf of Alaska (after Reed & Schumacher, 1986).

differ hydrographically depending on the degree of stratification and mixing (Schumacher & Stabeno, 1998). Productivity appears to be highest at the shelf-break front and phytoplankton blooms can begin in May and last throughout the summer (Springer, McRoy & Flint, 1996). Zooplankton is also most dense in the outer shelf region and consists primarily of large oceanic copepod species. The EBS shelf is one of the most productive regions in the world and sustains a high biomass of higher trophic level organisms (Loughlin, Sukhanova, Sinclair & Ferrero, 1999).

Numerous troughs and shallow banks characterize the topography of the western GOA. The shelf area, as defined by the 200 m isobath, is narrower (65-175 km) than the EBS shelf and drops abruptly to depths of 5000-6000 m in the Aleutian Trench, which parallels the shelf edge (Fig. 1). The Alaskan Stream, which flows southwesterly and roughly parallel to the shelf break at 50-100 cm/sec, dominates offshore, near-surface circulation. Near-shore, the Alaska Coastal Current (ACC) is the dominant feature (Reed & Schumacher, 1986). The upper layer flows southwesterly. With surface speeds of 25-100 cm/sec, the ACC in the vicinity of Shelikof Strait is one of the most vigorous and dynamic coastal currents in the world (Stabeno, Reed & Schumacher, 1995). Temperatures follow a clear seasonal pattern, with the coldest values occurring in March and the warmest values in August (Reed & Schumacher, 1986). Freshwater discharge into coastal waters peaks in the fall and strongly affects the circulation (Royer, 1998). This region has been referred to as the Coastal Downwelling Domain and is characterized by mainly onshore flow at the surface (Ware & McFarlane, 1989). A seasonal peak in phytoplankton production occurs first in the ACC, and then in the adjacent shelf area, during the first week in May (Napp, Incze, Ortner, Sieffert & Britt, 1996). Production of copepod nauplii and other zooplankton usually accelerates significantly at this time but because of low temperatures and low concentrations of gravid adults, does not reach its maximum until mid-summer (Cooney, 1986).

In contrast to the EBS and western GOA, the continental shelf is narrow off the U.S. West Coast (Fig. 2). Off Washington and northern Oregon, the shelf width is less than 70 km, whereas off southern Oregon and northern California it narrows to less than 30 km, reaching a minimum of about 10 km off Cape Mendocino. A series of submarine canyons intersect the shelf and slope off Washington and California. Off Oregon, rocky submarine banks occur along the shelf. The WC is part of an extensive Coastal Upwelling Domain that extends from Baja California to southern British Columbia (Ware & McFarlane, 1989). The oceanography of this region is characterized by the California Current system, a typical eastern boundary current regime (Hickey, 1989, 1998). The main California Current flows southwards along the U.S. West Coast, its sub-components include the northerly flowing California Undercurrent and the Davidson Current. The California Undercurrent consists of a jet-like northward flow with a subsurface maximum, whose core appears to be confined to the continental slope. The northerly flowing Davidson Current is a surface current that occurs on the coastal side of the California Current during winter. In winter, winds from the south drive this surface current, causing onshore Ekman transport of surface water and downwelling close to the coast. A transition from southerly to northerly winds occurs during spring, and by summer the prevailing conditions include a southward flowing coastal current, offshore Ekman transport and upwelling of cold, nutrient laden, water close to the coast. The intensity of Ekman transport and associated upwelling varies along the coast but tends to increase from north to south with a local maximum at Cape Mendocino off northern California (Parrish, Nelson & Bakun, 1981). The prevailing current patterns during spring off the WC are illustrated in Fig. 2 by a schematic that represents the spring transition from northward to southward flow along the coast. Annual sea-surface temperature minima and salinity maxima generally occur in summer after sustained upwelling-favorable winds. Phytoplankton blooms occur during relaxed upwelling conditions between upwelling periods during spring and fall (Small & Menzies, 1981). A zone of high zooplankton standing stock is generally observed 10-30 km offshore in summer and the community is dominated by copepods (Landry & Lorenzen, 1989).

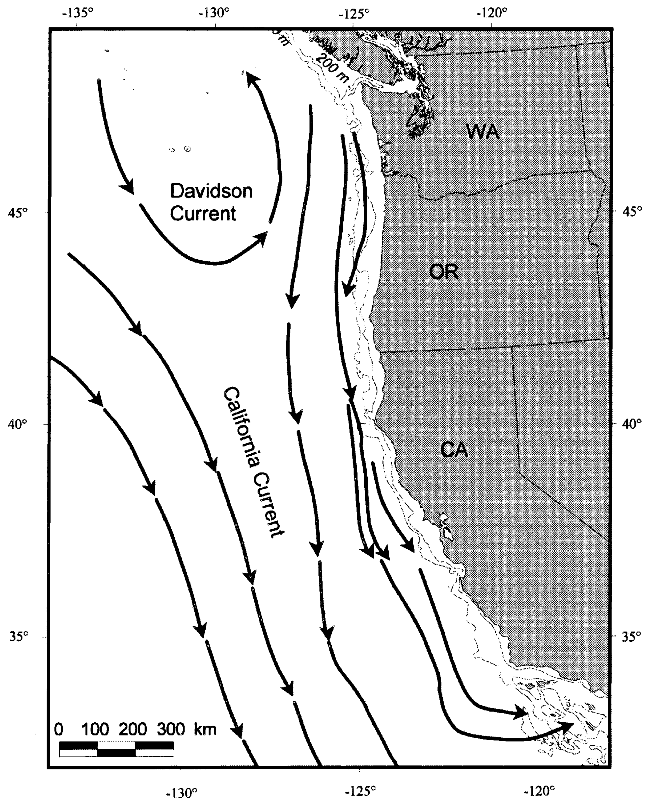

Fig. 2. Map of sampling area and prevailing pattern of circulation off the U.S. West Coast during spring (after Hickey, 1989, 1998).

2.2. Sample Collection

Data used in this study are derived from 950 ichthyoplankton tows sampled in spring on seven cruises from 1980 to 1994 in the EBS, GOA, and off the coasts of Washington, Oregon, and northern California (Table 1). These cruises were selected to represent best the prevailing occurrence and distribution of spring larval fish assemblages in each region. Sampling was most extensive geographically for these particular cruises and they also took place during, or close to, periods of maximum species diversity and abundance

Table 1
Sampling details for the seven cruises from which data were used in this study

Cruise	Vessel	Region	Dates	Number of Stations
4MF94	RV Miller Freeman (U.S.)	EBS	April 13 - 30, 1994	91
6MF95	RV Miller Freeman (U.S.)	EBS	April 16 - May 1, 1995	131
7MF95	RV Miller Freeman (U.S.)	EBS	May 3 - 18, 1995	134
1SH84	RV Shantar (Russian)	GOA	April 7 - May 4, 1984	157
2PO85	RV Poseydon (Russian)	GOA	May 16 - June 8, 1985	189
1TK80	RV Tikhookeanski (Russian)	WC	April 20 - May 15, 1980	125
1PO81	RV Poseydon (Russian)	WC	May 9 - June 2, 1981	123
			total	950

in the ichthyoplankton of each region. Standard MARMAP (Marine Resources Monitoring Assessment and Prediction) oblique tows (Smith & Richardson, 1977) were conducted to sample subsurface ichthyoplankton using 60-cm bongo samplers fitted with 0.505mm mesh nets (0.333mm mesh for cruise 2PO85). Flowmeters suspended in the mouths of the samplers were used to determine the volume of water filtered by each net. Plankton samples were preserved in the field using a 5% formalin-seawater solution buffered either with sodium tetraborate or crushed marble chips. Plankton samples were sorted at the Plankton Sorting and Identification Center in Sczcecin, Poland. Fish larvae were removed and identified to the lowest possible taxon, and enumerated. Up to 50 larvae were measured to the nearest 0.1 mm standard length (SL). Counts were converted to catch per $10m^2$ sea surface area. Identifications of fish larvae were accomplished using taxonomic information provided by Matarese, Kendall, Blood and Vinter (1989) and Busby (1998). Scientific names of pleuronectids follow Cooper and Chapleau (1998), Orr and Matarese (2000).

2.3. Data Analysis

Since our objective was to look for spatial patterns in the data rather than to test a specific hypothesis, this investigation primarily involved exploratory data analysis. For each cruise, we first eliminated rare species from the stations-by-species data matrix. The criterion was to include all species that occurred in more than 5% of the stations for each cruise. The distribution of catch per $10m^2$ was highly skewed to the right, and was therefore log-transformed using $\log_{10}(\text{catch}/10m^2+1)$ in order to de-emphasize the few species that were very abundant. A hierarchical cluster analysis was then performed on both stations and species, separately, using the relative Bray-Curtis dissimilarity coefficient as the distance measure. The Bray-Curtis, or Sorenson, distance measure works well for ecological community data because it retains sensitivity in heterogeneous data sets and gives less weight to outliers. The relative Bray-Curtis coefficient has a built in standardization by sample unit totals (McCune & Mefford, 1999) that allows sampling units to have equal weight (stations or species). This formula is slightly different from the normal Bray-Curtis coefficient. The relative Bray-Curtis distance between species i and h at p stations is given by

$$D_{i,h} = \frac{1}{2}\sum_{j-1}^{p}\left|\frac{a_{ij}}{\sum_{j=1}^{p} a_{ij}} - \frac{a_{hj}}{\sum_{j=1}^{p} a_{hj}}\right|$$

Ward's minimum variance clustering method, a popular hierarchical agglomerative method yielding well-defined clusters, can only be used with Euclidean distance, subsequently ruling out the choice of the Bray-Curtis distance measure (Romesburg, 1984). Therefore, the flexible beta method was chosen as the most appropriate agglomerative clustering algorithm with a beta value of -0.25, as suggested by Sneath and Sokal (1973), since this behaves similarly to the Ward's method. The 'distance' defined on the dendrogram scale (e.g., see Fig. 3) is actually Wishart's objective function (Wishart, 1969), not a simple distance measure. It is a measure of information loss as agglomeration (joining) proceeds. Objective and subjective criteria were used to determine the number and validity of species and station groups resulting from the classification of each data set. First, a line was drawn across the dendrogram tree at a level that transected a small number of distinct groups where the branches emerging from these groups were longest (representing the widest range of dissimilarity over which the groups remained constant). The original species-by-stations matrix of log-transformed abundance was then rearranged according to the dendrograms so that species/station groups were together, and a colored grid was made showing relative abundance among species groups and station groups. Station groups were then plotted on a map of the region sampled to see if they were geographically distinct. Levels of occurrence and abundance of species and geographical distinctness among species and station groups were then used as subjective criteria to fine-tune the identification of groups. Because our analysis was a specific-purpose classification rather than a general-purpose

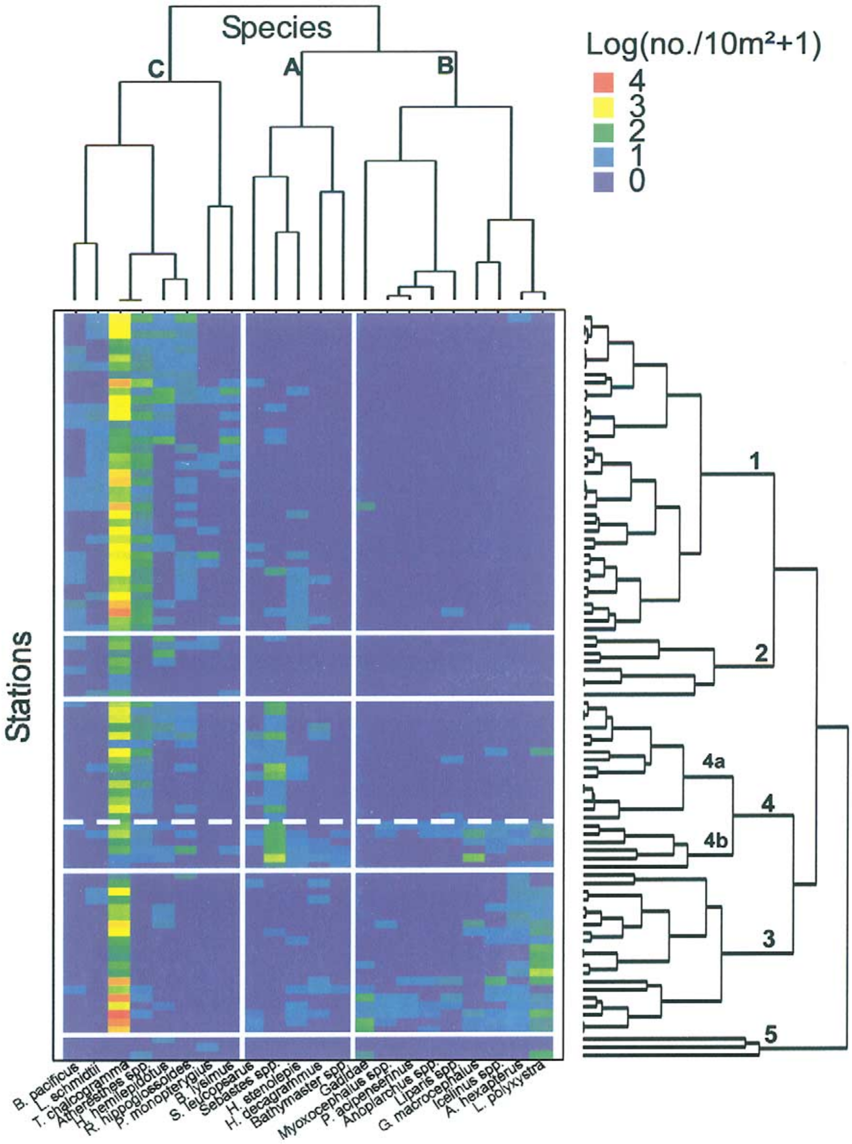

Fig. 3. Grid showing relative abundance among species and stations with dendrograms from two independent cluster analyses, one for species and one for stations for BS cruise 4MF94. Solid white lines divide the data into species/station groups while dashed white lines indicate subgroups.

one, this subjective interpretation of the cluster analysis results is considered appropriate (Romesburg, 1984). At this point, the dissimilarity level at which the dendrograms were cut could be decreased to include extra groups that appeared distinct in terms of species occurrence and abundance (species groups) or geographical location (station groups). Some groups that had a small number of poorly related species or stations then became outliers. In some instances, subgroups were identified among the primary groups. These subgroups were distinct according to the subjective criteria but not according to the objectively chosen dissimilarity level that yielded the primary groups. For further verification of the groups, nonmetric multidimensional scaling, an ordination technique, was used to look at the geometric patterns in the data. Again, the relative Bray-Curtis coefficient was used as the distance measure. The ordination scores for both stations and species were plotted to see if stations and species grouped in the same way in ordination space as they did in the cluster analysis. The r^2 value, the correlation of ordination scores with the original log-transformed data, was computed as a measure of proportion of variance explained by the ordination scores. For each cruise, stations were too numerous to yield informative ordination plots and so only species ordination plots are presented here. The software PC-ORD (McCune & Mefford, 1999) was used for both clustering and ordination methods. The relationship between water depth and station groups from the cluster analysis was explored by performing a one-way ANOVA using depth among station groups for each cruise. Post-hoc pairwise multiple comparisons of mean depths among station groups were also performed. The statistical software SYSTAT 7.1 for Windows (SPSS Inc., Chicago, IL.) was used to carry out the ANOVA calculations.

3. Results

3.1. Ichthyoplankton taxonomic composition

Species or taxa of fish larvae that occurred in less than 5% of samples collected during individual cruises are not considered to contribute significantly to the ichthyoplankton spatial patterns being investigated in this study and, therefore, are not included in the analyses. Of those taxa occurring in greater than 5% of samples from any cruise, 59 taxa were identified in a total of 20 families; 42 were identified to species level, 10 to genus and 6 to family level only (Table 2). Based on all AFSC collections, summaries of the geographical occurrence and bathymetric ranges of these 59 taxa of larvae are included in Table 2. The GOA and EBS samples from the present study were characterized by the dominance of the gadids *Theragra chalcogramma* and *Gadus macrocephalus* (mainly shelf dwellers), the ammodytid *Ammodytes hexapterus* and a variety of cottids, agonids, bathymasterids and stichaeids (shallow water and shelf), along with the pleuronectids *Lepidopsetta bilineata* and *Lepidopsetta polyxystra* (recently described by Orr & Matarese, 2000)(shelf), and *Atheresthes* spp, *Atheresthes stomias*, and *Hippoglossus stenolepis*, (shelf and slope). The pleuronectid *Hippoglossoides elassodon* was a numerically dominant species that occurred primarily in GOA samples, and likewise the pleuronectid *Reinhardtius hippoglossoides* occurred almost exclusively in the EBS collections. The ichthyoplankton fauna collected in the WC samples differed significantly from the GOA and EBS fauna and was characterized by the dominance of deep water species of myctophids, bathylagids, and the pleuronectid *Microstomus pacificus* and the occurrence of shallow water smelts (Osmeridae) and flatfishes *Citharichthys sordidus*, *Lyopsetta exilis*, *Parophrys vetula*, *Platichthys stellatus*, and *Psettichthys melanostictus*. The mesopelagic species *Bathylagus pacificus* and *Stenobrachius leucopsarus*, and the scorpaenids *Sebastes* spp., associated with slope waters, were common in samples from all three regions (Table 2).

3.2. Ichthyoplankton spatial patterns

3.2.1. Bering Sea

Cruise 4MF94: Sampling was carried out during the latter half of April at 91 stations covering the outer shelf, slope and deep water north of Unimak and Unalaska Islands (Table 1). Two slope/deep-water groups and one shelf group are apparent in the species cluster analysis of this data set (Figs. 3 and 4). Most of the sampling was off the shelf during this cruise and there was a dominance of deep-water species. *Theragra chalcogramma* was abundant throughout the sampling area and was grouped with *Bathylagus pacificus*, *Leuroglossus schmidti*, *Atheresthes* spp., *Reinhardtius hippoglossoides*, *Hemilepidotus hemilepidotus*, *Pleu-*

Table 2
Common taxa of fish larvae (occurred in >5% of samples from one or more cruises), associated abbreviation used in ordination plot figures, egg type (P = pelagic, D = demersal, V = viviparous), occurrence of taxa in samples collected from each area - based on all AFSC collections (GOA = Gulf of Alaska, EBS = Eastern Bering Sea, WC = U.S. West Coast, area in parentheses indicates scarcity of larvae in these collections), and association of taxa with different bathymetric ranges (C = coastal, S = shelf, OS = outer shelf, SL = slope, O = oceanic)

Abbrev. Name	**Family**	**Species/Taxon** (>5%occurrence)	**Common Name**	**Egg Type**	**Occurrence**	
					Geographic	**Bathymetric**
Nca	Argentinidae	*Nansenia candida*	bluethroat argentine	P	WC	OS, SL, O
Boc	Bathylagidae	*Bathylagus ochotensis*	popeye blacksmelt	P	WC	OS, SL, O
Bpa		*Bathylagus pacificus*	Pacific blacksmelt	P	EBS, GOA, WC	OS, SL, O
Lsc		*Leuroglossus schmidti*	northern smoothtongue	P	EBS.GOA	OS, SL, O
Osm	Osmeridae	Osmeridae	unidentified smelts	D	GOA. WC	C, S
Cma	Chauliodontidae	*Chauliodus macouni*	Pacific viperfish	P	(GOA), WC	OS, SL, O
Myc	Myctophidae	Myctophidae	unidentified lantemfishes	P	EBS, GOA, WC	OS, SL, O
Dth		*Diaphus theta*	California headlightfish	P	(GOA), WC	OS, SL, O
Lam		*Lampanyctus* spp.	genus of lanternfishes	P	WC	OS, SL, O
Ln		*Lampanyctus ritteri*	broadfin lampfish	P	WC	OS, SL, O
Lre		*Lampanyctus regalis*	pinpoint lampfish	P	WC	OS, SL, O
Pcr		*Protomyctophum crockeri*	California flashlightfish	P	WC	OS, SL, O
Pth		*Protomyctophum thompsoni*	northern flashlightfish	P	EBS, GOA, WC	OS, SL, O
Sle		*Stenobrachius leucopsarus*	northern lanternfish	P	EBS, GOA, WC	S, OS, SL, O
Tcr		*Tarletonbeania crenularis*	blue lanternfish	P	(GOA), WC	OS, SL, O
Gad	Gadidae	Gadidae	unidentified cods	P	EBS, GOA	S, OS, SL
Gma		*Gadus macrocephalus*	Pacific cod	D	EBS, GOA, (WC)	S, OS, SL
Mpr		*Microgadus proximus*	Pacific tomcod	P	GOA, WC	C, S
Tch		*Theragra chalcogramma*	walleye pollock	P	EBS, GOA, (WC)	S, OS, SL, O
Mel	Melamphaeidae	Melamphaeidae	unidentified bigscales	P	(GOA), WC	OS, SL, O
Seb	Scorpaenidae	*Sebastes* spp.	unidentified rockfishes	V	EBS, GOA, WC	S, OS, SL, O
Sbl		*Sebastolobus* spp.	unidentified thornyheads	P	(GOA), WC	S, OS, SL, O

(*continued on next page*)

Table 2 (*continued*)

Abbrev. Name	Family	Species/Taxon (>5%occurrence)	Common Name	Egg Type	Occurrence	
					Geographic	Bathymetric
Afi	Anoplopomatidae	*Anoplopoma fimbria*	sablefish	P	EBS, GOA, WC	S, OS, SL, O
Hde	Hexagrammidae	*Hexagrammos decagrammus*	kelp greenling	D	EBS, GOA, WC	S, OS, SL, O
Pmo		*Pleurogrammus monopterygius*	Atka mackerel	D	EBS, GOA	S, OS, SL, O
Cot	Cottidae	Cottidae	unidentified sculpins	D	EBS, GOA, WC	C, S, OS
Aha		*Artedius harringloni*	scalyhead sculpin	D	(EBS), GOA, WC	C, S
Hhe		*Hemilepidotus hemilepidotus*	red Irish Lord	D	EBS, GOA, WC	S, OS, SL, O
Ice		*lcelinus* spp.	genus of sculpins	D	EBS, GOA, (WC)	S, OS, SL
Myo		*Myoxocephalus* spp.	genus of sculpins	D	EBS, GOA	C, S, OS
Ras		*Radulinus asprellus*	slim sculpin	D	GOA, WC	C, S, OS
Ago	Agonidae	Agonidae	unidentified poachers	D	(EBS), GOA, WC	C, S, OS, SL
Bal		*Bathyagonus alascanus*	gray starsnout poacher	D	EBS, GOA, (WC)	C, S, OS
Pac		*Podothecus acipenserinus*	Sturgeon poacher	D	EBS, GOA, (WC)	C, S, OS
Lip	Liparidae	*Liparis* spp.	Genus of snailfishes	D	EBS, GOA, (WC)	C, S, OS
Bat	Bathymasteridae	*Bathymaster* spp.	Searcher/some ronquils	D	EBS, GOA	C, S, OS, SL
Bly	Stichaeidae	*Bryozoichthys lysimus*	Nutcracker prickleback	D	EBS. GOA	C, S, OS, SL
Lum		*Lumpenus* spp.	Genus of pricklebacks	D	EBS, GOA	C, S, OS
Lma		*Lumpenus maculatus*	Daubed shanny	D	EBS, GOA	C, S, OS
Pro		*Poroclinus rothrocki*	Whitebarred prickleback	D	EBS, GOA, (WC)	C, S, OS
Ano		*Anoplarchus* spp.	Genus of pricklebacks	D	(EBS), GOA	C, S, OS
Cal	Cryptacanthodidae	*Cryptacanthodes aleutensis*	Dwarf wrymouth	D	EBS, GOA, WC	S, OS, SL
Zsi	Zaproridae	*Zaprora silenus*	Prowfish	D	EBS, GOA	S, OS, SL
Ahe	Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	D	EBS, GOA, WC	C, S, OS, SL

Table 2 (*continued*)

Abbrev. Name	Family	Species/Taxon (>5%occurrence)	Common Name	Egg Type	Occurrence	
					Geographic	Bathymetric
Cso	Paralichthyidae	*Citharichthys sordidus*	Pacific sanddab	P	WC	S, OS, SL, O
Ath	Pleuronectidae	*Atheresthes* spp.	Genus of righteyed flounders	P	EBS, GOA	S, OS, SL, O
Ast		*Atheresthes stomias*	Arrowtooth flounder	P	EBS. GOA. (WC)	S, OS, SL, O
Gza		*Glyptocephalus zachirus*	Rex sole	P	(EBS), GOA, WC	S, OS, SL, O
Hel		*Hippoglossoides elassodon*	Flathead sole	P	EBS, GOA, (WC)	S, OS, SL
Hst		*Hippoglossus stenolepis*	Pacific halibut	P	EBS, GOA	S, OS, SL, O
Iis		*lsopsetta isolepis*	Butter sole	P	GOA, WC	C, S, OS
Lbi		*Lepidopsetta bilineata*	Southern rock sole	D	GOA, (WC)	C, S, OS, SL
Lpo		*Lepidopsetta polyxystra*	Northern rock sole	D	EBS, GOA	C, S, OS, SL
Lex		*Lyopsetta exilis*	Slender sole	P	(GOA), WC	C, S, OS, SL, O
Mpa		*Microstomus pacificus*	Dover sole	P	(EBS), GOA, WC	S, OS, SL, O
Pve		*Parophrys vetula*	English sole	P	GOA, WC	C, S, OS, SL
Pst		*Platichthys stellatus*	Starry flounder	P	(EBS), GOA, WC	C, S, OS
Pme		*Psettichthys melanostictus*	Sand sole	P	GOA, WC	S, S, OS
Rhi		*Reinhardtius hippoglossoides*	Greenland halibut	P	EBS, (GOA)	S, OS, SL, O

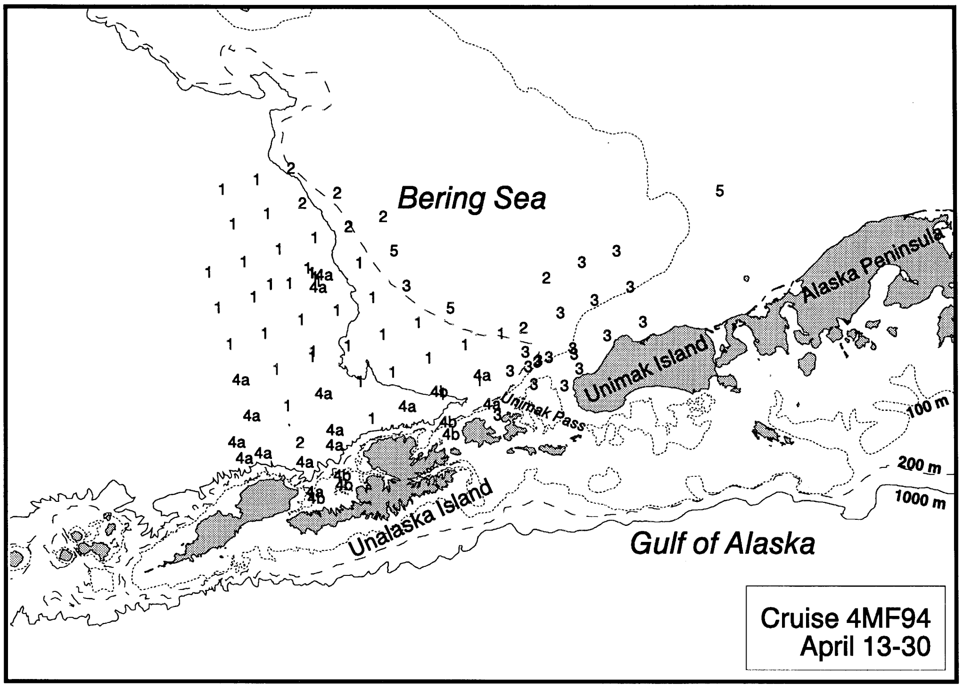

Fig. 4. Map showing position of station groups, by group number, resulting from cluster analysis of ichthyoplankton data from BS cruise 4MF94.

rogrammus monopterygius and *Bryozoichthys lysimus*. All the members of Species Group C were most abundant in Station Group 1 in deep water west of the shelf (Fig. 4). In addition to *T chalcogramma*, *Atheresthes* spp., *H. hemilepidotus*, and *R. hippoglossoides* were also prominent in Station Groups 4a and 4b along the shelf and in deep water to the north of Unalaska Island. Species Group A also included slope and deep water species (most notably *Stenobrachius leucopsarus*, *Sebastes* spp. and *Hippoglossus stenolepis*) all of which were most abundant in Station Groups 4a and/or 4b off Unalaska Island, except for *H. stenolepis*, which was equally abundant in Station Group 1. Shelf and coastal species, including *Gadus macrocephalus*, *Ammodytes hexapterus*, *Lepidopsetta polyxystra*, some cottids, agonids, liparids and stichaeids, make up Species Group B. They were associated almost exclusively with Station Group 3, on the shelf in the vicinity of Unimak Island and Unimak Pass, and Station Group 4b, on the shelf north of Unalaska Island.

Although the three species groups (cluster analysis) are discernable in the ordination plot for these data, they do not form tight clusters of points (Fig. 5). Group B taxa, representing the shelf assemblage, are plotted most closely together whereas the deep-water and slope species of Groups A and C are more scattered in the ordination space. This reflects the pattern of joining of species in the cluster analysis dendrogram where the shelf group was the first to be formed (Fig. 3).

The ANOVA of depth among the cluster analysis station groups indicates a significant group effect ($P<0.001$). At the 5% significance level, Station Groups 1 and 4a located along the outer shelf, slope and in the basin (Fig. 4) were significantly different (deeper; >1000 m) from the shelf Station Groups 2, 3, 4b and 5 according to the post-hoc multiple comparisons tests.

Cruise 6MF95: As in cruise 4MF94, sampling was carried out during the latter half of April for this 1995 cruise (Table 1) but this time the sampling extended further over the shelf. The grouping of species and stations in the cluster analysis reflects the dichotomy in distribution patterns of shelf and deep-water

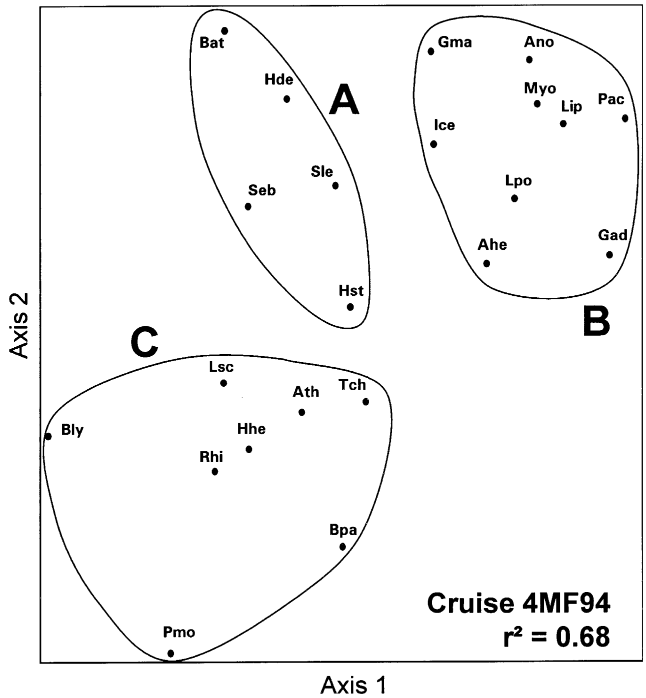

Fig. 5. Ordination plot of species scores using two-dimensional multidimensional scaling for BS cruise 4MF94. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

species (Figs. 6 and 7). Species Groups A and B were comprised of shelf species and *Theragra chalcogramma*, which was also abundant along the slope and over deep water. Unidentified gadids, *Gadus macrocephalus*, *Icelinus* spp. and *Ammodytes hexapterus*, belonging to Species Group A, were associated with Station Group 3a occurring in the vicinity of Unimak Pass and to the northwest of Unimak Island. *Theragra chalcogramma* and *Lepidopsetta polyxystra* (Species Group B) were more ubiquitous in their distribution. The former was abundant in Station Groups 3a and 3b on the shelf, as well as along the outer shelf, slope and deep water in Station Group 4. The latter was concentrated in Station Groups 1, 3a and 3b covering the inner and middle shelf. The stichaeids, *Lumpenus* spp., which also belong to Species Group B, occurred almost exclusively in the mid-shelf Station Group 3b. Group A taxa were associated with Station Group 3a, in the vicinity of Unimak Pass, and Station Group 4 extending from the outer shelf to deep water. These included *Stenobrachius leucopsarus*, *Hexagrammos decagrammus*, *Pleurogrammus monopterygius*, *Hippoglossus stenolepis*, *Atheresthes* spp. and *Reinhardtius hippoglossoides*, which were notably absent from the shelf Station Groups 1, 2 and 3b.

Group A taxa from the cluster analysis (Fig. 6), that were associated with the shelf close to Unimak Pass, plot closest together in the ordination diagram (Fig. 8). Species belonging to Groups B and C, representing a shelf/ubiquitous distribution and an outer-shelf/slope/deep-water distribution, respectively, are more scattered in ordination space. In fact, *T. chalcogramma* from Species Group B plots closer to *Hemilepidotus hemilepidotus* and *H. stenolepis* of Group C than to the other members of Group B, reflecting its abundance over deep water, as well as at shelf, stations.

The ANOVA using water depth shows a significant station group effect ($P<0.001$). The pairwise comparison of means, as expected, shows that Station Group 4 (outer shelf, slope and deep water; mean depth

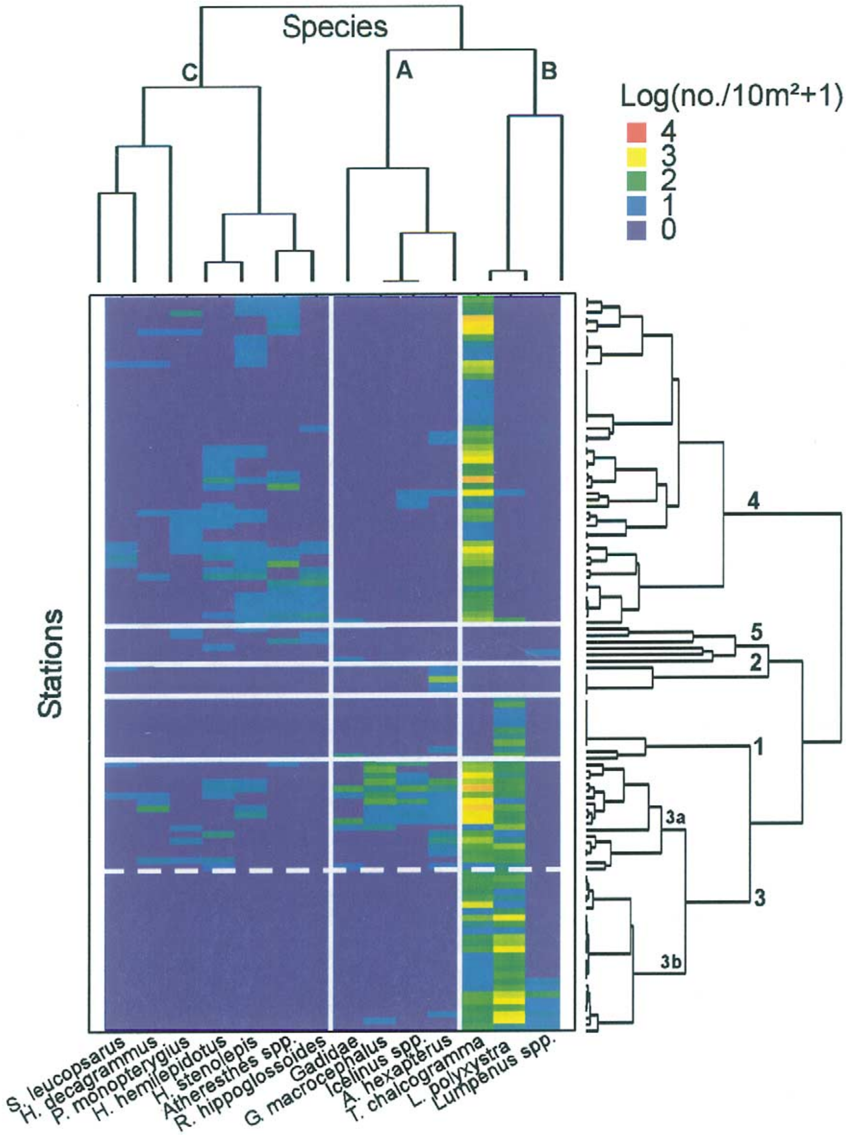

Fig. 6. Grid showing relative abundance among species and stations with cluster dendrograms from two independent cluster analyses, one for species and one for stations for BS cruise 6MF95. Solid white lines divide the data into species/station groups while dashed white lines indicate subgroups.

of 800 m) was significantly different from all of the shelf station Groups (mean depths <150 m), either at the 5% or 10% level.

Cruise 7MF95: This 1995 cruise was conducted almost immediately following cruise 6MF95, during the early half of May (Table 1). In contrast to cruises 4MF94 and 6MF95, the sampling during this cruise took place almost entirely on the continental shelf. Consequently, deep water species (e.g. bathylagids and myctophids) and slope species (*Atheresthes* spp. and *Sebastes* spp.) were either absent or scarce in these samples (Fig. 9). *Theragra chalcogramma* larvae were dominant and abundant throughout the sampling grid. They were grouped with unidentified gadids and *Lepidopsetta polyxystra* in Species Group A, which

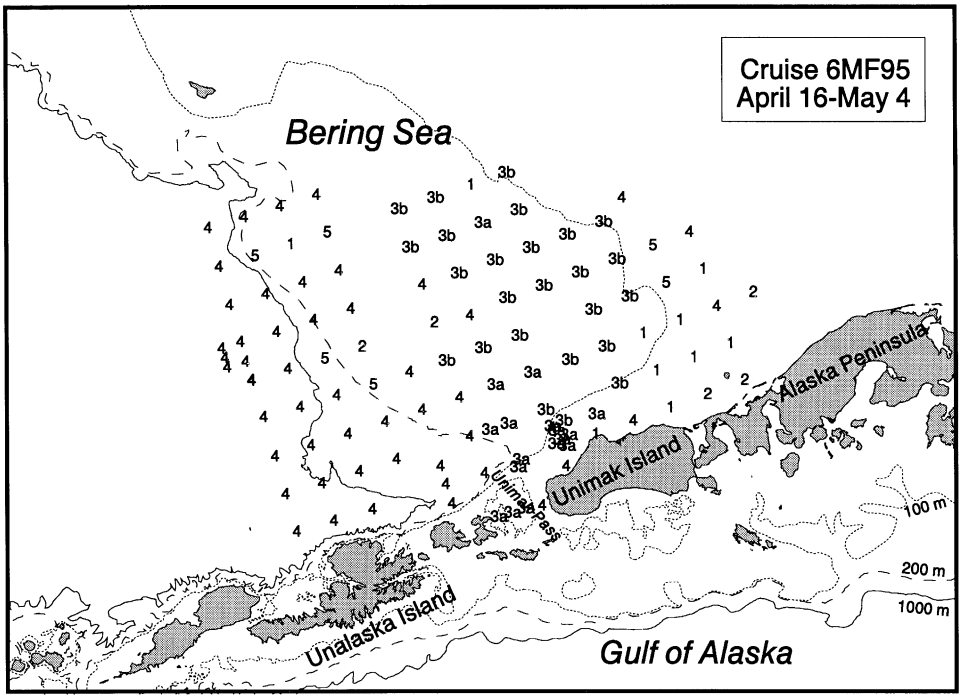

Fig. 7. Map showing position of station groups, by group number, resulting from cluster analysis of ichthyoplankton data from BS cruise 6MF95.

was associated with Station Groups 1 and 2 covering much of the shelf (Fig. 10). Species Group B including *Gadus macrocephalus*, some cottids, *Hippoglossus stenolepis*, *Sebastes* spp. and *Bathyagonus alascanus* were concentrated in Station Group 1 near Unimak Pass. In fact, the defining characteristic of Station Group 1 is its high species diversity. *Hemilepidotus hemilepidotus, Reinhardtius hippoglossoides, Poroclinus rothrocki* and *Lumpenus* spp. were loosely affiliated in Species Group C and had no strong affiliation to any Station Group. They were absent, however, from Station Group 3 that is characterized by water depths less than 100m. Larvae were scarce in Station Group 5 and these stations are considered outliers as they grouped very high up on the dendrogram and had no particular species association.

A gradation in clustering of the species group points on the ordination plot (Fig. 11) mirrors exactly the order of species groups on the dendrogram (Fig. 9). Group A taxa are plotted close together, Group C taxa are far apart and Group B taxa are at an intermediate level of closeness.

Even though a much narrower range of water depth was sampled on this cruise (almost all stations occurring on the shelf), ANOVA of depth among the station groups yields a significant group effect overall ($P<0.001$). The pairwise comparison of means shows Station Group 4, along the outer shelf (mean depth 180 m), to be significantly different from the middle and inner shelf Station Groups 2 and 3 (mean depths $<$100 m), at the 5% significance level.

3.2.2. Gulf of Alaska

Cruise 1SH84: A total of 157 stations were sampled along the shelf and slope to the northeast and southwest of Kodiak Island during early April through early May of 1984 (Table 1). Cluster analysis results for this data set are shown in Fig. 12 and the distribution of Station Groups is illustrated in Fig. 13. Three species groups were identified leaving one outlier, *Zaprora silenus*. Because of their ubiquitous distribution

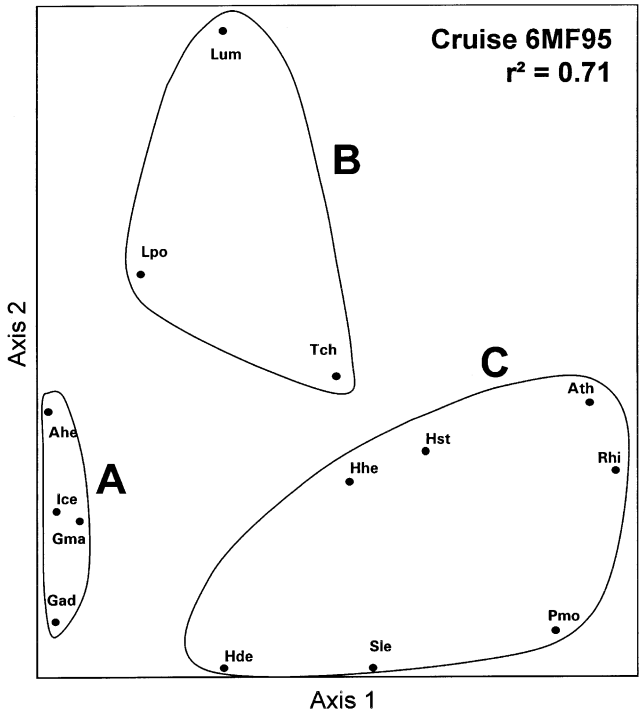

Fig. 8. Ordination plot of species scores using two-dimensional multidimensional scaling for BS cruise 6MF95. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

throughout the sampling area and their high densities, *Theragra chalcogramma* and *Ammodytes hexapterus* were linked at a very high level of similarity in Species Group A. The highest concentrations of *T chalcogramma* larvae were associated with Station Group 1 along the Alaska Peninsula coast and the sea valley extending from Shelikof Strait out to the slope. *Ammodytes hexapterus* larvae were equally abundant in Station Groups 1, 2 and 3 throughout the shelf zone. Species Group B was comprised of bathylagids, myctophids and the deep-water pleuronectids *Atheresthes stomias* and *Hippoglossus stenolepis*, all associated primarily with Station Group 4 that occurred along the shelf edge and slope. In contrast, Species Group C was comprised of shelf and shallow water species including *Gadus macrocephalus*, *Lepidopsetta polyxystra* and *Liparis* spp. These were concentrated primarily in Station Group 3, and to a lesser extent in Station Groups 1 and 2, along the shelf. Except for two occurrences of *Liparis* spp., these taxa were absent from Group 4 stations over deep water. Group 5 stations were scattered throughout the shelf and slope area and are considered outliers.

The clusters of species points in the ordination plot (Fig. 14) for these data reflect almost exactly the grouping of species in the dendrogram. *Theragra chalcogramma* and *A. hexapterus* plot close together in one group, and the other two groups represent the slope/deep-water group (myctophids, bathylagids and deep-water flatfish) and the shelf group, respectively. As for the cluster analysis results, the species *Z. silenus* emerged as an outlier.

The results of the one-way ANOVA of depth among station groups (from cluster analysis) reveals that there is a significant station group effect at the 5% level ($P<0.001$). Post-hoc pair-wise multiple comparisons of means shows that Station Group 4, located along the shelf edge and slope (mean depth 1000 m), was significantly different ($P<0.001$) from all the other station groups (mean depths 400m).

Cruise 2PO85: In 1985, species diversity (richness) was higher during this cruise because it took place

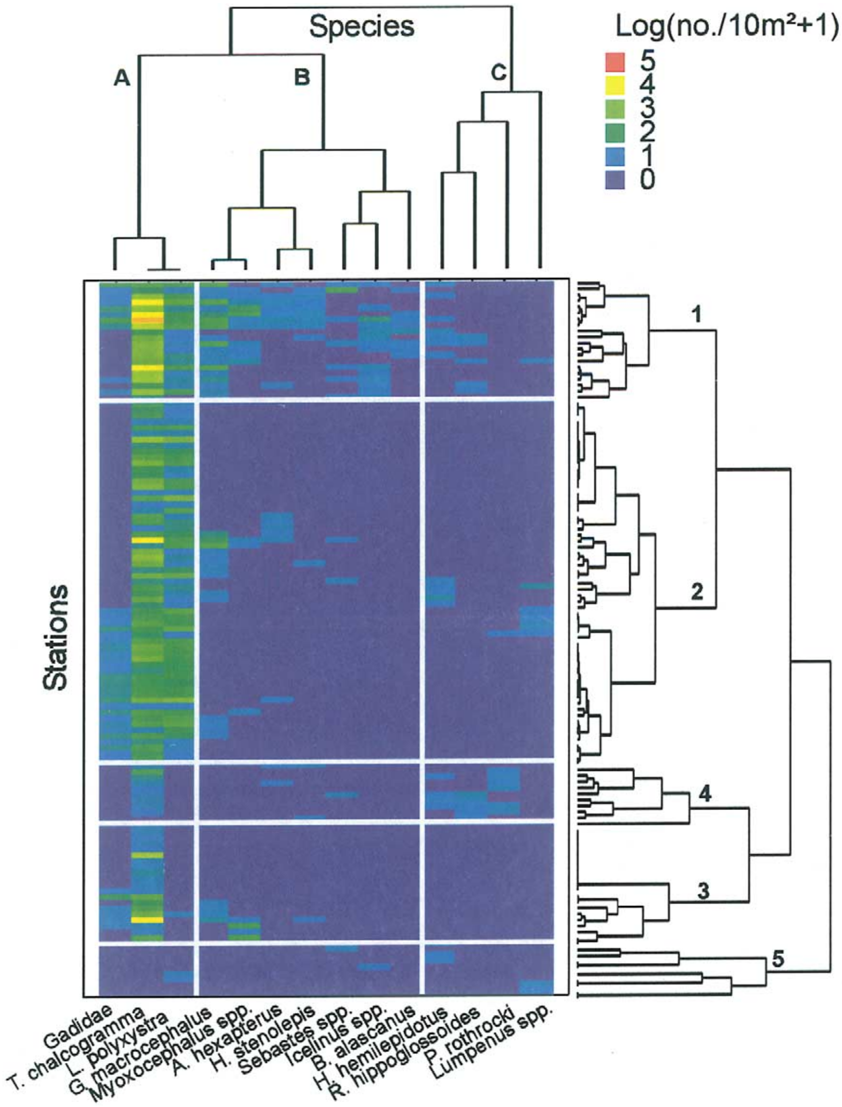

Fig. 9. Grid showing relative abundance among species and stations with cluster dendrograms from two independent cluster analyses, one for species and one for stations for BS cruise 7MF95. Solid white lines divide the data into species/station groups.

later in spring than cruise 1SH84 (Table 1), also the sampling was more extensive geographically. The primary division of the species reflects differences in levels of abundance (Fig. 15). Species in Groups B and C displayed low occurrences and low densities whereas Species Groups A1 and A2 were more ubiquitous and considerably more abundant. The next distinction between Species Groups B and C and between Groups A1 and A2 reflects a difference in distribution according to water depth. For instance, the mesopelagic *Bathylagus pacificus* and *Protomyctophum thompsoni* of Species Group B occurred mainly in Station Groups 2 and 4 along the slope and in deeper water, whereas the cottids, agonids and stichaeids of Species Group C were scarce in deep water (Station Groups 2, 4, and 6) and relatively abundant on the shelf, in Station Group 5 mainly (Fig. 16). Likewise, *Leuroglossus schmidti*, *Stenobrachius leucopsarus*, *Sebastes* spp., and the deep-water pleuronectids *Atheresthes stomias* and *Glyptocephalus zachirus* of Species Group

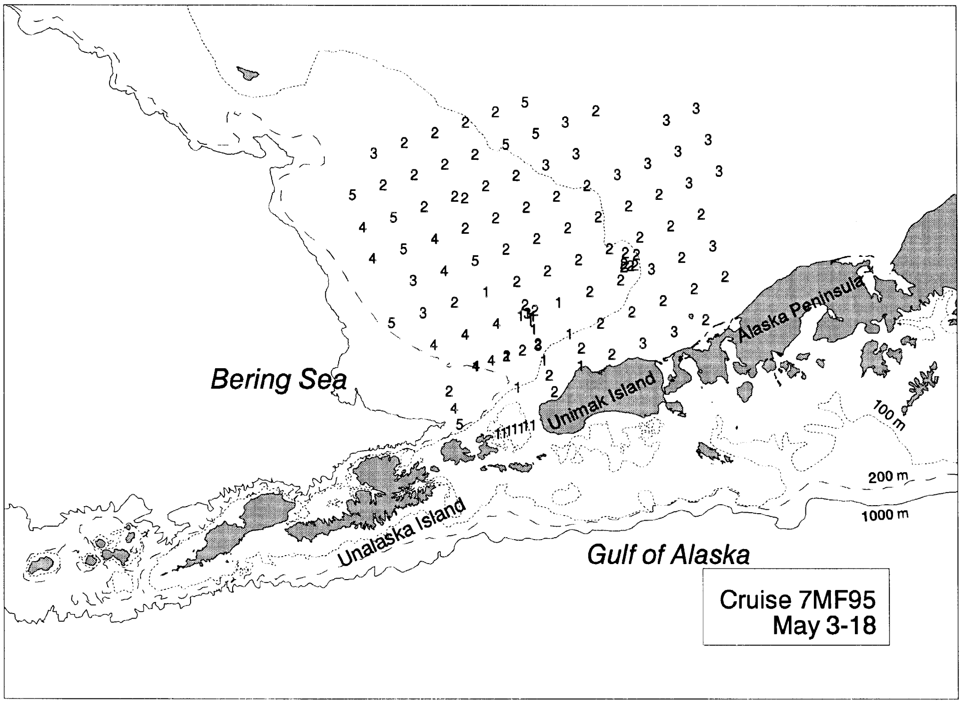

Fig. 10. Map showing position of station groups, by group number, resulting from cluster analysis of ichthyoplankton data from BS cruise 7MF95.

A1 were most abundant at the deep water stations (Groups 2 and 4) whereas the shelf species in Group A2 were least abundant, scarce or absent from deep water, particularly Station Group 4. An interesting feature of the distribution patterns in this data set is the co-occurrence of shallow-water, shelf and deep-water species in Station Group 5. This group of stations was characterized by highest concentrations of *Gadus macrocephalus*, *Lepidopsetta polyxystra*, *Theragra chalcogramma*, *Hippoglossoides elassodon*, *Ammodytes hexapterus* (Species Group A2), and all other taxa were also well represented here. The group was associated with the shelf to the north and northeast of Kodiak Island and with the Shelikof Strait sea valley that extends outwards to the slope south west of Kodiak. Stations belonging to Station Group 7 in this data set had no distinct geographic or species association and are considered outliers.

As on the species dendrogram (Fig. 15), Species Group A (comprised of the most abundant taxa) is most distinct on the ordination plot and the division of this group into a deep-water component (A1) and a shelf component (A2) is discernable (Fig. 17). Similarly, Species Groups B and C (representing low abundance deep water and shelf taxa, respectively) that were loosely grouped on the species dendrogram, do not form clearly defined clusters in the ordination plot.

Variance of water depth among the Station Groups is significant ($P<0.001$) as indicated by the ANOVA of these data. The pairwise comparison of means shows that Station Group 2 and Station Group 4 (mean depths >700m) were significantly different at the 5% level from all other station groups (mean depths <300m).

3.2.3. U.S. West Coast

Cruise 1TK80: During this 1980 cruise, ichthyoplankton sampling was carried out at 125 stations along the continental shelf, slope and deeper waters off the U.S. West Coast from late April to mid-May (Table

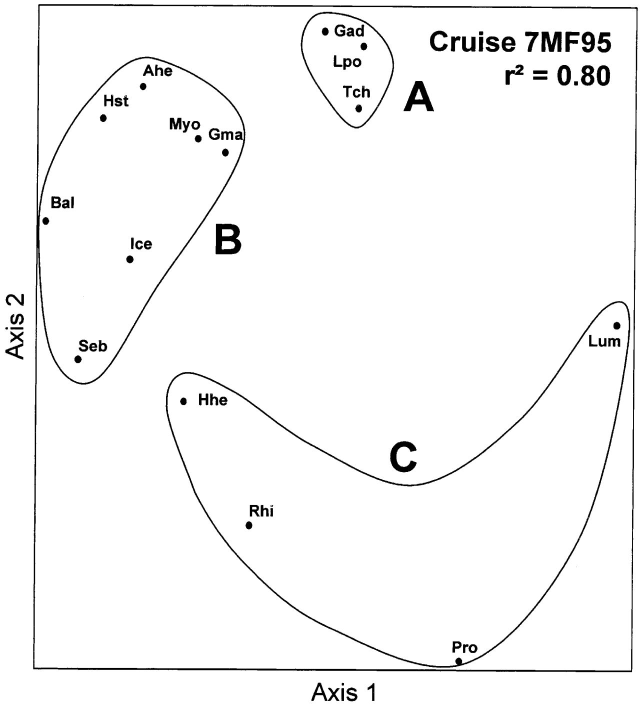

Fig. 11. Ordination plot of species scores using two-dimensional multidimensional scaling for BS cruise 7MF95. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

1). The family Osmeridae, the shallow-water pleuronectids *Isopsetta isolepis*, *Platichthys stellatus* and *Psettichthys melanostictus*, and the gadid *Microgadus proximus* are highly correlated in Species Group A for this data set (Fig. 18). These species were concentrated in Station Group 1, located primarily along the Washington coast, and to a lesser extent in Station Group 2, associated with the Oregon coast (Fig. 19). They were rare along the outer shelf and slope and absent over deep water (Station Groups 3, 4 and 5). *Liparis* spp., *Parophrys vetula*, and *Glyptocephalus zachirus* belonged to a second group of mainly shelf species, Species Group C. They were less abundant overall than taxa in Species Group A, and occurred infrequently in Station Groups 1 and 2 along the coast, and Station Group 5 along the outer shelf, slope and over deeper water. The most abundant species in this data set belong to Species Group B that includes *Stenobrachius leucopsarus*, *Bathylagus ochotensis*, *Sebastes* spp., and *Lyopsetta exilis*. Except for *L. exilis*, which was abundant along the Oregon coast (Station Group 2) as well as at slope stations, these taxa were concentrated in Station Groups 5 and 3, along the slope and over deeper water. *Sebastes* spp. larvae were more abundant in Group 5 stations (slope) than in the deep-water Station Group 3. Species Group D also consisted of deep-water taxa including myctophids, bathylagids, melamphaeids and *Chauliodus macouni*. Members of this group were less abundant than group B taxa but they displayed similar distribution patterns and were associated primarily with Station Groups 3 and 5. The 8 stations belonging to Station Group 6 were scattered throughout the sampling area and were last to cluster on the station dendrogram. These stations are considered outliers in this data set.

The coastal species in group A from the cluster analysis (Fig. 18) form a very close group near the middle of the first axis in the ordination diagram (Fig. 20). Further along axis 1 are the three members of Species Group C, displaying a coastal distribution but also extending into deeper water. The two deep-water Species Groups (B and D) plot high up on axis 2 and are less clearly defined – they are also more

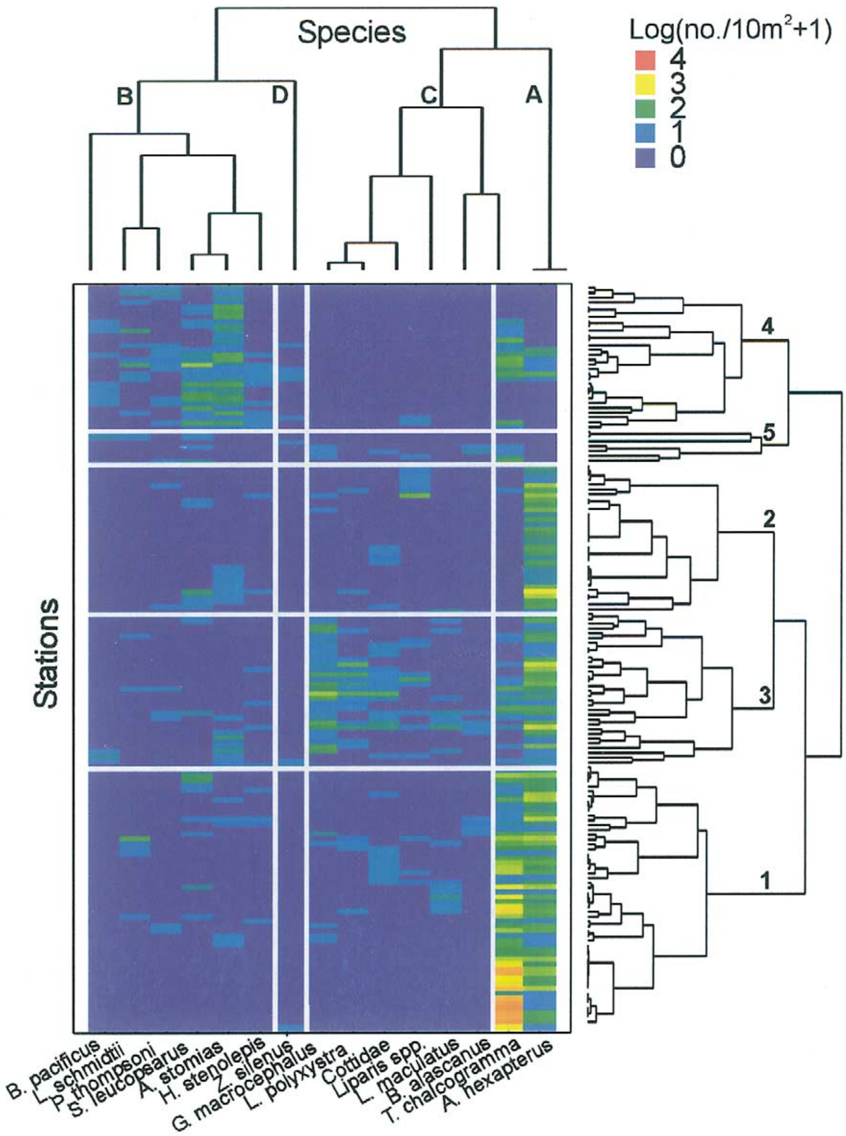

Fig. 12. Grid showing relative abundance among species and stations with cluster dendrograms from two independent cluster analyses, one for species and one for stations for GOA cruise 1SH84. Solid white lines divide the data into species/station groups.

loosely linked on the dendrogram. *Lyopsetta exilis*, belonging to Species Group B, is relatively abundant in Station Group 2 along the Oregon coast as well as in the deep-water Station Group 5 (Fig. 18). Its proximity to the coastal species groups, and the deep-water taxa, in the ordination plot reflects this bimodal type distribution pattern.

There is a significant station group effect ($P<0.001$) according to the one-way ANOVA based on water depth. The pair-wise comparison of means shows that station group 3 (mean depth >2000 m) was significantly different from all other station groups at the 5% level.

Cruise 1PO81: Sampling occurred later (May 9-June 2) during the 1981 cruise in comparison with cruise 1TK80 (Table 1) and fewer stations were sampled along the Washington coast. These differences seem to

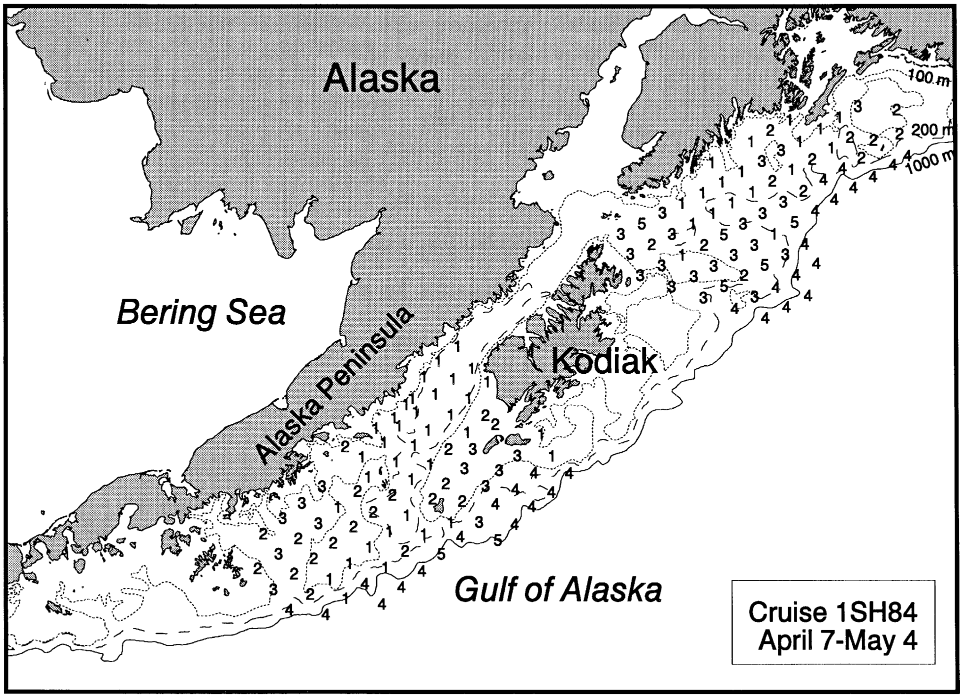

Fig. 13. Map showing position of station groups, by group number, resulting from cluster analysis of ichthyoplankton data from GOA cruise 1SH84.

be reflected in the occurrences of species and the species group structure resulting from analysis of the 1PO81 data (Figs. 21 and 22). Unlike 1TK80, no exclusively coastal species group resulted from cluster analysis of this data set and the coastal taxa Osmeridae, *Microgadus proximus* and *Psettichthys melanostictus* were absent from the samples. Three species groups were identified including two slope-associated groups (Groups A and C) and one deeper water group (Group B). Group A taxa included *Bathylagus pacificus*, *Glyptocephalus zachirus*, *Microstomus pacificus*, *Citharichthys sordidus*, *Nansenia candida*, and *Sebastolobus* spp. They all occurred in low densities and were associated primarily with Station Group 2 along the slope and extending into deep water. Among Group C taxa, *Sebastes* spp., *Lyopsetta exilis* and *Liparis* spp. larvae were most abundant and were concentrated in the slope Station Groups 2, 3 and 4. The pleuronectid *L. exilis* was also abundant in Station Group 3 along the coast. The other Species Group 3 members occurred at low densities in only a few samples. They included *Protomyctophum thompsoni*, which was scarce in the slope and deep-water Station Groups (2, 3, 4 and 5) and absent along the coast (Station Group 1), and *Isopsetta isolepis*, which mainly occurred in Station Groups 1 and 6 along the coast. The deep-water species in Group B, including bathylagids, myctophids and *Chauliodus macouni*, were concentrated in Station Groups 2 and 5 along the slope and in deep water. *Stenobrachius leucopsarus* was also abundant in Group 4 stations, along the slope and, to a lesser extent, at the coastal Group 1 stations.

Apart from *I. isolepis*, a coastal species that appears to be somewhat of an outlier, the three dendrogram species groups are not clearly defined in the ordination plot (Fig. 23). The contrast with the ordination plot for cruise 1TK80 mainly results from the absence of the exclusively coastal group of species, as mentioned above.

There is a significant station group effect according to the ANOVA of water depth among cluster analysis station groups ($P<0.001$). Pairwise comparisons of means show that Station Group 5 (mean depth >2500m) was significantly different from Station Groups 1 through 4 at the 5% level.

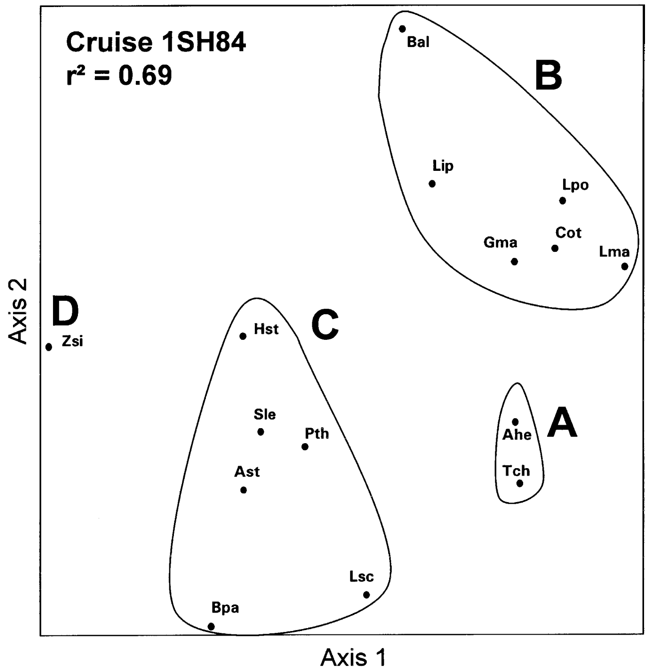

Fig. 14. Ordination plot of species scores using two-dimensional multidimensional scaling for GOA cruise 1SH84. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

3.3. Assemblages of fish larvae

Based on the results of the numerical classification and multidimensional scaling, the individual species of fish larvae were assigned to assemblages in each study region (Tables 3 to 5). Each assemblage was associated with either a specific geographical location or bathymetric range within the study regions, as indicated by the geographically distinct station groups that resulted from the numerical classification analysis. Most species occurred in more than one assemblage.

The two primary assemblages of fish larvae in the southeastern Bering Sea were identified as a General Shelf assemblage and a Slope/Deep-water assemblage (Table 3). The former occurred over the broad shelf of the southeast Bering Sea, as well as along the narrow shelf north of the Aleutian Islands. The latter was associated with the slope and deep water west of the Bering shelf and north of the Aleutian shelf. *Bathymaster* spp., *Lumpenus* spp., and *Poroclinus rothrocki* were unique to the General Shelf assemblage. Seven taxa were unique to the Slope/Deep-water assemblage including mesopelagic species, *Sebastes* spp., *Pleurogrammus monopterygius*, *Bryozoichthys lysimus*, and *Reinhardtius hippoglossoides*. A third assemblage identified in the Bering Sea was the Unimak assemblage that occurred on the shelf in the vicinity of Unimak Pass. It had the highest diversity of species including a combination of shelf and some slope species from the other two assemblages as well as the unique occurrence of *Icelinus* spp., *Liparis* spp., *Bathyagonus alascanus* and *Podothecus acipenserinus*. *Theragra chalcogramma* was notable for its occurrence in each assemblage. It was abundant and ubiquitous throughout the sampling area.

As in the Bering Sea, a General Shelf assemblage and a Slope/Deep-water assemblage of fish larvae, were identified in the Gulf of Alaska (Table 4). The General Shelf assemblage occurred throughout the shelf region along the Alaska Peninsula and the Slope/Deep-water assemblage occurred over, and seaward of the slope, from northeast of Kodiak Island to the Aleutian chain. Their constituent species were similar

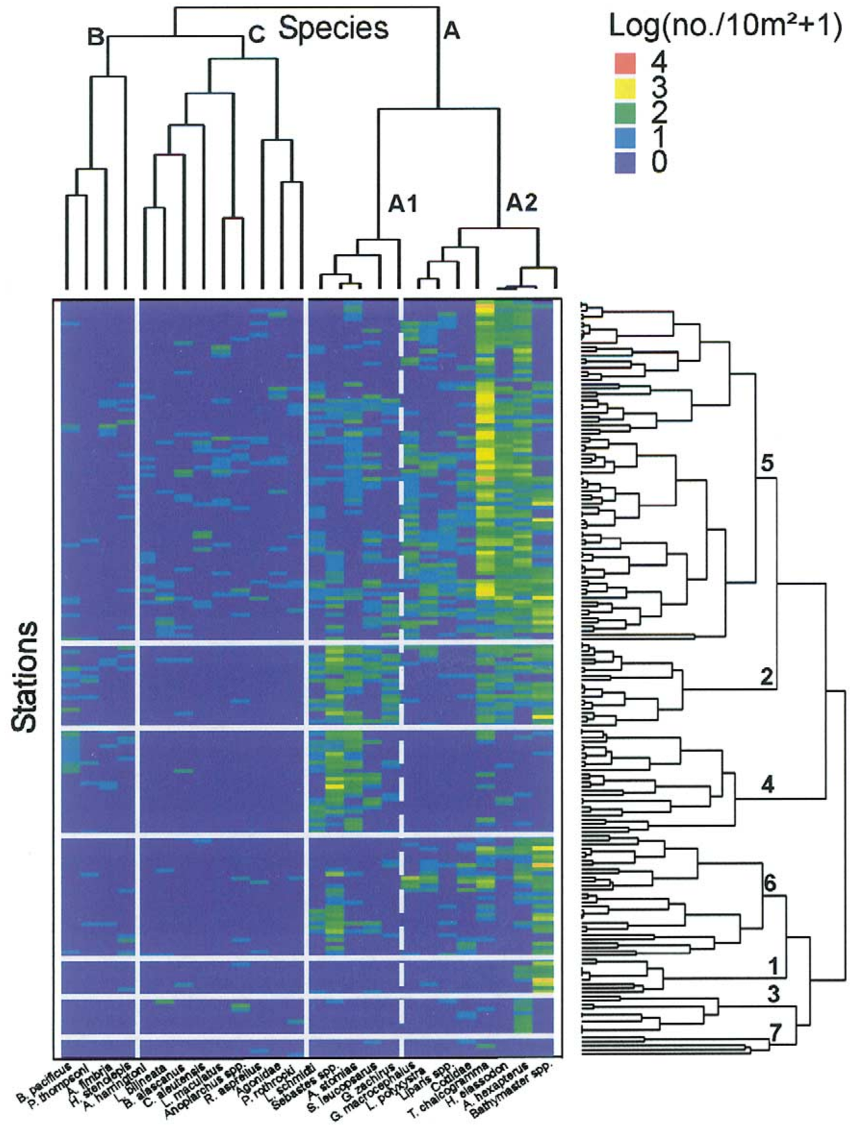

Fig. 15. Grid showing relative abundance among species and stations with cluster dendrograms from two independent cluster analyses, one for species and one for stations for GOA cruise 2PO85. Solid white lines divide the data into species/station groups while dashed white lines indicate subgroups.

to the shelf and slope assemblages in the Bering Sea (Table 3) but with higher diversity overall, especially among the Pleuronectidae which here included the deep-water species *Atheresthes stomias*, *Glyptocephalus zachirus*, *Hippoglossoides elassodon*, and *Hippoglossus stenolepis*. *Anoplopoma fimbria* was also added to the Slope/Deep-water assemblage in the GOA as was *Zaprora silenus* and the mesopelagic species *Protomyctophum thompsoni*. Except for the latter two species, the third assemblage identified in the GOA (Shelikof Sea Valley and Northeast Kodiak Shelf assemblage) included all the species from the General Shelf assemblage and the Slope/Deep-water assemblage as well as *Poroclinus rothrocki* and *Cryptacanthodes aleutensis* (Table 4). It was associated specifically with Shelikof Strait and the Shelikof Sea Valley,

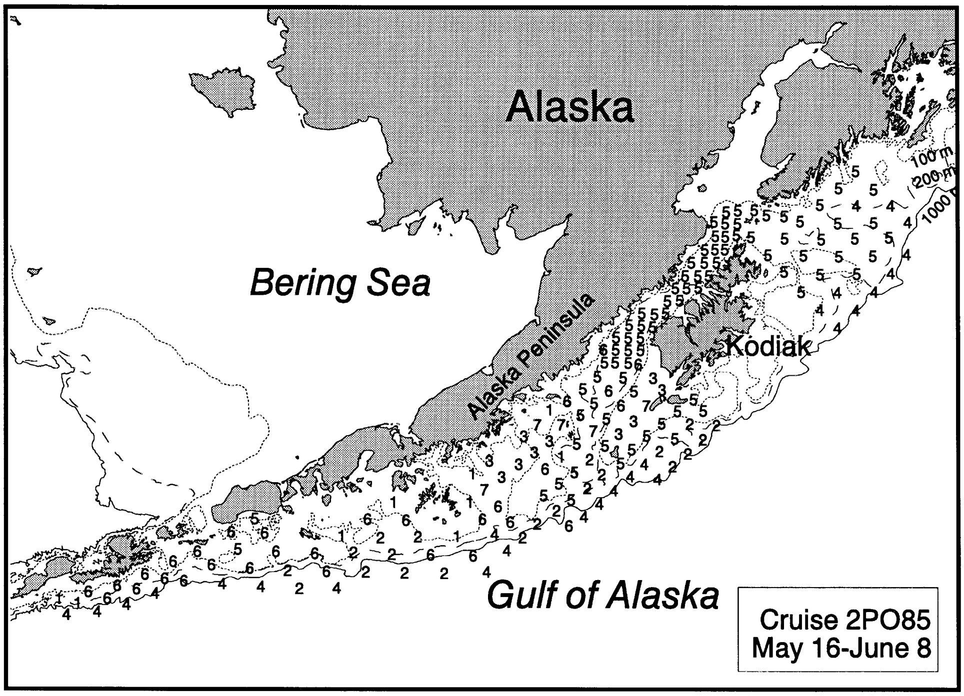

Fig. 16. Map showing position of station groups, by group number, resulting from cluster analysis of ichthyoplankton data from GOA cruise 2PO85.

west and southwest of Kodiak Island, where water depth ranges from 200 m to 300 m, and with the shelf area northeast of Kodiak. This assemblage represented an overlap in the distribution of the shelf and slope assemblages in the GOA. As in the EBS, the ubiquitous *T. chalcogramma* was prominent in all three assemblages in the GOA but as for many of the other species it was most abundant in the latter Shelikof assemblage. *Bathymaster* spp. was also prominent in all three GOA assemblages but was most abundant along the shelf and slope southwest of Kodiak (Fig. 15).

Coastal/Shelf, Slope and Oceanic assemblages were identified for the WC region (Table 5). Unique to the Coastal/Shelf assemblage, associated with the inner shelf area along the Washington and Oregon coasts, were the family Osmeridae, *Microgadus proximus*, and four species of shallow water Pleuronectidae. *Liparis* spp., *Glyptocephalus zachirus* and *Lyopsetta exilis* were also included in this assemblage as they occurred in shelf water as well as over the slope. Similarly, the ubiquitous *Stenobrachius leucopsarus* was also included in the Coastal/Shelf assemblage. The Oceanic assemblage identified along the WC was associated primarily with deep water beyond the shelf edge and slope, although the distribution of many of these species also extended into slope and outer shelf waters. It was comprised essentially of mesopelagic species but also included *Sebastes* spp., *Sebastolobus* spp., and *Citharichthys sordidus* whose distributions ranged from the shelf to the oceanic zone. Unique to the Slope assemblage here was *Microstomus pacificus*. It was most abundant at stations along the shelf edge and slope. *Sebastes* spp. and *Sebastolobus* spp. were also most abundant in this zone making them essential members of the Slope assemblage. The remaining members of the Slope assemblage represent a mixture of oceanic and shelf species whose distributions overlapped along the slope.

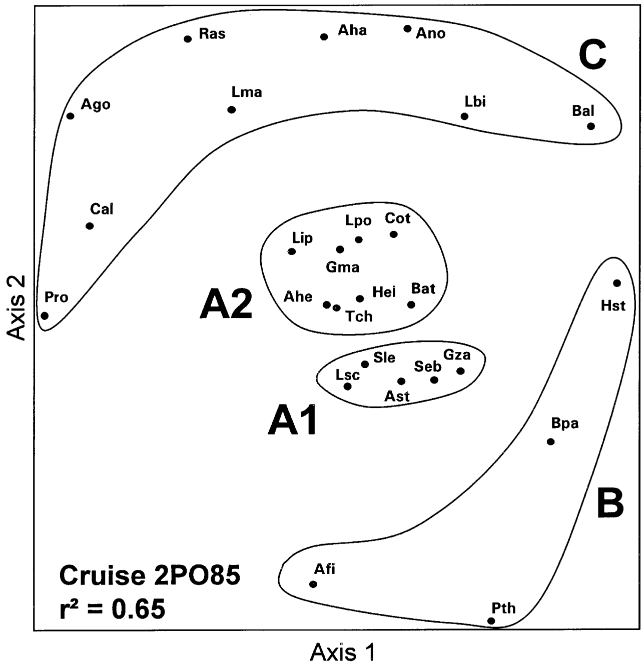

Fig. 17. Ordination plot of species scores using two-dimensional multidimensional scaling for GOA cruise 2PO85. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

4. Discussion

Most of the species encountered in this study have broad geographic ranges, often extending from the Bering Sea to the Baja California Peninsula off Mexico (Allen & Smith, 1988). However, the centers of abundance and reproductive ranges of the individual species tend to vary within this range and larval distributions are more restricted. The distinction between the ichthyoplankton fauna characteristic of the GOA and southeastern EBS and that characterizing the WC collections is primarily related to this north-south variation in adult distributions and reproductive ranges; water temperature appears to be a major environmental influence in this regard. Differences in local topography and habitat availability, however, may also contribute to the observed inter-regional differences in the ichthyoplankton. For instance, the dominance of the mesopelagic species, such as bathylagids and myctophids, in the WC collections can be related to the narrowness of the shelf off the WC; in contrast to the GOA and EBS where the shelf is broad. In addition, the coastlines of the GOA and, to a lesser extent, the southeastern EBS are heavily indented with many bays and the near-shore topography is rugged with a wide variety of substrate types, ranging from soft mud and sand to rock. Intertidal and subtidal rocky habitats are plentiful and these support a rich diversity of demersal species including cottids, agonids, liparids and stichaeids, all demersal spawners whose larvae are prominent in the ichthyoplankton of these regions. In general, the WC is characterized by a much smoother coastline with extensive areas of sandy bottom that support a less diverse shallow-water ichthyofauna, typically the Osmeridae (demersal spawners) and the coastal Pleuronectidae (pelagic spawners) whose larvae are dominant in the WC shelf samples.

The application of numerical classification to the species abundance data sets for each cruise elucidated spatial patterns in the ichthyoplankton that suggest the occurrence of two or more multi-species assemblages of fish larvae in each region. The identification of distinct species and station groups in each data set

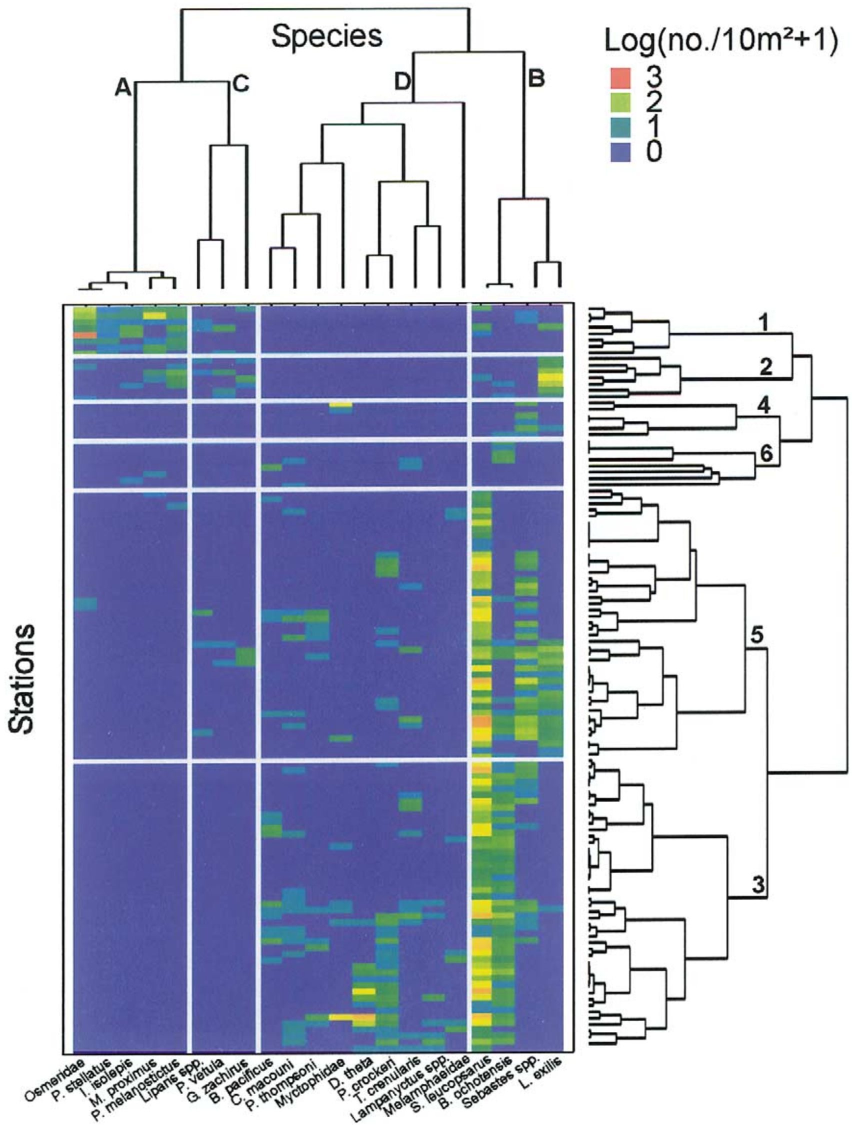

Fig. 18. Grid showing relative abundance among species and stations with cluster dendrograms from two independent cluster analyses, one for species and one for stations for WC cruise 1TK80. Solid white lines divide the data into species/station groups.

indicates that species of fish larvae are not randomly distributed throughout these regions. However, none of the species groups do represent a unique assemblage of fish larvae, nor does any station group describe a consistently exact pattern of distribution for a particular group of fish larvae. Rather there was variation among data sets in both the composition and distribution of species groups, that reflects the fluidity of the pelagic environment the fish larvae inhabit. In addition, distribution patterns among species groups tended to overlap and were seldom mutually exclusive. Furthermore, some species, such as *Theragra chalcogramma* in the EBS and GOA, were distributed widely in the study region whereas others were more confined in their occurrences. Nevertheless, there was a general tendency for species groups identified in the numerical classification results for each data set to be associated with one or more station groups

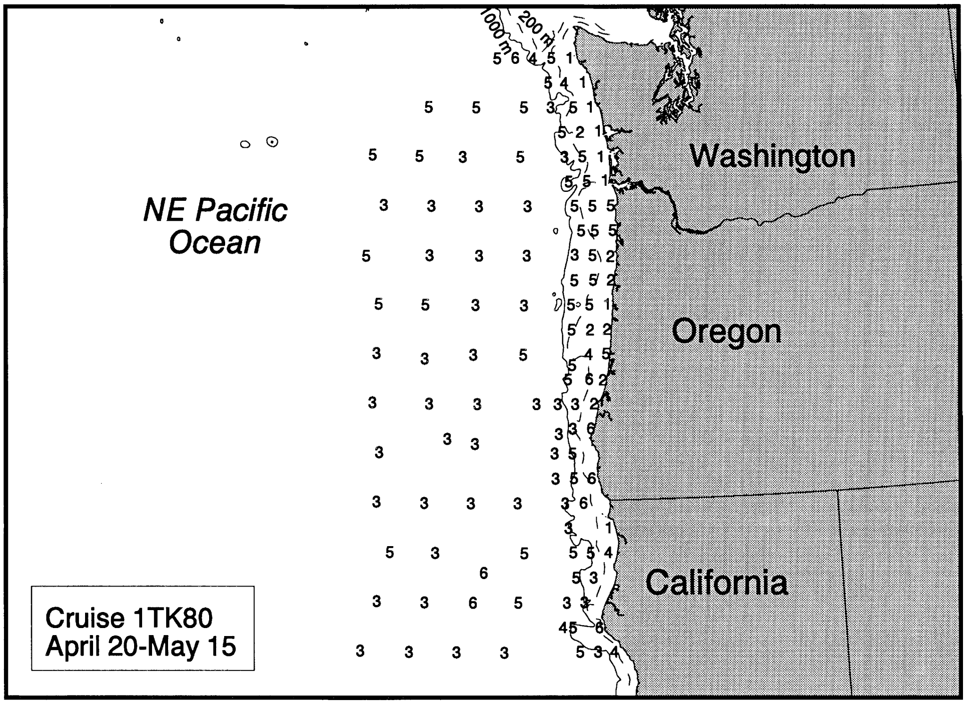

Fig. 19. Map showing position of station groups, by group number, resulting from cluster analysis of ichthyoplankton data from WC cruise 1TK80.

representing a specific geographical area or bathymetric range. In summarizing the results of the numerical analysis, it is possible then to assign individual species to spatially distinct assemblages. These assemblages represent the prevailing pattern of distribution and abundance of larval fish species in the different regions during spring of the years in which sampling was carried out (Tables 3-5).

For all three sampling regions, the grouping of species into geographically distinct assemblages is primarily related to bathymetry. This is supported by the results of the ANOVA of water depth among station groups that resulted from numerical classification of the ichthyoplankton abundance data. As indicated by observations in many regions of the world's oceans, ichthyoplankton assemblages generally display strong horizontal structure along the onshore-offshore axis (Richardson, Laroche & Richardson, 1980; Sabates, 1990; Cowen, Hare & Fahay, 1993; Doyle, Morse & Kendall, 1993; Leis, 1993; Loeb, Kellerman, Koubbi, North & White, 1993; Olivar & Shelton, 1993; Richards, McGowan, Leming, Lamkin & Kelley, 1993; Thorrold & Williams, 1996). This shelf-oceanic gradient in larval fish assemblages reflects the distribution and spawning patterns of adult fish populations. A considerable degree of complexity can be superimposed on this primary, depth-driven structure in ichthyoplankton assemblages by topographic features, regional and local currents, water-mass structure, fronts, eddies, upwelling regimes, estuarine influence and seasonal variation in the oceanographic environment (Moser & Smith, 1993a; Grothues & Cowen, 1999; Witting, Able & Fahay, 1999).

In the EBS and GOA, the clear distinction between the General Shelf assemblage and the Slope/Deepwater assemblage reflects the habitat preference and spawning location of the adult fish. The shelf assemblage is comprised essentially of shallow water and shelf species that spawn demersal eggs, including cottids, agonids, *Bathymaster* spp., stichaeids, *Ammodytes hexapterus* and the pleuronectids *Lepidopsetta bilineata* and *L. polyxystra*. *Gadus macrocephalus* is an exception to this group in that it spawns semi-

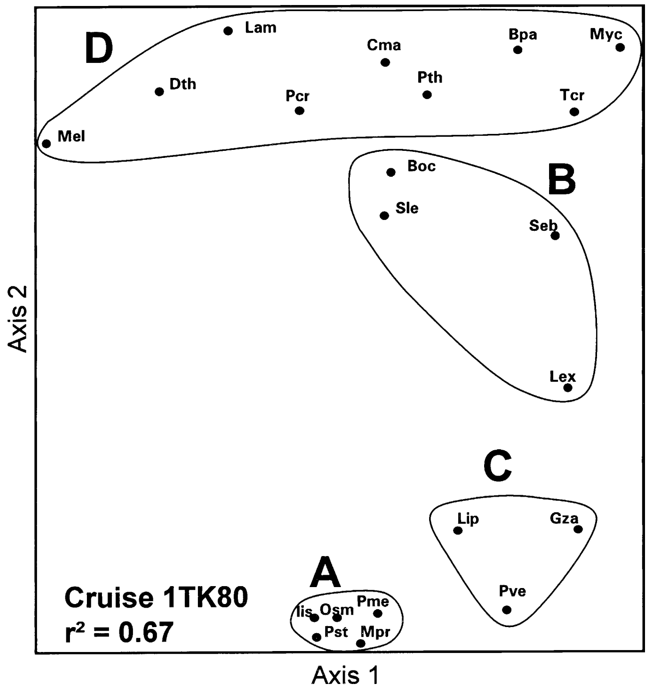

Fig. 20. Ordination plot of species scores using two-dimensional multidimensional scaling for WC cruise 1TK80. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

demersal eggs, depositing them just above the bottom. *Theragra chalcogramma* (pelagic eggs) is a member of this assemblage because of its ubiquitous distribution. Except for the viviparous *Sebastes* spp., the Slope/Deep-water assemblage of the EBS and GOA is made up of pelagic spawners including the mesopelagic species and the deep-water pleuronectids. The former live and spawn in deep oceanic and slope water and the latter seem to be associated primarily with, and spawn in, water over the shelf edge and slope (Matarese, Kendall, Blood & Vinter, 1989). In the GOA, larvae of the demersal spawning *Bathymaster* spp. are widespread in their distribution and therefore are also included in the deep-water assemblage here. The Unimak assemblage of fish larvae identified in the EBS and the Shelikof Sea Valley and Northeast Kodiak Shelf assemblage identified in the GOA seem to represent a more complex structure in the ichthyoplankton than that represented by the primary shelf/deep-water dichotomy. Both these assemblages are characterized by a high diversity of species including a mixture of members from the shelf and deep-water assemblages in addition to some species unique to them. The topography and current patterns in each region contributes to the complexity observed in these assemblages.

The proximity of Unimak Pass to the shelf edge and slope, and the eastward flow of the Aleutian North Slope Current over the slope and onto the shelf north of the pass are likely to enhance the occurrence of deep-water fish larvae at this location. In addition, it is known that a portion of the Alaska Coastal Current flows into the Bering Sea through Unimak Pass (Schumacher, Pearson & Overland, 1982; Stabeno, Scumacher & Ohtani, 1999) bringing GOA shelf water onto the shelf of the southeast EBS, and likely with it fish larvae from the GOA. The unique occurrence of GOA shelf assemblage taxa *Liparis* spp., *Anoplarchus* spp., and *Bathyagonus alascanus* in the Unimak assemblage in the Bering Sea is likely to be related to this transport of water northward through the pass. In the GOA, the Shelikof Sea Valley and NE Kodiak Shelf assemblage represents a complex mixture of shallow-water and shelf species with mesopelagic species and deep-water pleuronectids. Water depths in the central part of Shelikof Strait are >200 m and in the

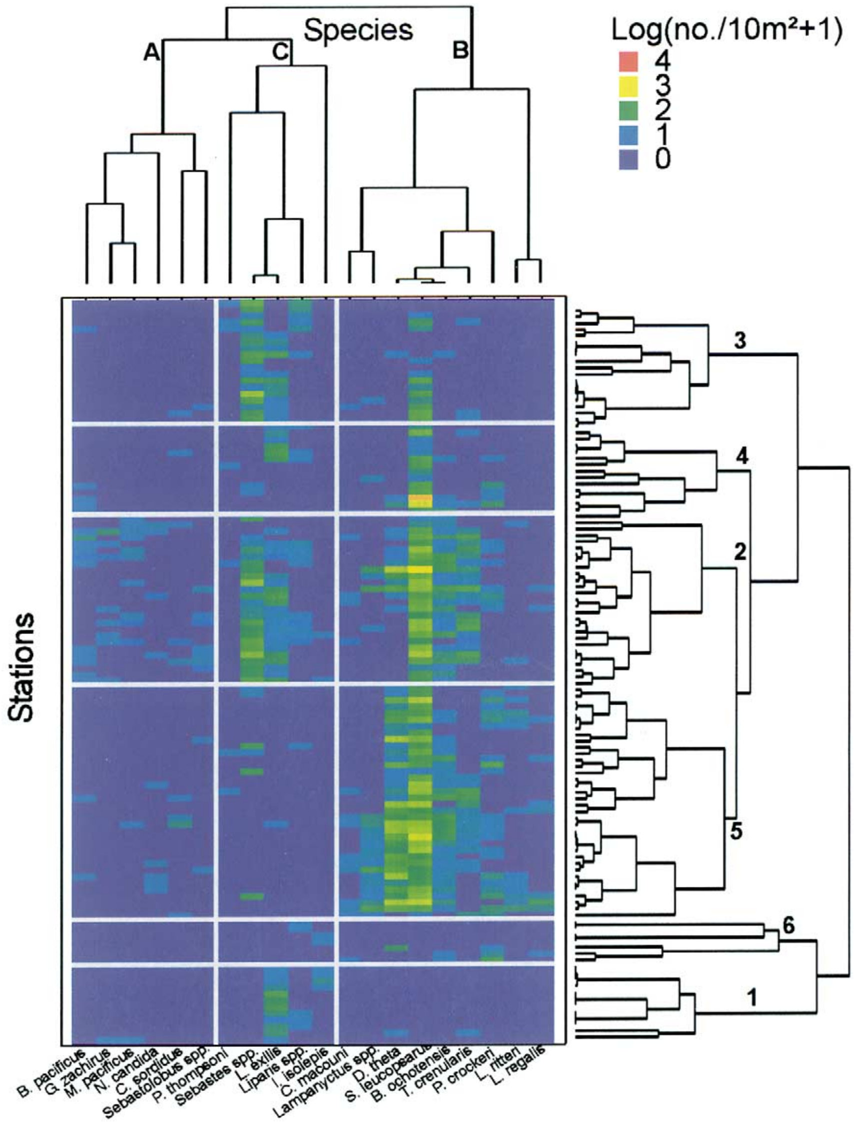

Fig. 21. Grid showing relative abundance among species and stations with cluster dendrograms from two independent cluster analyses, one for species and one for stations for WC cruise 1PO81. Solid white lines divide the data into species/station groups.

southwest extremity of the Shelikof Sea Valley reach 300 m. We speculate here that some spawning of deep-water taxa such as the mesopelagic species and the deep-water pleuronectids may occur in this area as well as along the slope. It is also possible that advection of these larvae into Shelikof Strait takes place in deep water along the Sea Valley, in the opposite direction to the main flow of the near surface waters (Kevin Bailey, personal communication). Numerous bays indent the north shore of Kodiak Island and the Alaska Peninsula coast in the vicinity of Shelikof Strait and support a diverse community of shallow water taxa such as cottids, agonids, liparids and stichaeids (Kendall & Dunn, 1985; Mueter & Norcross, 1999). Larvae of these taxa may be flushed out of the bays into the deeper water of Shelikof Strait by a combination of the Alaska Coastal Current and local tidal currents; thus the diversity of larval fish species is enhanced

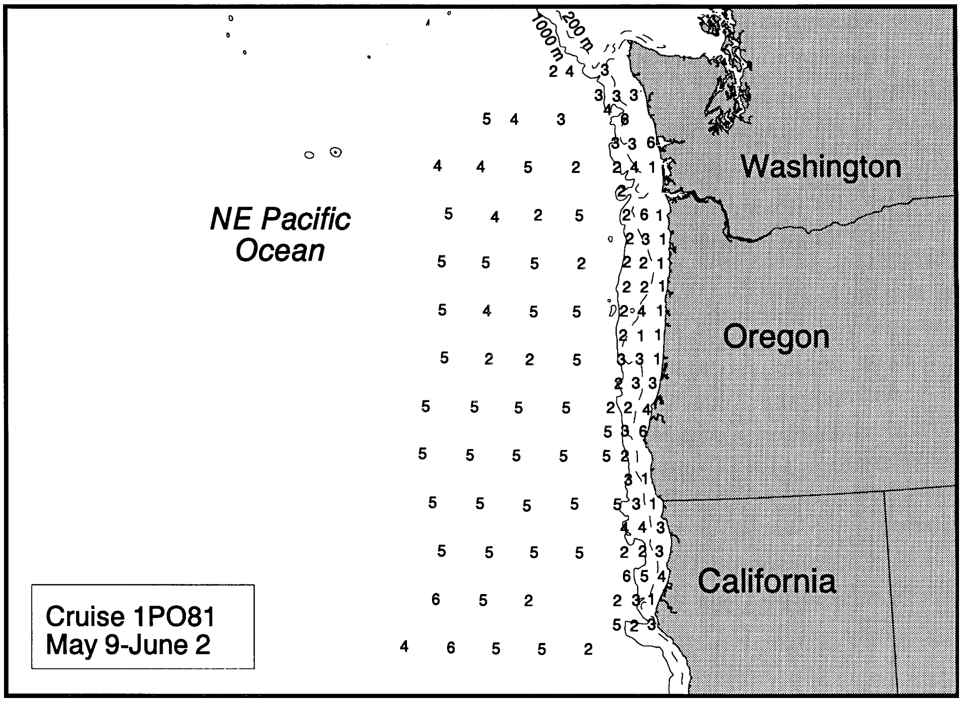

Fig. 22. Map showing position of station groups, by number, resulting from cluster analysis of ichthyoplankton data from WC cruise 1PO81.

in the Shelikof assemblage. The occurrence of a diverse assemblage on the shelf northeast of Kodiak Island seems more difficult to explain. However, deep-water taxa including the mesopelagic species and the deep-water pleuronectids may be transported onto the shelf in this region, from the slope, by the Alaska Stream that flows westwards along, and to a certain extent across, the slope to the northeast of Kodiak Island. This would explain the mixture of shelf and deep-water species here.

The data sets examined here and observations from other studies (Richardson, Laroche & Richardson, 1980; Doyle, Morse & Kendall, 1993; Doyle, 1995) indicate that the ichthyoplankton assemblages prevailing along the U.S. West Coast during spring are structured essentially according to water depth and reflect the distribution and habitat preference of the adults. They include a Coastal/Shelf assemblage, a Slope assemblage, and an Oceanic assemblage. The Slope assemblage represents a transition between the shelf and oceanic assemblages, containing some species from both. It is also uniquely characterized by peak abundances of *Sebastes* spp., *Sebastolobus* spp., and the pleuronectids *Glyptocephalus zachirus*, *Lyopsetta exilis* and the occurrence of *Microstomus pacificus*. The assemblage structure is also influenced by the upwelling regime in this northern region of the California Current system. The occurrence and timing of spawning of coastal species seems to be related to the occurrence and intensity of offshore surface Ekman transport in association with the seasonal variation in upwelling along the coast (Richardson, Laroche & Richardson, 1980; Doyle, Morse & Kendall, 1993; Doyle, 1995). The Coastal/Shelf assemblage, which is prominent off the Washington and northern Oregon coasts, is scarce or absent off southern Oregon and northern California. This seems to be related to the decreasing width of the shelf, and associated increase in intensity of summer upwelling and offshore Ekman transport, from north to south. Along-shore variation in occurrence and abundance of species within the Oceanic assemblage has also been observed during summer and seems to be related to temperature gradients (Doyle, Morse & Kendall, 1993; Doyle, 1995).

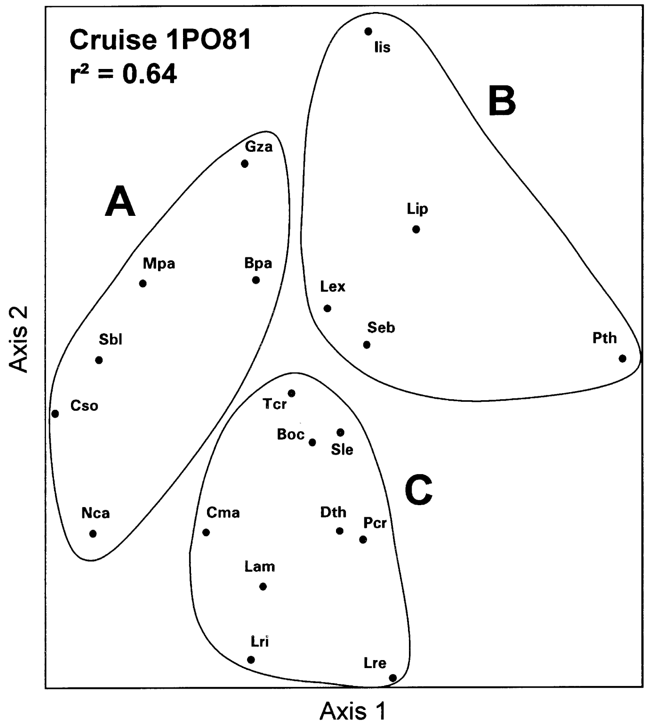

Fig. 23. Ordination plot of species scores using two-dimensional multidimensional scaling for WC cruise 1PO81. Species groups from the cluster analysis are circled on the plot. Species are identified by abbreviations shown in Table 2.

Table 3
Assemblages of fish larvae identified in the Bering Sea - based on the occurrence and abundance of individual species in these geographical locations as indicated by the species and station groups resulting from the numerical classification of the three data sets. Species unique to an assemblage are indicated in bold

Bering Sea Assemblages: **General Shelf**	**Unimak Shelf**	**Slope/Deep-water**
Gadidae	Gadidae	***Bathylagus pacificus***
Gadus macrocephalus	*Gadus macrocephalus*	***Leuroglossus schmidti***
Theragra chalcogramma	*Theragra chalcogramma*	***Stenobrachius leucopsarus***
Myoxocephalus spp.	*Hexagrammos decagrammus*	*Theragra chalcogramma*
***Bathymaster* spp.**	*Hemilepidotus hemilepidotus*	***Sebastes* spp.**
***Lumpenus* spp.**	***Icelinus* spp.**	*Hexagrammos decagrammus*
Poroclinus rothrocki	Myoxocephalus *spp.*	***Pleurogrammus monopterygius***
Ammodytes hexapterus	***Liparis* spp.**	*Hemilepidotus hemilepidotus*
Lepidopsetta polyxystra	***Anoplarchus* spp.**	***Bryozoichthys lysimus***
	Bathyagonus alascanus	*Hippoglossus stenolepis*
	Podothecus acipenserinus	***Reinhardtius hippoglossoides***
	Ammodytes hexapterus	
	Hippoglossus stenolepis	
	Lepidopsetta polyxystra	

Table 4
Assemblages of fish larvae identified in the Gulf of Alaska - based on the occurrence and abundance of individual species in these geographical locations as indicated by the species and station groups resulting from the numerical classification of the two data sets. Species unique to an assemblage are highlighted in bold

Gulf of Alaska Assemblages: **General Shelf**	**Shelikof Sea Valley and NE Kodiak Shelf**	**Slope/Deep-water**
Gadus macrocephalus	*Bathylagus pacificus*	*Bathylagus pacificus*
Theragra chalcogramma	*Leuroglossus schmidti*	*Leuroglossus schmidti*
Cottidae	*Stenobrachius leucopsarus*	***Protomyctophum thompsoni***
Artedius harringtoni	*Gadus macrocephalus*	*Stenobrachius leucopsarus*
Radulinus asprellus	*Theragra chalcogramma*	*Theragra chalcogramma*
Agonidae	*Sebastes* spp.	*Sebastes* spp.
Bathyagonus alascanus	*Anoplopoma fimbria*	*Anoplopoma fimbria*
Liparis spp.	Cottidae	*Bathymaster* spp.
Bathymaster *spp.*	*Artedius harringtoni*	***Zaprora silenus***
Lumpenus maculatus	*Radulinus asprellus*	*Atheresthes stomias*
Anoplarchus spp.	Agonidae	*Glyptocephalus zachirus*
Ammodytes hexapterus	*Bathyagonus alascanus*	*Hippoglossoides elassodon*
Lepidopsetta bilineata	*Liparis* spp.	*Hippoglossus stenolepis*
Lepidopsetta polyxystra	*Bathymaster* spp.	
	Lumpenus maculatus	
	Poroclinus rothrocki	
	Anoplarchus spp.	
	Cryptacanthodes aleutensis	
	Ammodytes hexapterus	
	Atheresthes stomias	
	Glyptocephalus zachirus	
	Hippoglossoides elassodon	
	Hippoglossus stenolepis	
	Lepidopsetta bilineata	
	Lepidopsetta polyxystra	

The prevailing patterns in ichthyoplankton assemblages of three regions in the Northeast Pacific Ocean described here form the basis for future investigations of spatial and temporal patterns in the ichthyoplankton of the subarctic Pacific. For the Gulf of Alaska and southeast Bering Sea, ichthyoplankton collections and oceanographic monitoring are ongoing since the 1980s as part of the NOAA research in these regions. It is hoped to examine seasonal and interannual variation in the occurrence and structure of ichthyoplankton assemblages in these regions in relation to the oceanographic environment, and to examine further spatial patterns in relation to spatial variation in the physical and biological environment. Fish egg data are also available for the above collections and it is intended to investigate spatial and temporal patterns in egg distribution and abundance of the dominant species in the GOA and EBS. This should further enhance our understanding of spawning strategies of the fish species in these regions and how the oceanographic environment may be influencing the early life history and subsequent survival to juvenile stage, among these fish populations.

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Table 5
Assemblages of fish larvae identified along the West Coast - based on the occurrence and abundance of individual species in these geographical locations as indicated by the species and station groups resulting from the numerical classification of the two data sets. Species unique to an assemblage are indicated in bold

West Coast Assemblages:

Coastal/Shelf	**Slope**	**Oceanic**
Osmeridae	*Nansenia candida*	*Nansenia candida*
Stenobrachius leucopsarus	*Bathylagus ochotensis*	*Bathylagus ochotensis*
Microgadus proximus	*Bathylagus pacificus*	*Bathylagus pacificus*
Liparis spp.	*Chauliodus macouni*	*Chauliodus macouni*
Glyptocephalus zachirus	Myctophidae	Myctophidae
Isopsetta isolepis	*Diaphus theta*	*Diaphus theta*
Lyopsetta exilis	*Lampanyctus* spp.	*Lampanyctus* spp.
Parophrys vetula	*Protomyctophum crockeri*	***Lampanyctus ritteri***
Platichthys stellatus	*Protomyctophum thompsoni*	***Lampanyctus regalis***
Psettichthys melanostictus	*Stenobrachius leucopsarus*	*Protomyctophum crockeri*
	Tarletonbeania crenularis	*Protomyctophum thompsoni*
	Sebastes spp.	*Stenobrachius leucopsarus*
	Sebastolobus spp.	*Tarletonbeania crenularis*
	Liparis spp.	**Melamphaeidae**
	Citharichthys sordidus	*Sebastes* spp.
	Glyptocephalus zachirus	*Sebastolobus* spp.
	Lyopsetta exilis	*Citharichthys sordidus*
	Microstomus pacificus	

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