Ichthyoplankton abundance, distribution, and assemblage structure in the Gulf of Alaska during September 2000 and 2001

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Abstract

Autumn ichthyoplankton assemblage structure in the Gulf of Alaska (GOA) region has not previously been characterized. Ichthyoplankton data from September 2000 and 2001 survey collections were analyzed to describe assemblages in the western GOA, to examine interannual variation in assemblages, and to relate observations to oceanographic conditions. Taxa with the highest frequency of occurrence (2000/2001) included Osmeridae (94/87%), *Hexagrammos lagocephalus* (57/45%), *Sebastes* spp. (35/47%) and *Bathymaster* spp. (27/57%). Through the use of clustering techniques and ordination, three identifiable larval assemblages common to both years were identified. Slope assemblages appeared well defined in both years, while nearshore and mid-shelf assemblages tended to be more loosely associated and variable between years. Analyses of environmental variables (temperature, salinity, water depth, distance from shore, and water transport) suggest ichthyoplankton assemblage structure is affected primarily by bathymetry and circulation. We demonstrate that early autumn ichthyoplankton assemblage structure in the GOA is fundamentally linked to variations in macro- (slope vs. shelf) and meso-scale topography (on-shelf proximity to land masses), and suggest that these intrinsic associations may be modified by spatial and temporal variations in local hydrographic conditions.

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1. Introduction

The Gulf of Alaska (GOA) is an important region for commercially valuable marine fish and shellfish populations and supports some of the most productive fisheries in the United States. It is also an important spawning area for many fishes and supports a diverse array of larval fish species throughout the early spring to late autumn months. The shelf region southwest of Kodiak Island is characterized by a complex bottom topography, including numerous banks and troughs and an abrupt shelf break (Fig. 1). Circulation in this region is dominated by two southwestward-moving currents. The nearshore Alaska Coastal Current (ACC) dominates flow along the coast and shelf, and obtains surface speeds of up to 25–100 cm s⁻¹ (Royer, 1981; Stabeno et al., 1995). This current usually reaches its maximum transport in the autumn (September/October), and is driven primarily by winds and coastal runoff. It receives pulses of freshwater flux along the entire coast from May to October, with freshwater runoff generally peaking in October (Royer, 1982; Wilson and Overland, 1986). The other major current in this region is the

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Alaska Stream (AS), which runs roughly parallel to the shelf-break, dominates offshore circulation along the slope and remains relatively constant at speeds of 50–100 cm s\(^{-1}\) (Reed and Schumacher, 1986).

Spring ichthyoplankton abundance and diversity in the GOA is well characterized (Brodeur and Rugen, 1994; Doyle et al., 2002); however, comparatively little is known about factors affecting larval fish assemblages in the early autumn. Kendall and Dunn (1985) reported species-specific ichthyoplankton distribution and abundance data in the GOA in autumn, but no data are available on autumn larval fish assemblages for this area. Many species whose larvae are present in autumn (e.g. capelin) provide a food source for commercially and ecologically important fishes, birds and mammals in this area (Baird, 1990; Hansen, 1997; Byrd et al., 1997; Merrick et al., 1997). Knowledge of the distributions and associations of these larvae with key hydrographic features and other biotic components of the ecosystem is needed to help understand factors influencing the distribution of adults. The ecology of larval assemblages present during early autumn may be particularly relevant since, compared with spring-spawned species, these summer-spawned individuals have relatively less time for growth prior to the onset of their first winter, a critical interval influencing survival and recruitment to the juvenile stage.

The objectives for this study were to describe ichthyoplankton abundance, distribution and assemblage structure in the GOA in early autumn (September); examine interannual variations in these factors between 2000 and 2001; and relate evident patterns to oceanographic conditions.

2. Materials and methods

2.1. Study area and sampling procedure

The geographic region of focus for this study was the GOA southwest of Kodiak Island along the Alaska Peninsula (Fig. 1). Samples characterized as early autumn were collected during two research cruises conducted from 2 to 20 September 2000, and 2 to 19 September 2001. Samples examined included 109 collections from 2000, and 93 from 2001. A 1-m\(^2\) Tucker trawl was used to collect samples on a fixed grid of stations (33 km apart) from near-shore to the outer shelf in the area between Shelikof Strait and the Shumagin Islands. Oblique samples were obtained by opening and closing the two Tucker nets (333-\(\mu\)m mesh). Net one fished from 200 m or 10 m above bottom (whichever was shallowest) to just below the thermocline, and net two fished from the thermocline to the surface. Each station was sampled during both daylight and dark hours. In...
order to focus on the geographic distribution of larvae and allow for comparison with historical catches using obliquely towed bongo nets (Kendall and Dunn, 1985), catch from nets one and two were summed to yield one continuous oblique sample at each station. In addition, day and night samples were averaged to provide integrated information on the ichthyoplankton present at each station during a full 24-h period. Our focus here is on geographic (horizontal) distribution of assemblages, a subsequent investigation may focus on vertical distribution and diurnal variations in distribution.

Real-time data on net depth, salinity and water temperature were collected at each station during the Tucker trawls using a Sea-Bird SBE 19 CTD profiler attached in-line between the wire terminus and the net. Mechanical flowmeters fitted in the mouth of each net were used to determine the volume of water filtered for that net. Contents of each cod end were immediately fixed in 5% formalin for later quantitative sorting. Ichthyoplankton samples were sorted, identified to the lowest possible taxon, measured for standard length (mm), and enumerated at the Plankton Sorting and Identification Center in Szczecin, Poland.

2.2. Analyses

The percent frequency of occurrence and mean abundance (no. 10 m$^{-2}$) of species across stations in each year were calculated. Inclusion of species in assemblage structure analyses (described below) were limited to those occurring at 5% or more of the stations. However, in 2000 the catch data for Bathymasteridae (3.9%), which is comprised exclusively of Ronquilus jordani and Bathymaster spp. (A. Matarase, personal communication), were combined with the catch data for Bathymaster spp. (27.5%) to reach the 5% threshold for the former.

To investigate the distribution of assemblages, a flexible-beta (beta = −0.25) cluster analysis of stations was performed using Bray–Curtis similarity coefficients of stations with fourth root transformed abundance data (no. 10 m$^{-2}$). This transformation down-weighted the common species. The resulting distribution of station assemblages were mapped. To investigate the taxonomic composition of assemblages, a cluster analysis of species, using Bray–Curtis similarity coefficients of species with untransformed abundance data standardized by species totals, was also performed. Standardization allows for species with similar patterns, though the numbers may be very different in scale, to show up as similar. Species clusters were determined using a combination of cluster stability (longer branches in dendogram suggest more stability) and ecological plausibility of species association. Differences in species and station clustering between 2000 and 2001 were compared and contrasted in a matrix relating species clusters and overall species abundance to station assemblage groups. Cluster groups were further corroborated using the non-metric multidimensional scaling (NMDS) ordination method (McCune and Mefford, 1999).

To interpret the ecological significance of station assemblages we used nonparametric, multivariate analyses to examine environmental (depth-integrated estimates of temperature and salinity) and station (water depth and distance from shore) effects on species composition. BIO-ENV (biological-environmental) and ANOSIM (analysis of similarity), both of which are permutation techniques within the multivariate software PRIMER, were used for these analyses (Clarke and Green, 1988). BIO-ENV uses a stepwise procedure to determine the best subset of environmental variables that maximizes the rank correlation between the Bray–Curtis similarity matrix of biotic variables and the Euclidean distance matrix of continuous environmental variables. The ANOSIM procedure is analogous to ANOVA but uses similarity matrices. The $R$ statistic in ANOSIM is based on the difference between the average rank similarities between groups and the average rank similarities among groups, just as in an ANOVA; the $F$ statistic is based on the ratio of the mean squared error between groups and the mean squared error among groups. The $R$ statistic is also an indication of how different groups are: the closer to 1, the greater the difference.

For ANOSIM testing purposes, each station was assigned to a discrete temperature and salinity category. Contour maps showing the extent of these categories were created for both years. In addition, two water-depth [shallow (<200 m), deep (>200 m)] and distance-from-shore [nearshore (<25 km from shore), offshore (>25 km from shore)] categories were originally assigned. However, the GOA is characterized by a complex bottom topography, and water depth and distance from shore are not linearly related in this system. Accordingly, we assigned each station to one of three combined water-depth/distance-from-shore categories; Shallow-Nearshore (S-N), Shallow-Offshore (S-O) or Deep-Offshore (D-O), to test for differences in species composition in a two-way crossed ANOSIM. Note: no Deep-Nearshore stations occurred. We followed each of these analyses with a SIMPER (similarity percentages—species contribution) analysis to determine which species were primarily responsible (discriminating species) for the differences found in the ANOSIM categories (Clarke, 1993). In addition, the correspondence of temperature, salinity, water depth and distance from shore with individual taxa was tested using Pearson correlation coefficients.

We related patterns in station assemblage structure to fluctuations in water transport for August–September 2000 and 2001. Estimates of total transport (Sv) were
calculated from grid point data along a line in lower Shelikof Strait that is part of a sigma-coordinate primitive equation model (SPEM) of circulation and salinity in this area. The SPEM shows the extent of eddying and the degree of variability of overall flow in each year (Hermann et al., 1996a,b).

3. Results

3.1. Relative abundance and species associations

Of the taxa occurring in greater than 5% of the stations in 2000 and 2001, 17 taxa were identified from a total of 9 families: 13 were identified to species, 3 to genus, and 1 to family level only (Table 1). Both years were characterized by a dominance of Osmerid larvae, with abundance at stations over the shelf region reaching an order of magnitude higher than other species. Taxa with the highest frequency of occurrence across stations (2000/2001) included Osmeridae (94/87%), Hexagrammos lagocephalus (57/45%), Sebastes spp. (35/47%), Bathymaster spp. (31/57%), Hexagrammos octogrammus (28/23%) and Ronquillus jordani (18/26%).

Cluster analysis showed that three species groups (A, B and C) were associated with six station assemblages in 2000, and four species groups (D, E, F and G) were associated with four station assemblages in 2001 (Table 1). Similar species and station groupings resulted from NMDS ordination analysis (results not shown). Species group A (2000) and G (2001) shared three core species: Leuroglossus schmidtii, Protomyctophum thompsoni and Stenobrachius leucopsarus (Table 1). With few exceptions, highest abundances in this group tended to be associated with the station assemblage located primarily over the slope area (Fig. 2A, Assemblage 6; Fig. 2B, Assemblage 2). Some individuals were also associated with stations located in the midsection of Shelikof Trough (Fig. 2A and B, select stations in Assemblage 4 over the trough). In both years the station assemblage associated with this species group remained largely over the slope. However, in 2000 it extended further up the trough exiting Shelikof Strait, while in 2001 it moved up Shumagin Trough on the opposite side of the sampling grid.

In contrast to the relatively consistent slope species group described above, species groups B and C in 2000 were split into groups D, E and F in 2001 (Table 1). Although species in these groups were generally associated with stations located over the shelf, none of these species groups showed consistent fidelity to any specific station assemblage over the shelf or nearshore areas. However, cluster analysis of stations showed that, in both years, a nearshore assemblage occurred primarily over shallow depths and bordered the coastline (Fig. 2A, Assemblage 2; Fig. 2B, Assemblage 1). Several widely scattered mid-shelf assemblages also occurred in each year, spanning a large and variable area from the coastline up to the edge of the shelf break (Fig. 2A, Assemblages 1, 4 and 5; Fig. 2B, Assemblages 3 and 4). In general the mid-shelf assemblages in 2000 tended to be more interspersed with the nearshore assemblage than in 2001, although one of the mid-shelf assemblages in 2000 consisted of stations restricted to a localized area (Fig. 2A, Assemblage 5).

3.2. Physical factors

Contour maps of depth-integrated temperature and salinity data revealed differences across the shelf between September 2000 and 2001 (Fig. 3). Although conditions along the shelf break (slope) appeared similar in each year (3.27–33.1 psu), the cross-shelf horizontal profile in 2001 was more stratified when compared to 2000. Specifically, a warm (30.4–30.9 °C), low salinity (10.1–11.5 psu) water mass was observed adjacent to the Alaska Peninsula in 2001, that was not present in 2000. The presence of this relatively fresh, coastal water mass was likely due to a greater degree of riverine runoff in September 2001. In addition, there is evidence of slope water intrusion up Shelikof, and to a lesser extent, Shumagin Trough in both years.

When tested individually, only four of the 17 taxa were significantly correlated with environmental variables in either year (Table 2). Interestingly, three of these four taxa were Leuroglossus schmidtii, Protomyctophum thompsoni and Stenobrachius leucopsarus, which also comprised the core of species group A/G, occurring primarily over the slope region. In both years these slope associated species were negatively correlated with temperature, and positively correlated with salinity, water depth, and distance from shore. The only other taxon correlated with environmental variables was the widespread and abundant family Osmeridae. In contrast to the slope species, Osmeridae was positively correlated with temperature, and negatively correlated with salinity, and distance from shore.

Species composition showed correspondence with both environmental and station variables in both years. In 2001, water depth and salinity combined had the highest correlation with species composition, with a Spearman correlation coefficient of $r_s = 0.48$ [note: temperature and salinity were highly inversely correlated ($r_s = -0.94$)]. ANOSIM testing revealed that salinity had a significant effect on species composition in 2000 ($p = 0.007, R = 0.145$), while temperature ($p = 0.001, R = 0.280$) and salinity ($p = 0.001, R = 0.312$) had significant effects on species composition in 2001. Whether a station was categorized as Shallow-Neashore (S-N), Shallow-Offshore (S-O) or Deep-Offshore (D-O) also significantly affected species composition in both 2000 ($p = 0.001, R = 0.291$) and 2001 ($p = 0.001, R = 0.319$). Pairwise testing suggested that between the shelf and slope regions, water depth appeared to be the
Table 1

Matrix of species groups and station assemblages resulting from cluster analysis. Matrix numbers are mean abundance (no. 10 m$^{-2}$) of taxon for each station assemblage; $-$ = taxon not present. Total ichthyoplankton (mean and standard deviation) for each station assemblage represents all species, including rare taxa not included in the cluster analysis. Numbers in parentheses are total number of stations in each station assemblage. Letters in parentheses represent outliers that lay near a species group.

<table>
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<th>2000 station assemblages</th>
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<td>2.05 4.33 6.39</td>
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<td>Protonectus thompsoni</td>
<td>A</td>
<td>G</td>
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<td>2.05 4.33 6.39</td>
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<td>2.45 17.46 7.66</td>
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<td>47.97 75.03 10.95 4.45 246.56</td>
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<td>4.60 2.77 10.94 2.59</td>
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<td>E</td>
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<td>Outlier</td>
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<td>4.28 42.84</td>
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</table>

Total ichthyoplankton
Mean 19.36 75.97 15.55 30.53 6.59 5.43 103.80 4.12 13.90 9.81
Standard deviation 30.31 111.93 27.02 78.28 6.30 9.10 270.77 4.03 18.97 16.32
defining factor (Table 3A; S-O vs. D-O), while over the relatively shallow shelf region, distance from shore determined differences in species composition (S-N vs. S-O). Pairwise testing of the temperature and salinity categories showed that in both years species composition in the highest salinity area was significantly different when compared to any other respective area (Table 3B). Furthermore, in 2001 species composition in the lowest salinity area, as well as the lowest and highest temperature areas, was significantly different from all other areas. Overall, BIO-ENV analyses indicated stronger correlation between species composition and environmental variables in 2001, as compared to 2000 (Spearman correlation for best 10 subsets of variables ranged from 0.38 to 0.48 for 2001, and from 0.20 to 0.26 for 2000).

Fig. 2. Station assemblages for 2000 (A) and 2001 (B). Numbers are not analogous between years and correspond to station assemblages presented in Table 1.
SIMPER analysis revealed that the average dissimilarity between environmental and station categories was higher (i.e. species composition between categories was more distinct) in 2001, as compared to 2000. Osmeridae was the greatest contributor to the dissimilarity between categories in both 2000 (contributed 15–23% to the overall dissimilarity), and 2001 (18–42%). Other primary discriminating species between categories in 2000 were *Hexagrammos lagocephalus*, *Lepidopsetta bilineata*, *Stenobrachius leucopsarus*, and *Liparis fucensis*. In 2001, the primary discriminating species, in addition to Osmeridae, included *H. lagocephalus*, *Sebastes* spp., *Bathymaster* spp., *H. octogrammus*, *L. schmidtii*, and *R. jordani*.

SPEM model estimates of transport through lower Shelikof Strait showed striking differences between August–September of 2000 and 2001 (Fig. 4). Net flow appeared to be near zero or towards the northeast for part of the pre-sampling and sampling periods in 2000. In fact, mean transport in 2000 (−0.1 Sv) was 1.5 standard deviations below the 25-year mean (+0.7 Sv). It is important to note here that if north-eastward flow is strong enough (e.g. when a large eddy is present), the

![Fig. 3. Temperature and salinity contours for 2000 (A) and 2001 (B). Contour numbers correspond to categories used in ANOSIM pairwise testing presented in Table 3.](image)

<table>
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<tr>
<th>Taxon</th>
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<th>2001</th>
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<tbody>
<tr>
<td>Temperature</td>
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<td>Water depth</td>
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<tr>
<td>-------------------------------</td>
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</tr>
<tr>
<td>Leuroglossus schmidtii</td>
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<td>Stenobrachius leucopsarus</td>
<td>−0.482**</td>
<td>0.584***</td>
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* p < 0.05.  
** p < 0.01.  
*** p < 0.001.
net south-westward transport may be zero while the current at any given point is far from stagnant. However, on average, the net flux of water is to the southwest in Shelikof Strait. In contrast, mean flow in 2001 (0.6 Sv) more closely tracked the 25-year mean. Although the strength of the current fluctuated somewhat in 2001, net transport remained almost entirely out of the southwest, both in the weeks prior to and during the sampling period.

4. Discussion

Early autumn ichthyoplankton assemblage structure in the western GOA appears to be related primarily to large-scale topographic features (Table 3). Previous studies have linked springtime ichthyoplankton assemblage structure to specific bathymetric ranges (e.g. shelf, slope, and deep-water) (Kendall and Dunn, 1985; Doyle et al., 2002). This study suggests that GOA autumnal assemblages are similarly influenced by large-scale bathymetric features (shelf, slope). However, our study also demonstrates that within sub-regions of the continental shelf, larval fish assemblages are affected by land mass proximity, suggesting that mesoscale variations in landscape features can also have substantial impacts on larval fish associations. Superimposed on this fairly persistent association with macro- and mesoscale topography, ichthyoplankton assemblages in the GOA shelf region also appear to be subject to transient perturbations by local flow patterns (similar results were reported for spring assemblages by Doyle et al., 2002). Specifically, we demonstrate that autumn ichthyoplankton assemblages on the GOA shelf vary in accordance with spatial and temporal fluctuations in the ACC, promoting horizontal mixing of larvae in this region.

The distinction between slope and shelf assemblages was supported by environmental and station variables (Table 3), and the slope assemblage appeared relatively stable and consistent between 2000 and 2001 (Fig. 2). In both years, the group of species defining the slope assemblage included *Leuroglossus schmidti*, *Stenobrachius leucopsarus*, and *Protomyctophum thompsoni* (Table 1). Kendall and Dunn (1985) describe a similar group of larval fish that occurred primarily over the slope southeast of Kodiak Island during autumn. As adults, these species are generally associated with the shelf edge and deep slope waters and produce pelagic eggs (Matarese et al., 1989; Mecklenburg et al., 2002). The fact that their larvae were negatively correlated with temperature and positively correlated with salinity, water depth and distance from shore (Table 2) is consistent with their ecology.

Although centered mainly over the shelf break, the slope assemblage extended into troughs penetrating the shelf in both years (Fig. 2A, Assemblage 6 up Shumagin Trough in 2000; Fig. 2B, Assemblage 2 up Shelikof Trough in 2001). Kendall and Dunn (1985) noted that during the autumns of 1978 and 1979, small numbers of slope species were found over trough regions bisecting the shelf southeast of Kodiak Island and suggested intrusion of oceanic water to inshore areas as a mechanism for extension onto the shelf. Bailey and

![Fig. 4. Estimates of net water flux through lower Shelikof Strait in 2000 and 2001 (±0.6 Sv) more closely tracked the 25-year mean. Although the strength of the current fluctuated somewhat in 2001, net transport remained almost entirely out of the southwest, both in the weeks prior to and during the sampling period.](image)
Picquelle (2002) suggested a similar transport mechanism as a pathway for deepwater flatfish larvae to juvenile nursery grounds on the GOA shelf. It is likely that intrusion of the mesopelagic, slope assemblage onto the shelf in our study is a result of the same mechanism; there is evidence of cold, saline slope water moving up both Shumagin and Shelikof Troughs in both years (Fig. 3). This supports the notion that water-mass structure and fronts can influence larval distribution in this area (Bailey and Picquelle, 2002).

Although differences between shelf and slope larval fish assemblages were primarily related to bathymetry, factors associated with topography appeared to characterize associations within the shelf region itself. Over the relatively shallow shelf, distance from shore determined differences in species composition in both years (Bailey and Picquelle, 2002). This area is subject to periodic disruption of these shelf ichthyoplankton assemblages as the result of perturbations in the dynamic flow of the ACC. We observed that species groups occurring primarily over the shelf split from three broad clusters in 2000, to four smaller clusters in 2001 (Table 3A), indicating that proximity to land was consistently important to assemblage structure. These observations, coupled with those noted above, lead us to conclude that landscape features (bottom depth, landmass proximity) have leading influences on distributions and associations of larval fishes in the GOA. However, we also suggest that periodic disruption of these shelf ichthyoplankton assemblages occurs as the result of perturbations in the dynamic flow of the ACC. We observed that species groups occurring primarily over the shelf split from three broad clusters in 2000, to four smaller clusters in 2001 (Table 3A). Interestingly, between 2000 and 2001 there were also major differences in the speed and direction of the ACC exiting Shelikof Strait (Fig. 4), as well as differences in the horizontal profile of temperature and salinity across the shelf (Fig 3). Anomalies in the August–September 2000 flow of the ACC (relative to the 25-year time series presented in Fig. 4) likely resulted in mixing of cross shelf waters. Similar flow patterns were characterized in a study during May 1996, when satellite-tracked drifters were used concurrently with ichthyoplankton sampling to describe unusual patterns of water transport and larval fish advection in the GOA shelf region (Bailey et al., 1999). These authors suggest that flow in May 1996 was anomalously weak and disorganized, and we hypothesize that the flow field in September 2000 may have been comparable (Fig. 4). Although drifter data is lacking in our study, the more diffuse temperature and salinity contours in 2000 compared to 2001 (Fig 3A vs. B), coupled with the observed greater degree of mixing of the nearshore and mid-shelf station assemblages (Fig. 2) in 2000, support this assertion.

In contrast to the weak flow conditions in September of 2000, the ACC flow environment on the shelf in September of 2001 appeared stronger and more organized (Fig. 4). Throughout the majority of the pre-sampling and sampling periods, net flow was vigorous in the south-westward direction. In addition, a large influx of riverine runoff into the Shelikof Strait occurred during this time period. The salinity and temperature signature of this freshwater input, and a much more horizontally stratified shelf, is apparent in Fig. 3B. The relatively large net south-westward flux of water through Shelikof Strait likely resulted in a more clearly defined and structured pattern of nearshore and mid-shelf station assemblages in 2001 (Fig. 2). Note also the prominent northeast-southwest alignment of these two assemblages. Correlation between salinity and assemblage structure was also stronger in 2001 versus 2000. In addition, differences in species composition between the environmental variables was more distinct in this year than in 2000, suggesting the ichthyoplankton assemblage structure in 2001 reflected the more organized abiotic environment.

In addition to the abiotic environment, many other factors could potentially influence larval fish associations. For example, the unique life history traits of autumn assemblage species likely influence their abundance and distribution. Many of the ichthyoplankton species present in the shelf region occupy intertidal, coastal, demersal, and other shelf areas as adults, while species associated with the shelf edge and deeper slope waters are reflected in the slope larval assemblages (Matarese et al., 1989; Mecklenburg et al., 2002). Feeding ecology and predator/prey relationships also likely play important roles in the ecology of autumn larvae, though these factors are not directly addressed here.

Many of the same taxa found in this study were also found in the nearby Kodiak Island area during historical autumn surveys (Kendall and Dunn, 1985). Overall, 15 out of the 17 taxa which occurred in our samples were documented by Kendall and Dunn (1985). In contrast, only five taxa from our autumn surveys matched those found during their summer cruises. In addition, our ichthyoplankton assemblages differed from those sampled in virtually the same location during the summer months by Brodeur et al. (1995), although a larger mesh size was used in that study. These differences in taxonomic diversity suggest that the GOA ichthyoplankton assemblage structure may change significantly in just a few months (June to September) and highlights the potential uniqueness of the autumn larval fish assemblages in this area. Interestingly, although the community structure was quite different, Brodeur et al. (1995) also found inshore, mid-shelf and offshore station assemblage structure in their summer sampling.

Dominance of Osmeridae on the shelf was apparent in both years of this study (Table 1). These larvae are likely Mallotus villosus, as reported spawning times and the presence of osmerid larvae in late summer and throughout the autumn in the GOA are consistent with this species (Kendall and Dunn, 1985; Doyle et al., 2002). Based on meristics, distribution, and timing of larval abundance, it is likely that the Sebastes spp.
sampled in both years of this study are *S. aleutianus* (A. Kendall, AJALA Enterprises, personal communication). However, identification of larvae to the species level is presently possible for only a few *Sebastes* species, and larval *S. aleutianus* have not yet been described. As adults, *S. aleutianus* usually inhabit depths between 100 and 500 m, are live-bearing with pelagic larvae, and are thought to be spring spawners (Matarese et al., 1989; Mecklenburg et al., 2002).

Two taxa from the family Bathymasteridae were collected in this study: *R. jordani* and *Bathymaster* spp. Three species of the genus *Bathymaster* (*B. signatus*, *B. leurolepis*, and *B. caeruleofasciatus*) are found as adults in this study area and spawn during the summer months, making it likely their larvae would be prevalent in September. Although we cannot distinguish between the larvae of the above species at this time, juvenile *Bathymaster* spp. identified from this area in September have generally been *B. signatus* (A. Matarese, AFSC, personal communication).

In summary, we demonstrate that early autumn ichthyoplankton assemblage structure in the G OA is fundamentally linked to variations in macro- (slope vs. shelf) and meso-scale topography (on-shelf proximity to land masses), and suggest that these intrinsic associations may be modified by spatial and temporal variations in local hydrographic conditions. These observations may be particularly relevant given the recent resurgence of interest in the potential effects of climate variation on biological associations. If climate-induced shifts in the strength, direction, or timing of prevailing current patterns in the G OA region is sufficient to reorganize larval fish distribution patterns, disrupt sensitive species-specific groupings, or breakdown critical geographic associations, the result could be a mis-match between fish, prey, and recruitment to juvenile nursery habitat.

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References


