# Neustonic ichthyoplankton in the western Gulf of Alaska during spring*

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**Abstract.**—Species diversity and abundance of fish eggs in shelf waters of the western Gulf of Alaska were similar in both surface neuston net tows and subsurface bongo net tows, but a unique group of fish larvae appear to be associated with the neuston in this region. The dominance of larvae of an osmerid, several hexagrammids, cottids, bathymasterids, *Anoplopoma fimbria*, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus* in this group resembles the neustonic assemblage of fish larvae found in the California Current region along the U.S. west coast and most of these taxa are considered obligate members of the neuston. Several taxa, however, appear to be abundant in the neuston only at night suggesting a facultative association with the neuston through a diel pattern of vertical migration. The facultative association of certain species of larvae with the neuston varies with larval size.

The distribution patterns observed for most taxa of fish larvae in the neuston during this study suggest that during spring, spawning and emergence of larvae into the plankton and subsequently into the neuston take place mainly around Kodiak Island (except along the seaward side) and along the Alaska Peninsula to the southwest. Analysis of multispecies spatial patterns using recurrent group analysis and numerical classification did not reveal the existence of more than one neustonic assemblage of fish larvae in the study area. Apart from perhaps *Pleurogrammus monopterygius* larvae, which are known to occur throughout the Gulf of Alaska, and to a lesser extent *A. fimbria* and *Hemilepidotus hemilepidotus*, members of this neustonic assemblage of larvae are not commonly found in the oceanic zone.

The ecological significance of a neustonic existence for larvae of fish that are primarily demersal spawners in the Gulf of Alaska is considered to be trophic in nature. Neustonic fish larvae seem to be able to exploit to their advantage the unique feeding conditions which exist at the sea surface.

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The Fisheries Oceanography Coordinated Investigations (FOCI) is a long-term cooperative research program conducted by National Oceanic and Atmospheric Administration (NOAA) biological and physical scientists to describe processes leading to recruitment variability of commercially important fish and shellfish stocks of the Gulf of Alaska and Bering Sea (Schumacher and Kendall, 1991). To date, most effort has concentrated on walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, specifically in Shelikof Strait and along the Alaska Peninsula. Understanding the dynamics of the spring spawning of this species in Shelikof Strait and the subsequent hatching, drift, growth, and survival of the larvae, in interaction with the physical and biological oceanographic environment, have been the primary goals of FOCI.

Ancillary to the information collected on the early life history stages of walleye pollock, are data on the distribution and abundance patterns of eggs and larvae of other fishes that spawn in the coastal waters and adjacent deeper waters of the western Gulf of Alaska. These observations can contribute to our understanding of the biology and ecology of fish populations in this region and the relationships between their life history strategies and the environment.

Prior to the onset of FOCI investigations in the early 1980's, plankton collections in the vicinity of Kodiak Island were generally limited in scope but still yielded information on species composition and spatio-temporal patterns in abundance of fish eggs and larvae (Rogers et al., 1979; Kendall and Dunn, 1985; Kendall et al.[1]). Based on early FOCI plankton collections, large-scale patterns in the ichthyoplankton have been documented for a more extensive portion of the continental shelf along the Alaska Peninsula (Rugen and Matarese[2]; Rugen[3]). There remains, however, considerable data from the more recent FOCI spring cruises, the analysis of which may improve our understanding of the ecological relationships among the fish populations inhabiting this region.

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[2] Rugen, W. C., and A. C. Matarese. 1988. Spatial and temporal distribution and relative abundance of Pacific cod (*Gadus macrocephalus*) larvae in the western Gulf of Alaska. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA, 98115. Proc. Rep. 88-18, 53 p.

[3] Rugen, W. C. 1990. Spatial and temporal distribution of larval fish in the western Gulf of Alaska, with emphasis on the period of peak abundance of walleye pollock. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA, 98115. Proc. Rep. 90-01, 162 p.

During the 1970's and 1980's, several investigations of ichthyoplankton in the neuston were conducted in the northeast Pacific Ocean, primarily off the coasts of Washington and Oregon but also extending to southern California waters (Ahlstrom and Stevens, 1976; Shenker, 1988; Brodeur, 1989; Doyle 1992). These studies established that larvae of many fish are abundant at the surface as well as deeper in the water column and that an additional group of species is almost exclusively neustonic. Doyle (1992) identified obligate and facultative members of the neuston among the larvae and juveniles of fish collected off Washington, Oregon, and northern California and attributed their association with the neuston primarily to the unique trophic conditions that prevail in this environment. Clearly, the neustonic realm is important in the early life history of many fish species (Zaitsev, 1970; Hempel and Weikert, 1972; Moser, 1981; Tully and O'Ceidigh, 1989; Doyle 1992). The level of importance, however, varies with geographical area and local conditions.

Rogers et al. (1979), Kendall and Dunn (1985), Kendall et al.[1], and Rugen[3] identified a unique surface component in the ichthyoplankton of the western Gulf of Alaska and concluded that the larvae of several species, mainly hexagrammids and cottids, are primarily neustonic. This finding merits further investigation concerning the ecological significance of a neustonic existence, particularly in this shelf area where there is a dynamic surface zone with a vigorous flow field (Reed et al., 1988; Reed and Schumacher, 1989). The present paper focuses on the neustonic ichthyoplankton in the western Gulf of Alaska. During seven of the spring cruises (1981–86), neuston as well as subsurface bongo net sampling was carried out. Data from these collections were used 1) to examine species composition and relative abundance of ichthyoplankton taxa in the neuston and to compare these with subsurface ichthyoplankton collected concurrently; 2) to identify obligate and facultative members of the neustonic ichthyoplankton; 3) to investigate diel variation in catches of larvae in the neuston; 4) to compare size distributions among the neustonic and subsurface larvae; and 5) to describe horizontal distribution patterns of the dominant neustonic ichthyoplankton species and to relate these to the oceanography of the western Gulf of Alaska.

## Methods

In 1981, the National Marine Fisheries Service (NMFS) initiated studies on the early life history of walleye pollock in the northwestern Gulf of Alaska. These studies included cooperative cruises with the Soviet Pacific Research Institute (TINRO, Vladivostok). Although the primary purpose of these cruises was to assess the spatial distribution and abundance of walleye pollock and to understand the dynamics of their planktonic stages, all taxa collected were identified and measured. For the present study, we used data from seven cruises during which both neuston net and bongo net samples were collected at each station. These cruises were conducted during spring months of the years 1981 to 1986 (Table 1). The survey area extended from the Kenai Peninsula (145°W), southwest along the Alaska Peninsula and Kodiak Island to Unimak Pass (165°W). The topography of the study area in the western Gulf of Alaska is characterized by numerous troughs and shallow banks (Fig. 1). The shelf area, as defined by the 200-m isobath, is generally wide (65–175 km) and drops abruptly to depths of 5,000–6,000 m in the Aleutian Trench, which parallels the shelf break (Fig. 1). A detailed description of the physical oceanography of the region is provided by Reed and Schumacher (1986).

The neuston was sampled at a total of 898 stations (Table 1). Station locations varied for each cruise because of specific objectives and are given in Dunn and Rugen.[4] Neuston net samples were collected with a Sameoto sampler (Sameoto and Jaroszynski, 1969)

**Table 1**

Summary of neuston collections by cruise conducted during spring of 1981 to 1986 in the western Gulf of Alaska.

| Cruise | Inclusive dates | Number of collections | Longitudinal range (°W) |
|---|---|---|---|
| 1SH81 | 5–18 March 1981 | 130 | 148–164 |
| 2SH81 | 16–24 April 1981 | 60 | 151–159 |
| 1CH83 | 16–31 May 1983 | 62 | 154–159 |
| 1SH84 | 17 April–9 May 1984 | 157 | 145–159 |
| 1PO85 | 29 March–21 April 1985 | 151 | 150–158 |
| 2PO85 | 16 May-8 June 1985 | 189 | 148–168 |
| 1GI86 | 30 March–20 April 1986 | 149 | 138–166 |

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[4] Dunn, J. R., and W. C. Rugen. 1989. A catalog of Northwest and Alaska Fisheries Center ichthyoplankton cruises, 1965–1988. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA, 98115. Proc. Rep. 89–04, 197 p.

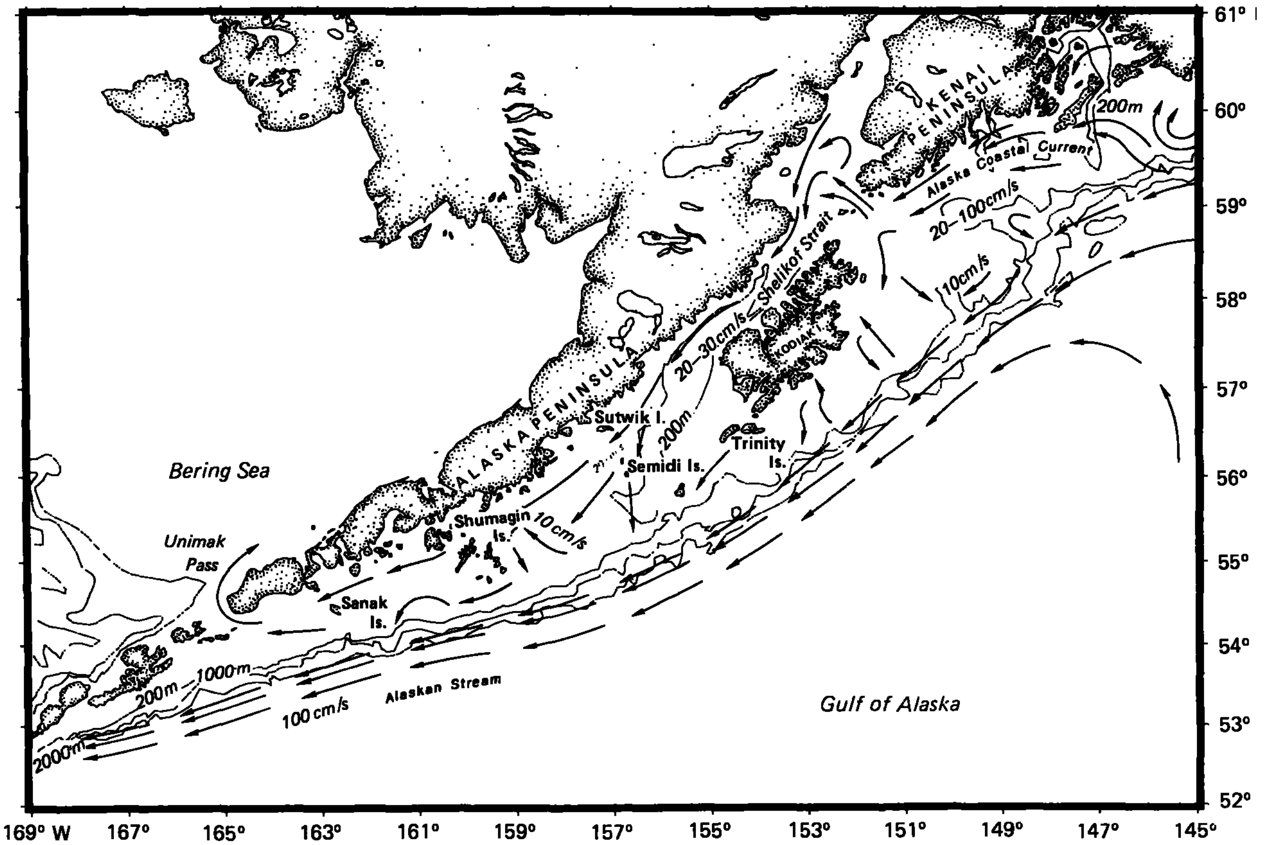


**Figure 1**

Near surface currents and some geographic and bathygraphic features of the western Gulf of Alaska. Currents based on Reed and Schumacher (1986).

with a mouth opening of 0.3 m × 0.5 m and with a 0.505-mm mesh net. Ship speed was 2 knots. Standard MARMAP (Marine Resources Monitoring Assessment and Prediction) oblique tows (Smith and Richardson, 1977) were conducted to sample subsurface ichthyoplankton with 60-cm bongo samplers fitted with 0.505-mm mesh nets. In shelf waters, tows were made to a depth close to the bottom, usually around 5 m above, and in deep water to a maximum depth of approximately 200 m. Calibrated flowmeters in the mouths of the samplers were used to determine the volume of water filtered by each net.

Counts of fish eggs and larvae were converted to densities per 1,000 $m^3$ for neuston collections, as follows:

$$(n)(1{,}000)/[(h)(w)(l)],$$

where $n$ = number of organisms in sample;
$h$ = effective fishing height of net opening (0.15 m);
$w$ = width of net opening (0.5 m);
$l$ = length of tow in meters (calculated from flowmeter).

In order to determine the importance of the neustonic layer relative to that of the entire water column, we compared the paired catches of neuston and bongo tows from the same stations following the approach derived by Hobbs and Botsford (1992). This approach accounts for the differences in surface area sampled between the neuston tows and the bongo tows. The method solves for the density of larvae per unit area in the $i$th sample ($\lambda_i$) and the portion of total water column larvae in the neuston ($\theta$) simultaneously in an iterative fashion. We first calculated the surface area (in $m^2$) sampled by the neuston ($A_{ni}$) and bongo ($A_{bi}$) net as:

$$A_{ni} = \frac{h \times w \times l}{d}$$

and

$$A_{bi} = \frac{r^2 \times \pi \times l}{d},$$

where $r$ = radius of net opening (0.3 m for bongo net);
$d$ = depth of water column sampled.

The maximum likelihood estimates of $\lambda$ and $\theta$ for $k$ sample pairs are derived as follows:

$$\hat{\lambda} = \frac{S_{ni} + S_{bi}}{A_{ni}\,\hat{\theta} + A_{bi}}$$

and

$$\hat{\theta} = \min\left( 1;\ \frac{\sum_{i=1}^{k} S_{ni}}{\sum_{i=1}^{k} A_{ni}\,\hat{\lambda}_i} \right),$$

where $S_{ni}$ = number of larvae in the $i$th neuston sample;
$S_{bi}$ = number of larvae in the $i$th bongo sample.

This method assumes that the sample pairs are drawn from a population that is distributed randomly in the horizontal plane but stratified vertically (Hobbs and Botsford, 1992).

Plankton samples were preserved in the field with a 5% formalin-seawater solution buffered with sodium tetraborate. Ichthyoplankton were sorted at the Polish Plankton Sorting Center in Szczecin, Poland. All fish eggs and larvae were removed and identified to the lowest possible taxa. Identifications were later verified at the NMFS laboratory in Seattle. Up to 50 larvae per taxon per station were measured to the nearest 0.1 mm standard length (SL).

Since sampling patterns and positions were different for each cruise, the study area was subsequently divided into 298 sectors of approximately 215 mi$^2$ (347 km$^2$). Data from stations within each sector were pooled so that average distribution patterns could be determined for the dominant neustonic taxa. The number of tows in each sector over all seven cruises are illustrated by various levels of stippling (Fig. 2). The mean densities of individual taxa were calculated for each sector by dividing the summed

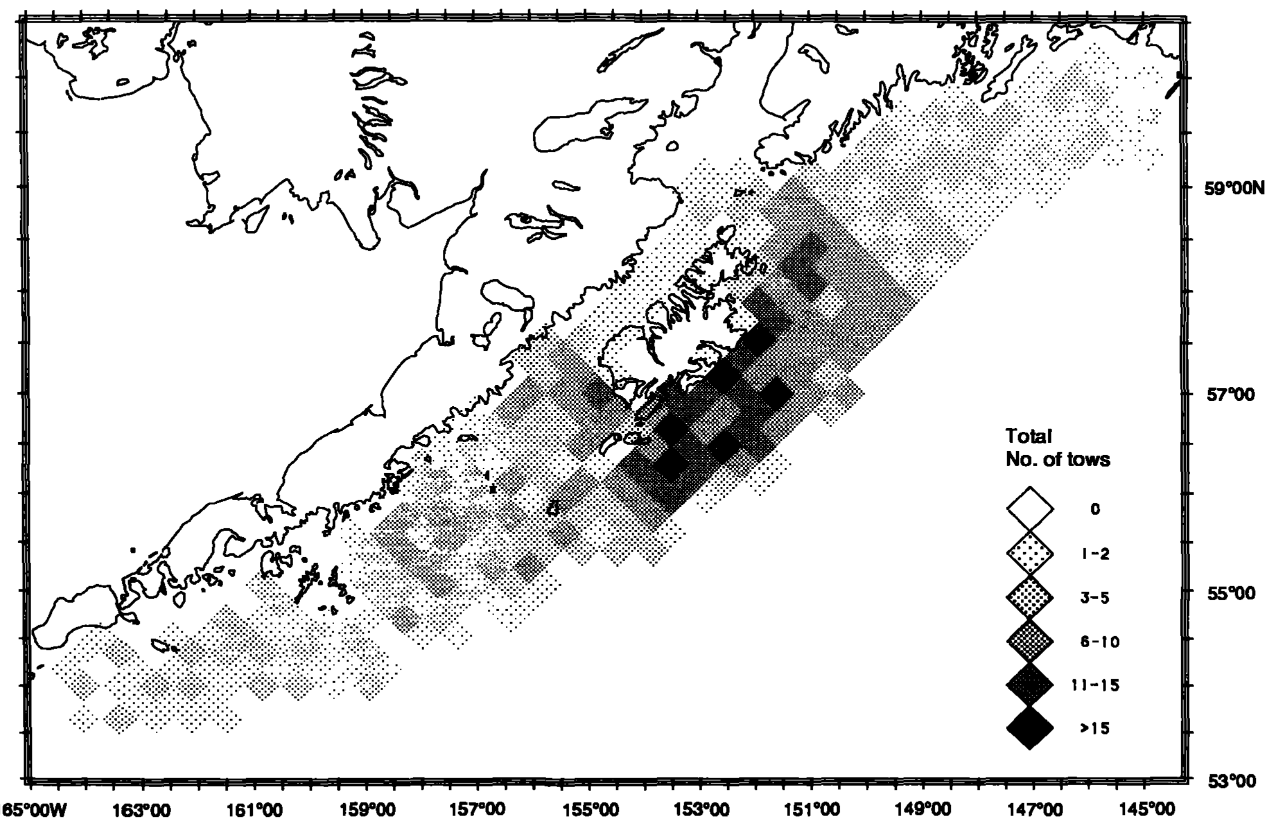


**Figure 2**

Neuston sampling coverage and intensity per sector for all seven cruises combined (1981–86).

abundance in each sector by the total number of stations sampled within that sector.

Cooccurrences of larval fish taxa in the neuston net samples were determined by using recurrent group analysis (Fager, 1957). This analysis identifies groups of taxa that occur together relatively frequently and considers only joint occurrences and not abundance. The procedure involves two steps: the calculation of indices of affinity for each pair of taxa and the formation of groups of taxa based on a chosen minimum index value. The equation for the affinity index is

$$I = \frac{N_j}{\sqrt{N_a N_b}} - \frac{1}{2\sqrt{N_b}},$$

where $I$ = the affinity index (range 0–1);
$N_j$ = the number of joint occurrences;
$N_a$ = the number of occurrences of taxon $a$, the less common taxon;
$N_b$ = the number of occurrences of taxon $b$, the more common taxon.

For this study, minimum index values for the formation of recurrent groups were set at 0.3 and 0.4, respectively, for two separate runs of the analysis. One or both of these values have been chosen previously by other workers who applied this method to ichthyoplankton data (Kendall and Dunn, 1985; Moser et al., 1987).

Numerical classification was used to investigate multispecies spatial patterns among the fish larvae in the neuston. It involves grouping similar entities based on numerical data such as, in this instance, species abundance at a range of stations (Clifford and Stephenson, 1975). An agglomerative, hierarchical technique was chosen. Normal and inverse classifications were carried out on the data sets (i.e. both the species and stations were classified into groups). Only the dominant larval fish taxa occurring in >4% of the samples were included in this analysis, as scarce taxa did not contribute significantly to spatial patterns overall. The numerical classification was performed on each individual data set from the seven neuston cruises, as well as on data combined for all the cruises (i.e. mean abundance of larval fish species in each of the previously chosen geographical sectors). The data were log-transformed prior to analysis.

The first step in the classification procedure comprised the calculation of correlation coefficients for each pair of species or stations in a data set. The Bray-Curtis dissimilarity measure was used. An agglomerative, hierarchical sorting strategy produced dendrograms depicting clusters of stations and species. The "flexible sorting" strategy was used and a recommended value of –0.25 was chosen as the clustering intensity coefficient (Lance and Williams, 1967).

To aid in identification of groups from the dendrograms, the original data sets (species abundance × stations) were rearranged into two-way tables according to the order that species and stations appeared in the dendrograms. In this manner, it was possible to see how a group of stations was characterized by the occurrence or definitive range of abundance of a particular species or group of species. After the final species and station groups were chosen, the two-way tables were reduced by calculating the mean abundance of each species, within the different species groups, for each station group. The station groups were then plotted on maps of the sampling area to aid in the identification of geographically distinct groups of fish larvae.

## Results

### Taxonomic composition and density

A total of 24,327 fish eggs were collected in the neuston samples. Eggs of 12 species representing five families were identified from the samples (Table 2). The numerically dominant taxa included the gadid *Theragra chalcogramma* and several pleuronectids, mainly *Errex zachirus*, *Hippoglossoides elassodon*, *Microstomus pacificus*, and other unidentified Pleuronectidae. *Theragra chalcogramma* was the only taxon whose eggs occurred in greater than 10% of all the samples. Although the density of *Clupea pallasi* eggs was relatively high, this taxon occurred in less than 1% of the samples. It is likely that the presence of these demersal eggs in the neuston was due to clumps of eggs breaking off the substrate and floating to the surface. The low diversity and generally low density of fish eggs in the neuston (relative to the diversity and density of fish larvae) was indicative of the scarcity of species that spawn pelagic eggs in this region.

In total, 41,157 specimens of larvae or early juveniles were caught in the neuston. The taxonomic diversity and overall density were higher than for the eggs (Table 3). Thirty-five species were identified representing a total of 18 families. Apart from *T. chalcogramma* and *Anoplopoma fimbria*, which spawn pelagic eggs close to the bottom, the numerically dominant taxa among the larvae were demersal spawners.

Among the dominant larvae, the families Hexagrammidae and Cottidae were best represented. The

**Table 2**

Summary of all fish eggs collected in neuston gear during spring cruises from 1981 to 1986 in the western Gulf of Alaska.

| Scientific name | Common name | Percent occurrence ($n$=895) | Mean abundance (no./1000m$^3$) |
|---|---|---|---|
| *Clupea pallasi* | Pacific herring | 0.37 | 22.83 |
| *Theragra chalcogramma* | walleye pollock | 28.12 | 205.59 |
| *Sebastalobus* spp. | unidentified thornyhead | 1.39 | 1.04 |
| *Chirolophis nugator* | mosshead warbonnet | 0.09 | 0.03 |
| *Trachipterus altivelis* | king-of-the-salmon | 0.74 | 0.16 |
| *Eopsetta exilis* | slender sole | 0.09 | 0.01 |
| *Errex zachirus* | rex sole | 6.38 | 5.50 |
| *Hippoglossoides elassodon* | flathead sole | 7.12 | 10.69 |
| *Microstomus pacificus* | Dover sole | 5.46 | 33.50 |
| *Platichthys stellatus* | starry flounder | 1.57 | 1.22 |
| *Pleuronectes asper* | yellowfin sole | 0.09 | 0.03 |
| *Pleuronectes isolepis* | butter sole | 0.37 | 0.20 |
| *Pleuronectes quadrituberculatus* | Alaska plaice | 5.83 | 12.67 |
| *Pleuronectes vetulus* | English sole | 0.46 | 0.49 |
| Pleuronectidae | unidentified flounder | 5.83 | 12.67 |
| Teleost Type A | unidentified teleost | 4.07 | 2.07 |
| Teleost Type H | unidentified teleost | 0.09 | 0.01 |

most abundant species by far was the hexagrammid *Hexagrammos decagrammus*, which was present in 71% of all the samples collected and had a mean density of 234 larvae/1,000 m$^3$ (Table 3). Less abundant were the hexagrammids *H. stelleri* and *Pleurogrammus monopterygius*. The category *Hexagrammos* spp. was also numerically important. Many of these larvae were most likely *H. decagrammus*, but the condition of the specimens made specific identification impossible. The most important taxa among the cottids were *Hemilepidotus hemilepidotus*, *H. jordani*, *H. spinosus*, *Hemilepidotus* spp., and *Myoxocephalus* spp. *Hemilepidotus hemilepidotus* was the third most abundant species overall, present in 20% of the samples with a mean density of 60 larvae/1,000 m$^3$. *Ammodytes hexapterus* was the second most abundant taxon with a mean density of 148 larvae/1,000 m$^3$ and was present in 14% of the samples. With a mean density of 43 larvae/1,000 m$^3$, *Cryptacanthodes aleutensis* was ranked as the fourth most abundant larval taxon and it was present in 21% of the samples collected. The remaining larval taxa each were found in less than 10% of the samples and had a mean density of less than 20 larvae/1,000 m$^3$. Most important among these were *Mallotus villosus*, *Theragra chalcogramma*, the hexagrammids and cottids mentioned above, *Bathymaster* spp., and the family Stichaeidae. The rest were scarce, mostly with a mean density of less than 1 larva/1,000 m$^3$ and a percent occurrence of less than 2%.

A comparison of the occurrence of dominant taxa of ichthyoplankton in the neuston samples with their occurrence in bongo samples, and estimates of the fraction of each taxon in the neuston, indicate that most of the dominant larval taxa in the neuston were scarce or absent in the subsurface zone (Table 4). In contrast, the dominant taxa of eggs were the same for both neuston and subsurface samples. *Theragra chalcogramma* eggs were by far the most abundant and accounted for 69% of all eggs caught in the neuston and 95% in the bongo samples. Eggs of pleuronectids, mainly of *Microstomus pacificus*, *Hippoglossoides elassodon*, and *Errex zachirus*, were the only other eggs to be significantly abundant in either gear, again indicating the paucity of pelagic spawners in this region. The estimated fractions ($\theta$) of these eggs occurring in the neuston were moderately high (9–26%) merely showing that positively buoyant eggs tend to accumulate in the surface layer.

The only taxa of larvae well represented in both neuston and bongo samples were *T. chalcogramma*, *A. hexapterus*, and *Bathymaster* spp. (Table 4). All three occurred in much fewer of the neuston net than the bongo net samples, however. In addition, the fractions of these taxa occurring in the neuston were low (<13%) suggesting that they were only occasionally abundant in the neuston. Among the less abundant taxa in the neuston, *Mallotus villosus*, Stichaeidae, *Zaprora silenus*, and *Myoxocephalus* spp. were only slightly better represented in neuston net than in

**Table 3**

Summary of all fish larvae collected in the neuston during spring cruises from 1981 to 1986 in the western Gulf of Alaska.

| Scientific name | Common name | Percent occurrence ($n$=895) | Mean abundance (no./1000m$^3$) |
|---|---|---|---|
| *Mallotus villosus* | capelin | 5.83 | 8.90 |
| Osmeridae | unidentified smelt | 0.09 | 0.03 |
| *Nansenia candida* | bluethroat argentine | 0.09 | 0.01 |
| *Oncorhynchus keta* | chum salmon | 0.09 | 0.01 |
| Bathylagidae | unidentified deepsea smelt | 0.09 | 0.01 |
| *Stenobrachius leucopsarus* | northern lampfish | 0.09 | 0.01 |
| *Gadus macrocephalus* | Pacific cod | 0.65 | 0.15 |
| *Theragra chalcogramma* | walleye pollock | 6.75 | 13.66 |
| Gadidae | unidentified gadid | 0.56 | 0.24 |
| *Sebastes* spp. | unidentified rockfish | 1.67 | 2.68 |
| *Hexagrammos decagrammus* | kelp greenling | 59.11 | 194.84 |
| *Hexagrammos lagocephalus* | rock greenling | 0.46 | 0.09 |
| *Hexagrammos octogrammus* | masked greenling | 1.85 | 0.26 |
| *Hexagrammos stelleri* | whitespotted greenling | 8.14 | 1.87 |
| *Ophiodon elongatus* | lingcod | 1.76 | 0.53 |
| *Pleurogrammus monopterygius* | Atka mackerel | 3.61 | 1.76 |
| *Hexagrammos* spp. | unidentified greenling | 3.52 | 5.94 |
| Hexagrammidae | unidentified greenling | 0.28 | 0.04 |
| *Anoplopoma fimbria* | sablefish | 5.00 | 15.37 |
| *Blepsius bilobus* | crested sculpin | 0.09 | 0.01 |
| *Enophrys bison* | buffalo sculpin | 0.09 | 0.01 |
| *Hemilepidotus hemilepidotus* | red Irish lord | 16.84 | 50.25 |
| *Hemilepidotus jordani* | yellow Irish lord | 5.55 | 3.63 |
| *Hemilepidotus spinosus* | brown Irish lord | 6.38 | 5.80 |
| *Hemilepidotus* spp. | unidentified Irish lord | 3.70 | 5.47 |
| *Leptocottus armatus* | Pacific staghorn sculpin | 0.09 | 0.01 |
| *Myoxocephalus* spp. | unidentified sculpin | 2.59 | 1.04 |
| *Radulinus boleoides* | darter sculpin | 0.09 | 0.01 |
| Cottidae | unidentified sculpin | 0.65 | 0.10 |
| Agonidae | unidentified poacher | 0.28 | 0.04 |
| Cyclopteridae | unidentified snailfish | 0.37 | 0.06 |
| *Bathymaster* spp. | unidentified ronquil | 4.63 | 6.68 |
| *Chirolophis decoratus* | decorated warbonnet | 0.19 | 0.05 |
| *Chirolophis* spp. | unidentified warbonnet | 0.56 | 0.16 |
| *Lumpenella longirostris* | longsnout prickleback | 0.09 | 0.02 |
| Stichaeidae | unidentified stichaeid | 1.57 | 4.90 |
| *Cryptacanthodes aleutensis* | dwarf wrymouth | 17.76 | 36.13 |
| *Cryptacanthodes giganteus* | giant wrymouth | 1.67 | 0.53 |
| *Zaprora silenus* | prowfish | 2.78 | 1.09 |
| *Ammodytes hexapterus* | Pacific sand lance | 11.75 | 123.75 |
| *Atheresthes stomias* | arrowtooth flounder | 0.19 | 0.04 |
| *Errex zachirus* | rex sole | 0.46 | 0.08 |
| *Hippoglossoides elassodon* | flathead sole | 0.93 | 0.15 |
| *Hippoglossus stenolepis* | Pacific halibut | 1.67 | 0.48 |
| *Microstomus pacificus* | Dover sole | 0.09 | 0.01 |
| *Platichthys stellatus* | starry flounder | 0.19 | 0.05 |
| *Pleuronectes bilineatus* | rock sole | 0.56 | 0.12 |
| *Pleuronectes vetulus* | English sole | 0.09 | 0.01 |
| *Psettichthys* spp. | unidentified sole | 0.19 | 0.02 |
| *Reinhardtius hippoglossoides* | Greenland turbot | 1.48 | 0.55 |

**Table 4**

Comparison of percent occurence and percent of total abundance (based on no./1000 m$^3$) of the dominant taxa in the neuston and bongo collections and fraction of each taxon occurring in the neustonic layer ($\theta$). Taxa ranked in order of percent occurrence in neuston.

| | Neuston | | Bongo | | |
|---|---|---|---|---|---|
| Taxa | Percent occurrence | Percent total abundance | Percent occurrence | Percent total abundance | Fraction in neuston |
| **Eggs** | | | | | |
| *Theragra chalcogramma* | 33.85 | 69.40 | 46.90 | 95.10 | 0.013 |
| *Hippoglossoides elassodon* | 8.69 | 3.61 | 21.06 | 0.72 | 0.091 |
| *Errex zachirus* | 7.68 | 1.86 | 18.07 | 0.77 | 0.155 |
| Pleuronectidae | 7.02 | 4.28 | 8.54 | 2.10 | 0.261 |
| *Microstomus pacificus* | 6.57 | 11.31 | 13.08 | 0.87 | 0.209 |
| **Larvae** | | | | | |
| *Hexagrammos decagrammus* | 71.16 | 40.15 | 4.99 | 0.22 | 0.930 |
| *Cryptacanthodes aleutensis* | 21.38 | 7.44 | 3.22 | 0.08 | 0.861 |
| *Hemilepidotus hemilepidotus* | 20.27 | 10.35 | 2.33 | 0.09 | 0.890 |
| *Ammodytes hexapterus* | 14.14 | 25.50 | 73.84 | 29.92 | 0.053 |
| *Hexagrammos stelleri* | 9.80 | 0.79 | 0.11 | <0.01 | 0.989 |
| *Theragra chalcogramma* | 8.13 | 2.82 | 48.78 | 46.05 | 0.009 |
| *Hemilepidotus spinosus* | 7.68 | 1.19 | 0.55 | 0.01 | 0.932 |
| *Mallotus villosus* | 7.02 | 1.83 | 5.10 | 0.18 | 0.568 |
| *Hemilepidotus jordani* | 6.68 | 0.75 | 0.00 | 0.00 | 1.000 |
| *Anoplopoma fimbria* | 6.01 | 3.17 | 2.33 | 0.04 | 0.689 |
| Stichaeidae | 5.79 | 0.32 | 2.33 | 0.10 | 0.728 |
| *Bathymaster* spp. | 5.57 | 1.38 | 17.74 | 6.47 | 0.121 |
| *Hemilepidotus* spp. | 4.45 | 1.13 | 2.33 | 0.04 | 0.638 |
| *Pleurogrammus monopterygius* | 4.34 | 0.38 | 0.11 | <0.01 | 0.974 |
| *Hexagrammos* spp. | 4.23 | 1.22 | 0.00 | 0.00 | 1.000 |
| *Zaprora silenus* | 3.34 | 0.22 | 2.55 | 0.05 | 0.541 |
| *Myoxocephalus* spp. | 3.12 | 0.22 | 1.88 | 0.08 | 0.596 |

bongo net samples perhaps also reflecting a facultative association with the neuston (i.e. concentrated at the surface only during certain hours). However, the high (54–73%) fraction occurring in the neuston suggests a strong association by these species with the surface zone.

The remaining dominant taxa of larvae in the neuston were absent or scarce in the bongo samples and all except *Hemilepidotus* spp. had a $\theta$ value of >85% (Table 4). It seems that their association with the neuston was obligative (i.e. permanent presence in the surface zone). These obligative taxa included the hexagrammids and cottids as well as *Cryptacanthodes aleutensis* and *Anoplopoma fimbria*. They formed a unique community of fish larvae in the neustonic realm.

Most of the dominant taxa of fish larvae that inhabit the subsurface zone of the western Gulf of Alaska were absent or rare in the neuston, including *Gadus macrocephalus* and *Sebastes* spp., and species of Bathylagidae, Myctophidae, Cyclopteridae, Agonidae, and Pleuronectidae (Kendall and Dunn, 1985; Rugen[3]).

## Diel variation in catches of larvae

To examine diel variation in catches of larvae for both the neuston and bongo samplers, stations were grouped by hour of the day, and mean densities of larvae for each of the 24 hours were calculated. Because of the substantial variability in day length over the 3-month sampling period, it was not possible to assign a specific sunrise and sunset time that could be used for all cruises. For the purposes of this analysis, we assumed that the daytime period lasted from 0700 to 1900 hr and the nighttime from 2200 to 0400 hr. The intervening periods of 0400 to 0700 h and 1900 to 2200 h were presumed to have been twilight, including dawn and dusk, respectively.

For all neuston catches combined, both the total mean density and the number of hauls in which larvae were caught were higher at night than during the day (Fig. 3A). This pattern was not apparent for the bongo catches taken from the same stations (Fig. 3B). Some of the highest catches of larvae in the bongo samples were taken during daylight. The ratio of night:day catches for the neuston was 9.1:1, whereas it was 1.6:1 for the bongo tows. The high ratio of night:day catches in the neuston may be attributed to two factors: 1) vertical migration of larvae into the neuston at night and 2) enhanced avoidance of the neuston sampler during daylight. One or both of these factors may operate among the species of larvae in the neuston.

Diel variation in catches among all the dominant taxa of neustonic larvae suggested a daytime decrease in density in the neuston. All larvae, except *Hexagrammos decagrammus* and *Theragra chalcogramma*, had lowest occurrences in neuston samples during the day (Fig. 4). Sampler avoidance by the larvae during daylight probably contributed significantly to this pattern. The taxa *Hemilepidotus jordani*, *H. spinosus*, *Myoxocephalus* spp., *Bathymaster* spp., and *Zaprora silenus* were absent from neuston samples during most daylight hours but were relatively abundant in twilight or nighttime samples. Because the latter three of these taxa were relatively common in bongo samples (Table 4), indicating a facultative association with the neuston, their scarcity in the neuston during the day may have been at least in part due to a diel pattern of vertical migration with larvae moving toward the surface zone at night. This may have also been true for *T. chalcogramma* and *Ammodytes hexapterus* whose larvae were extremely abundant in the bongo net samples (Table 4) but abundant in the neuston samples only at night (Fig. 4). *Mallotus villosus* larvae were also relatively common in bongo samples (Table 4), although they were most abundant in the neuston at night (Fig. 4).

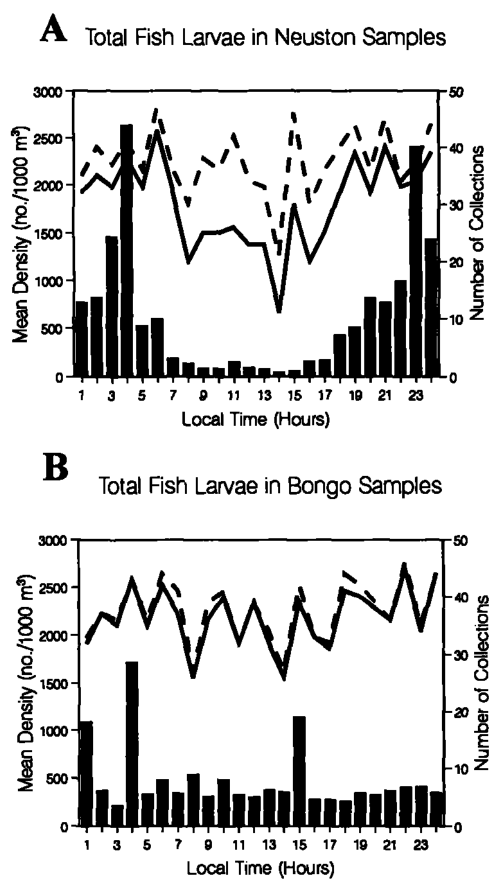


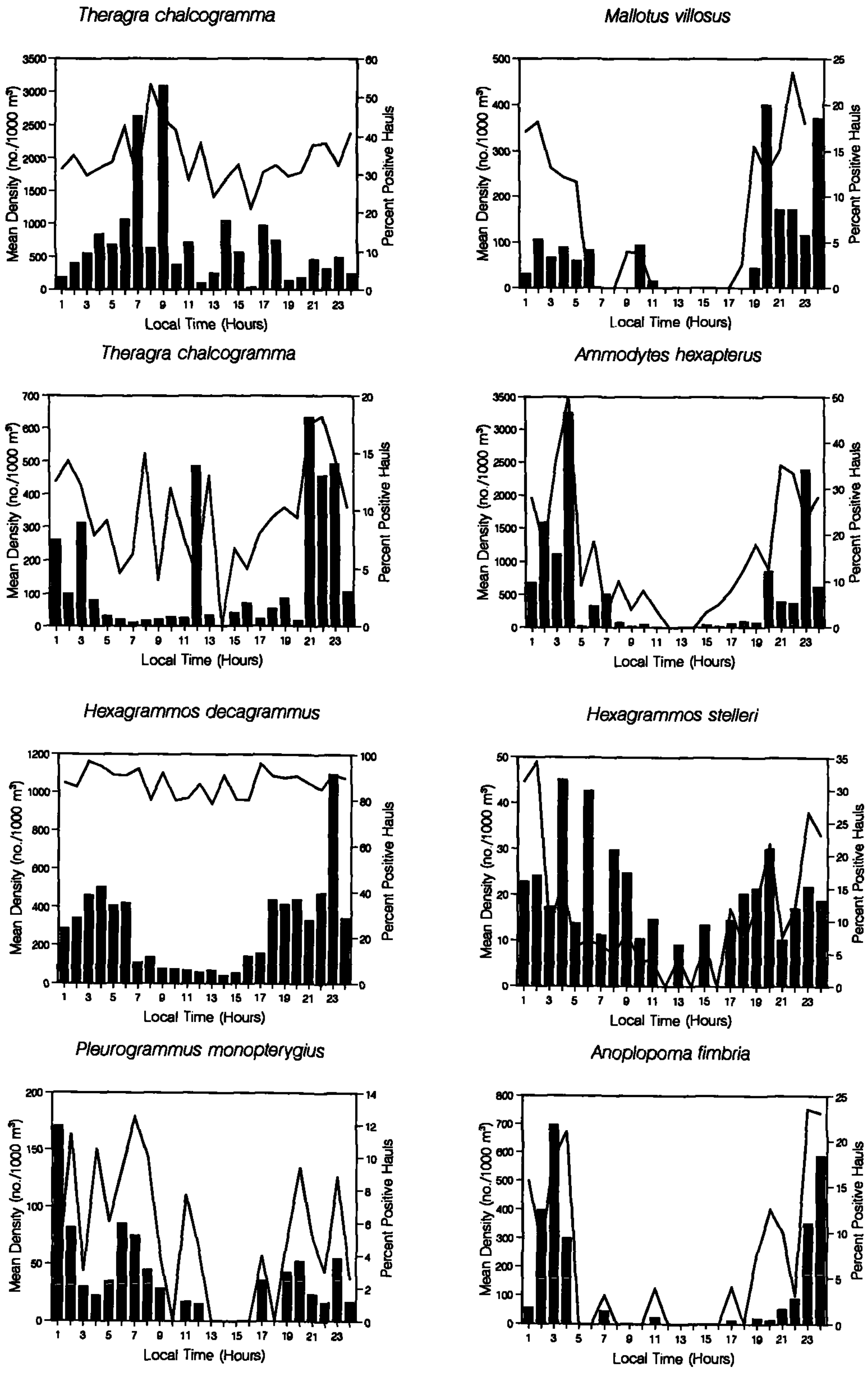
**Figure 3**

Diel variation in density and occurrence of total fish larvae in (**A**) neuston samples and (**B**) bongo samples for all cruises combined (1981–86). Bars represent mean density of fish larvae; dashed line represents total number of collections; solid line represents the number of hauls that collected fish larvae.

As expected, catches of *T. chalcogramma* eggs showed no discernable diel variation in either density or frequency of positive hauls. The large mean densities during two periods of the day are most likely due to spatial variation of egg densities rather than to any biological factor.

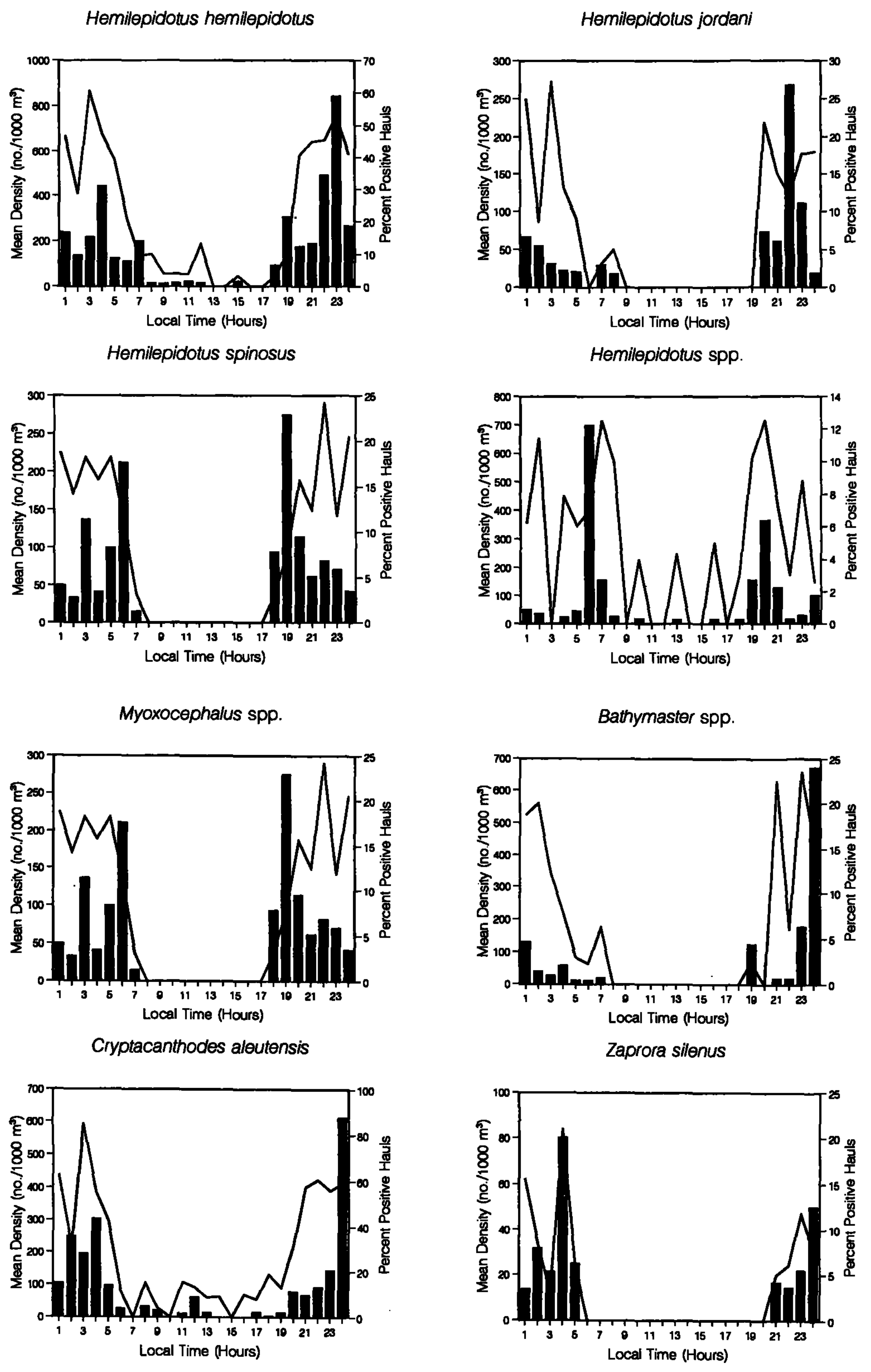
## Length distributions of dominant neustonic taxa

Standardized length distributions were plotted for the dominant neustonic taxa (Fig. 5). Comparisons were made with the corresponding length distributions of larvae in the subsurface zone for six of these taxa that were sufficiently represented in the bongo samples. For all these six taxa, greater median lengths were documented for larvae in the neuston than in the bongo hauls, especially in the case of *Mallotus villosus* and *Ammodytes hexapterus*. *Mallotus villosus* seemed unusual in that all larvae caught in both neuston and bongo net samples were >25 mm SL indicating a predominance of postflexion larvae. This is most likely due to species identification capabilities, as it is not possible to identify small osmerids to species until the pectoral fin rays are completely developed. With the exception of *Bathymaster* spp., the larvae caught in the neuston were also significantly larger than those caught in the bongo collections (Kolmogorov-Smirnov (*K-S*) 2-sample tests; all $P<0.01$). For *A. hexapterus*, it seemed that only the large postflexion larvae and early juveniles (mostly >20 mm SL) migrated into the neuston, mainly at night; most *A. hexapterus* larvae



## Figure 4

Diel variation in density and occurrence of walleye pollock, *Theragra chalcogramma*, eggs and individual dominant taxa of fish larvae in neuston samples, for all cruises combined (1981–86). Bars represent mean density; solid line represents the percent of hauls that caught larvae.



*Hemilepidotus hemilepidotus*

*Hemilepidotus jordani*

*Hemilepidotus spinosus*

*Hemilepidotus* spp.

*Myoxocephalus* spp.

*Bathymaster* spp.

*Cryptacanthodes aleutensis*

*Zaprora silenus*

**Figure 4 (continued)**

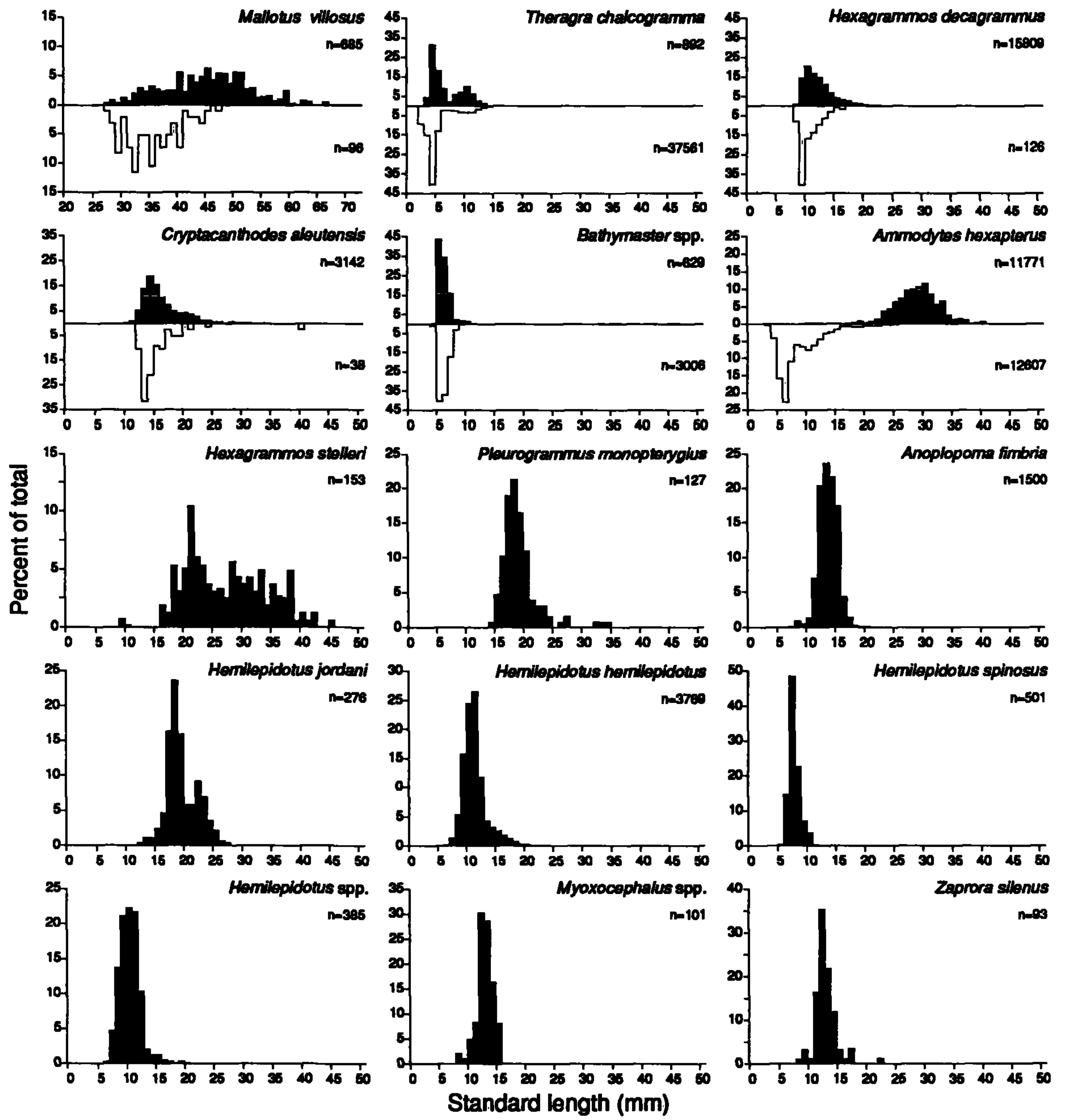


**Figure 5**

Length-frequency distributions for the dominant taxa of fish larvae in neuston samples and, where comparable, in bongo samples (open histograms), for all cruises combined (1981–86).

caught in the bongo samples were <15 mm SL. In contrast, larvae of *Bathymaster* spp. that were common in the neuston at night did not differ significantly in size from those occurring in the bongo samples; all were small, mostly <10 mm SL. *Theragra chalcogramma* larvae were also relatively small (all <15 mm but mostly <10 mm SL) both in bongo and neuston catches.

Among the remaining neustonic taxa, most larvae caught were >10 mm SL, and length distributions generally displayed one dominant mode within a relatively short length interval. The predominant length range for the taxa *Hexagrammos decagrammus*, *Cryptacanthodes aleutensis*, *Anoplopoma fimbria*, *Hemilepidotus hemilepidotus*, *Myoxocephalus* spp., and *Zaprora silenus* was 10–20 mm. *Hexagrammos stelleri*, *Pleurogrammus monopterygius*, and *Hemilepidotus jordani* larvae were larger with predominant length ranges of 15–40 mm, 15–25 mm, and 15–30 mm, respectively. In contrast, larval sizes for the cottids, *Hemilepidotus spinosus* and *Hemilepidotus* spp., were relatively small with a predominant length range of 5–15 mm.

Daytime catches of larvae in the neuston were sufficient to make diel comparisons in length distributions for only three of the dominant taxa. There was no significant day-night difference in the length distribution of *Hexagrammos decagrammus* larvae (*K-S* test; $Z$=0.07, $P$>0.05). *Theragra chalcogramma* larvae caught at night (median length=6 mm) were slightly, but significantly, larger (*K-S* test; $Z$=1.52, $P$=0.02) than those caught during the day (median length=5 mm). Day-night differences were much greater for *Ammodytes hexapterus* larvae for which the median length caught at night was 24 mm and the median day length was 13 mm (*K-S* test; $Z$=4.99, $P$<0.001). Migration of the larger larvae and juveniles to the surface at night may have been the cause of this difference, but it is also likely that enhanced sampler avoidance during daylight by large larvae and juveniles reduced the daytime median larval length significantly.

## Horizontal patterns of distribution

Patterns of distribution illustrated here for total and individual dominant taxa of neustonic larvae were based on data combined for all cruises. The distribution maps therefore represent general patterns of horizontal distribution for these species during spring in this region and did not take into account day-night, monthly, or interannual differences in catches.

The pattern for total fish larvae in the neuston indicated that highest concentrations generally occurred to the southwest of Kodiak Island, in Shelikof Strait, and off the northern tip of Kodiak Island (Fig. 6A). Southwest of the Shumagin Islands and northeast of Kodiak Island, high densities of larvae were more scattered. Despite the high intensity of sampling seaward of Kodiak Island (Fig. 2), mean larval concentrations tended to be low in this region. Based on data which incorporated sampling during all seasons, Kendall and Dunn (1985) and Rugen[3] frequently recorded high concentrations of various species of larvae in the neuston seaward of Kodiak Island. The apparent scarcity of larvae here may therefore be characteristic of spring in the sampling area.

Larvae of the osmerid *Mallotus villosus* were taken primarily southwest of Kodiak Island along the Alaska Peninsula as far southwest as the Shumagin Islands (Fig. 6b). They were scarce southwest of the Shumagin Islands and seaward of Kodiak Island and absent in the northeastern part of the sampling area. This pattern is similar to that described by Rugen[3] except that the latter study plus Kendall and Dunn's (1985) observations indicated a greater presence of larvae seaward of Kodiak Island. These studies also showed that *M. villotus* larvae were relatively scarce both in bongo and neuston samples during spring; the main spawning season seems to be late summer through fall (Kendall and Dunn, 1985).

*Theragra chalcogramma* larvae were usually most abundant in the upper 50 m of the water column in the southern Shelikof Strait area and along the Alaska Peninsula during spring (Schumacher and Kendall, 1991). Spawning takes place primarily in the sea valley in Shelikof Strait during late March and early April. Rugen[3] has also documented the occurrence of pollock larvae on occasions in large concentrations to the northeast of Kodiak Island. These patterns were reflected in the distribution of pollock larvae in the neuston documented during the present study (Fig. 6C). The scarcity of larvae within Shelikof Strait may have been due to the low number of samples from that region. Pollock larvae were absent or scarce along the outer shelf and slope indicating that most of the larvae in the surface zone were retained on the shelf.

Neustonic larvae of *Anoplopoma fimbria* were most abundant during late spring and summer in the western Gulf of Alaska where they were associated with the shelf edge (Kendall and Dunn, 1985; Rugen[3]). The general distribution pattern documented here for the spring months showed them to be most abundant close to the shelf edge southwest and northeast of Kodiak Island, as well as around the northern and northwestern perimeter of Kodiak Island (Fig. 6D). As with pollock, this species is a pelagic spawner in deep water, and the distribution pattern of larvae suggested that spawning occurred mainly in outer shelf and slope waters, a pattern which is consistent with what is known about the early life history of this species (Kendall and Matarese, 1987; Doyle, 1992).

The dominant hexagrammid species whose larvae were abundant in the neuston of the sampling area all spawn in coastal waters (Matarese et al., 1989). In the Gulf of Alaska region, spawning of these species seems to occur from fall through spring (Kendall and Dunn, 1985; Rugen[3]). Larvae of the most abundant species, *Hexagrammos decagrammus*, were found to be dominant in the neuston during most of the year; during the summer months there was a large decrease in density. They were distributed widely throughout the sampling area, but greater concentrations were found in the southwestern re-

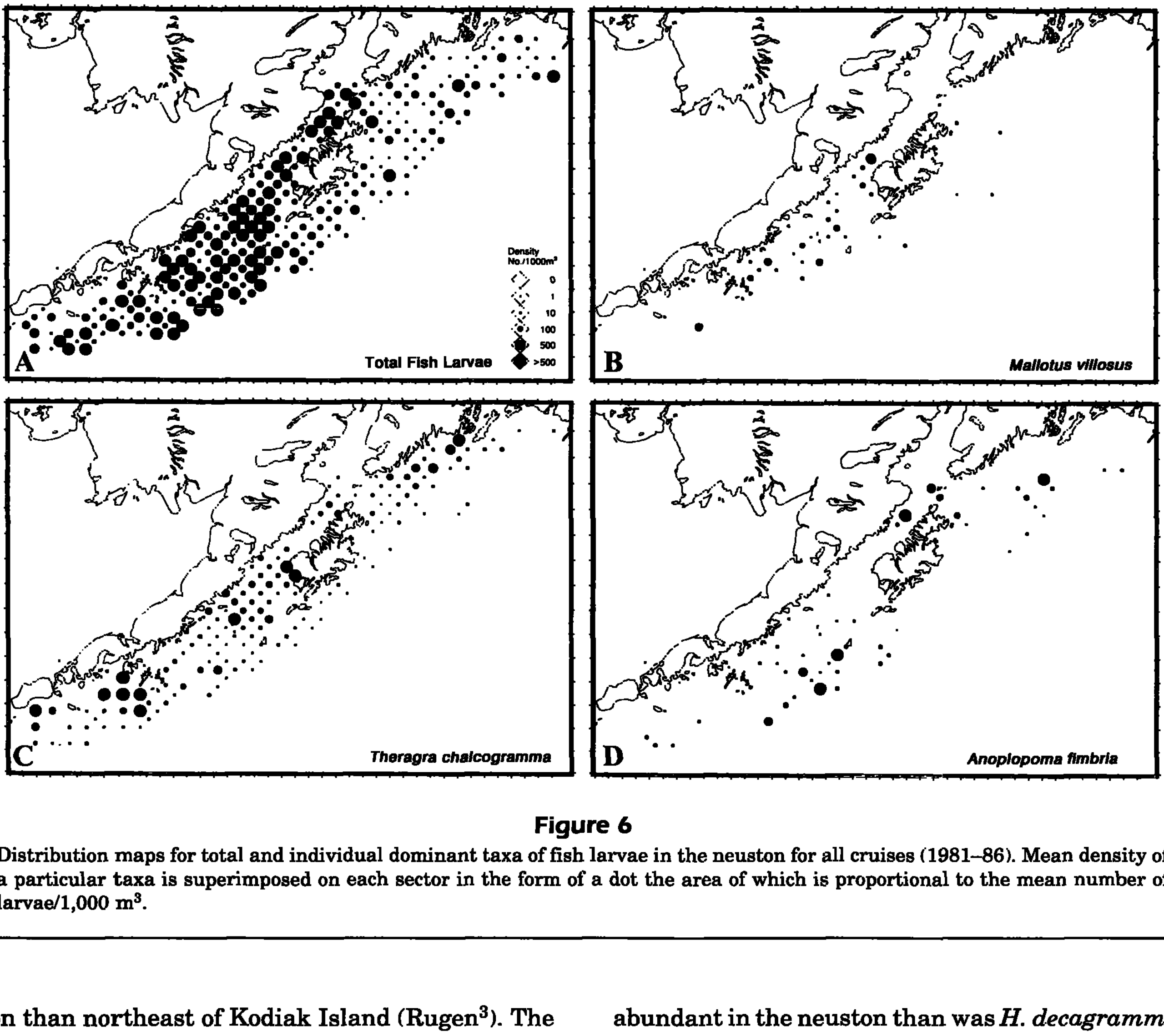


**Figure 6**

Distribution maps for total and individual dominant taxa of fish larvae in the neuston for all cruises (1981–86). Mean density of a particular taxa is superimposed on each sector in the form of a dot the area of which is proportional to the mean number of larvae/1,000 m$^3$.

gion than northeast of Kodiak Island (Rugen[3]). The same pattern was apparent from the spring data presented here (Fig. 6E). Larvae were most abundant to the north of Kodiak Island and to the southwest beyond the Shumagin Islands, whereas densities were lowest to the northeast and offshore of Kodiak Island. Kendall and Dunn (1985) documented widespread distribution around Kodiak Island but mainly at nearshore and midshelf stations early in the spawning season during fall. Advection of larvae in the neuston is probably extensive throughout winter and spring months in this region. Patterns in seasonal occurrence and spatial distribution of *H. stelleri* larvae were similar to those for *H. decagrammus* (Fig. 6F), and as found in previous studies (Kendall and Dunn, 1985; Rugen[3]), densities were much lower than those for *H. decagrammus*.

The third dominant hexagrammid species, *Pleurogrammus monopterygius*, was also considerably less abundant in the neuston than was *H. decagrammus*. Although the spawning season appears to extend from fall through spring, maximum densities of these larvae have been recorded during late October in the Kodiak Island region (Kendall and Dunn, 1985). The distribution of *P. monopterygius* larvae during the spring months of the present study extended from the Kodiak Island region southwest to the Shumagin Island area; most records were in the vicinity of the shelf edge from Kodiak Island to the Shumagin Islands (Fig. 6G). Kendall and Dunn (1985) and Rugen[3] also recorded highest densities of these larvae over the outer shelf and slope in the Kodiak Island region. The former authors also documented fingers of occurrence of these larvae extending shoreward associated with the troughs seaward of Kodiak Island. Although the larvae of this species usually display an offshore and oceanic distribution, spawning is known to take place in shallow water where currents

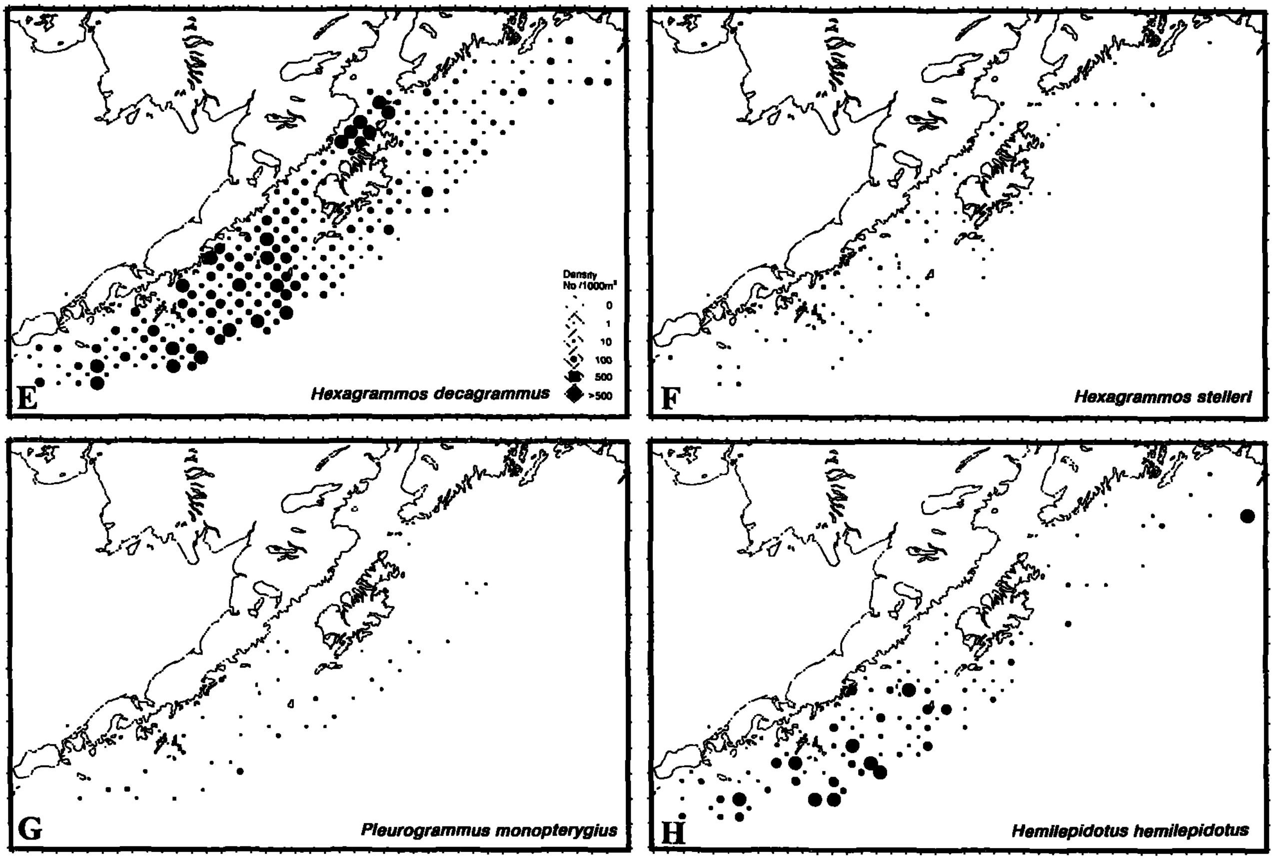


**Figure 6 (continued)**

are strong, primarily at 10–30 m depth, following an onshore migration by the mature adult fish during summer (Gorbunova, 1962; Macy et al.[5]). Gorbunova (1962) describes the oceanic occurrence of *P. monopterygius* larvae in the Pacific Ocean and Bering Sea and suggests that they migrate out to sea after hatching in shallow water, thus explaining the primarily offshore distribution pattern observed for these larvae.

The predominant cottid species in the sampling area were members of the genus *Hemilepidotus*. As with the hexagrammids, these species are inshore coastal dwellers that spawn demersal eggs and have neustonic larvae (Matarese et al., 1989). In the study area, spawning seems to occur from fall through spring; peak densities of larvae occur in the neuston during fall (Kendall and Dunn, 1985). The most abundant cottid recorded during the present study was *H. hemilepidotus*. Highest densities of this species occurred to the southwest of Kodiak Island, extended beyond the Shumagin Islands, and had a tendency to be associated with the mid- to outer-shelf region (Fig. 6H). Larvae were scarce northeast of Kodiak Island. The same pattern of distribution was observed for this species by Rugen[3] from samples taken during all seasons. The less abundant *H. jordani* displayed a similar distribution pattern (Fig. 6I) as did *Hemilepidotus* spp. (Fig. 6K). *Hemilepidotus spinosus*, however, had a more northerly distribution. Most larvae were caught northeast of Kodiak Island (Fig. 6J), suggesting that this is the main spawning area for this species.

Kendall and Dunn (1985) found larvae of the cottid *Myoxocephalus* spp. to be most abundant during summer to the south of Kodiak Island. The samples from the present study yielded low numbers of these larvae; when present they were found in the mid-shelf region

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[5] Macy, P. T., J. M. Wall, N. D. Lampsakis, and J. E. Mason. 1978. Resources of the non-salmonid pelagic fishes of the Gulf of Alaska and eastern Bering Sea. Part 1: Introduction, general fish resources and fisheries, and review of literature on non-salmonic pelagic fish resources. Part of Final Report for Contracts R7120811 and R7120812, Task A-7, Research Unit 64/354, Outer Continental Shelf Environment Assessment Program, U.S. Dep. Interior, Bureau of Land Management, 355 p.

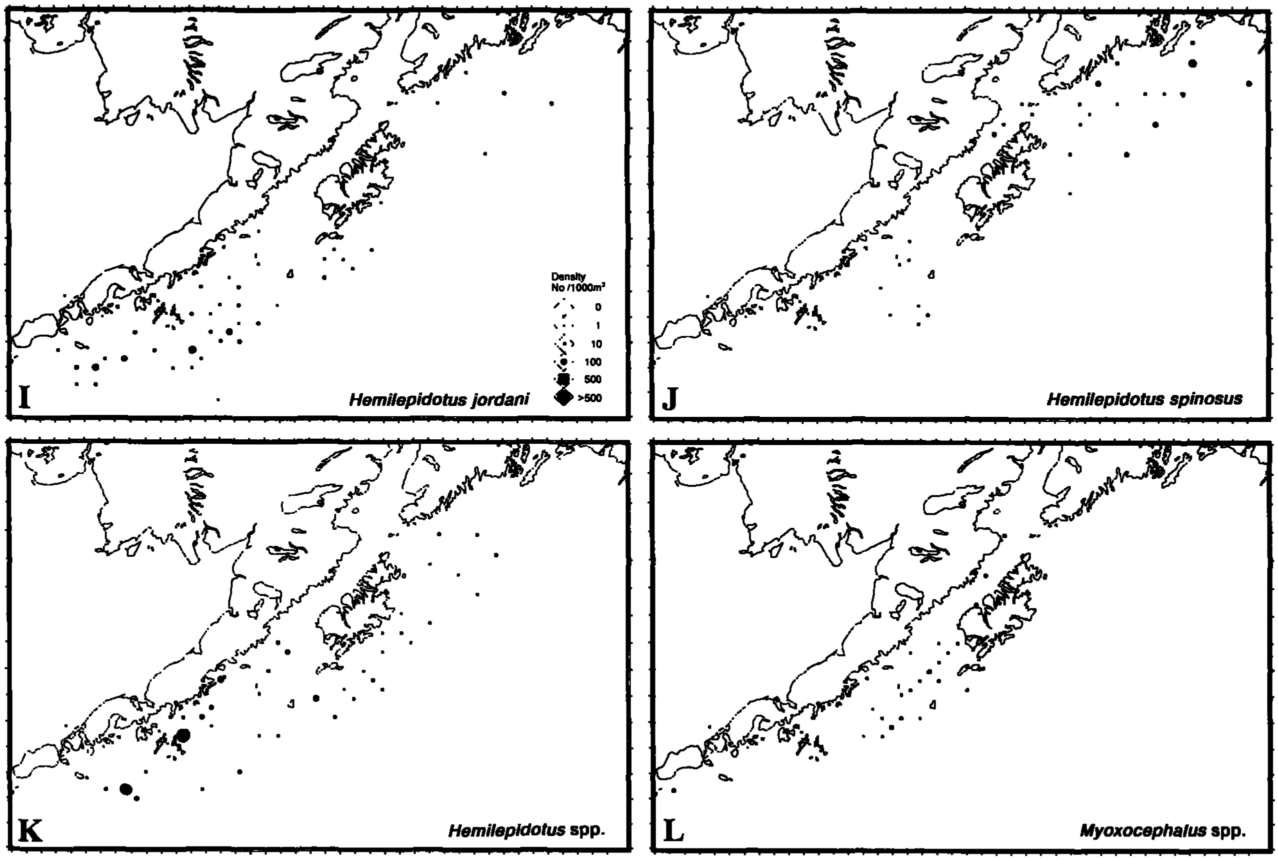

Figure 6 (continued)

between Kodiak Island and the Shumagin Islands (Fig. 6L). Spawning may be centered in this region.

Three species of bathymasterids belonging to the genus *Bathymaster* are known to occur in the sampling area: *B. caeruleofasciatus*, *B. leurolepis*, and *B. signatus* (Rogers et al., 1979; Rugen[3]). They are coastal demersal spawners. At the larval stage, it is not possible to identify these to species and they are included here in the taxon *Bathymaster* spp. The distribution of these larvae during spring was centered southwest of Kodiak Island (Fig. 6M) suggesting that this may be a primary spawning area. Occurrences were scarce northeast of Kodiak Island and southwest of the Shumagin Islands. It seems, however, that spring is a period when *Bathymaster* larvae are relatively scarce in the neuston. Previous studies have found these larvae to be most abundant in subsurface samples from May to October with a peak in summer (Kendall and Dunn, 1985; Rugen[3]). In the neuston, however, larvae did not become abundant until late June. Although Rugen[3] found *Bathymaster* larvae to be most abundant from Kodiak Island to the Shumagin Islands, he also found them to be abundant seaward of Kodiak Island, particularly during the summer, as did Kendall and Dunn (1985). There may be a northeasterly progression in spawning activity in the sampling area from spring to summer.

The wrymouth *Cryptacanthodes aleutensis* is epi- and meso-benthic in shelf and slope waters and spawns demersal eggs during spring and summer (Matarese et al., 1989). Larvae are associated mainly with the neuston (Kendall and Dunn, 1985; Doyle, 1992; Rugen[3]). The distribution of *C. aleutensis* larvae during the spring months of the present study was associated primarily with Kodiak Island and southwest to the Shumagin Islands (Fig. 6N), similar to that documented by Rugen.[3] Densities were higher in the inner- and mid-shelf region than along the shelf edge and slope.

The Pacific sand lance, *Ammodytes hexapterus*, is a pelagic, schooling species common to coastal and shelf waters and it spawns demersal eggs. Its larvae have been found to be facultative members of the neuston along the U.S. west coast where the well-

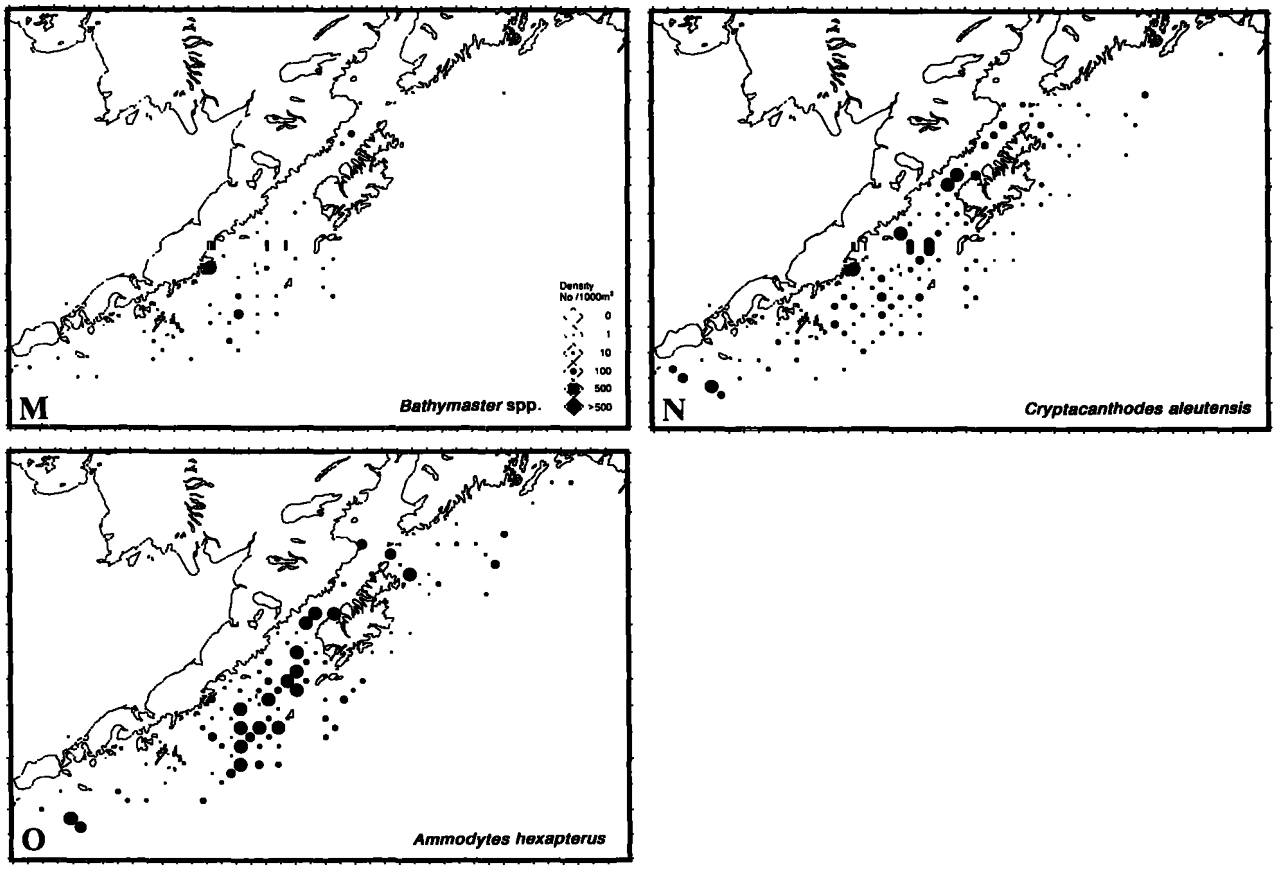

**Figure 6 (continued)**

developed larvae are abundant in the neuston mainly at night (Doyle, 1992). They are common in the neuston and subsurface zone in the western Gulf of Alaska from winter to summer (Kendall and Dunn, 1985; Rugen[3]). Mean larval lengths tended to be greater in the neuston, however, and densities were highest in the neuston during late spring and summer. As with many of the other species, *A. hexapterus* larvae were most abundant during spring in the mid-shelf area from southern Kodiak Island to the Shumagin Islands (Fig. 6O). They were scarce to the northeast and seaward of Kodiak Island and southwest of the Shumagin Islands. Kendall and Dunn (1985) and Rugen[3] found them to be more widely distributed in subsurface samples, including high numbers northeast and seaward of Kodiak Island, implying that spawning is widespread throughout the sampling area.

## Multispecies spatial patterns

Three recurrent groups of larval fish taxa were identified by using Recurrent Group Analysis on data from all cruises (Fig. 7). Constituent members of these groups displayed affinity levels of ≥0.4 with each other. Individual species from these groups were also associated with individual species from other groups, or from outside the groups, at affinity levels of ≥0.3 or ≥0.4.

The largest group contained four taxa, *Cryptacanthodes aleutensis*, *Hemilepidotus hemilepidotus*, *Mallotus villotus*, and Stichaeidae, which frequently occurred together in the same samples. A second group comprising *Ammodytes hexapterus* and *Hexagrammos decagrammus*, the two most abundant larval species in the neuston, was connected to Group 1 via individual linkages among all taxa except Stichaeidae. The result, two groups and their associated weak linkages, suggested the existence of a loosely affiliated assemblage of larval species in the neuston for this region.

*Pleurogrammus monopterygius* and *Hemilepidotus* spp. belonged to a third recurrent group which did not display any linkages with other species or groups of species. This may reflect the unusual association

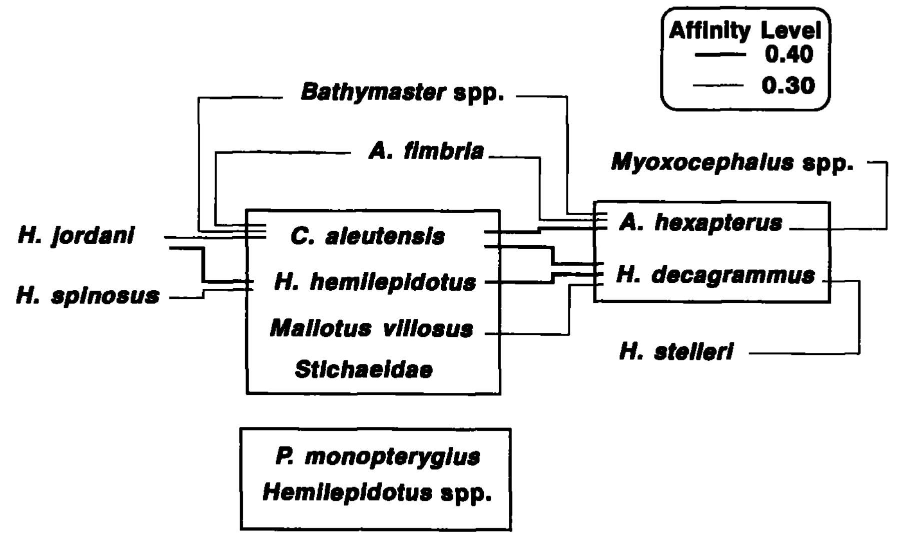

**Figure 7**

Results of recurrent group analysis on neuston data (larvae) for all cruises (1981–86). Boxes enclose members of recurrent groups that have affinity levels of 0.4 or higher with each other. Lines connect taxa with affinities outside their groups.

of *P. monopterygius* larvae with the outer shelf and slope particularly off Kodiak. *Hemilepidotus* spp. had a similar pattern of distribution.

Two species which were included in the analysis, but did not display significant affinities with any of the other taxa, were *Theragra chalcogramma* and *Zaprora silenus*. It seemed that at least in the neuston, *T. chalcogramma,* which is the dominant larval taxon in this region, had a unique pattern of occurrence, largely dissimilar to the other neustonic larvae. The lack of affinity of *Z. silenus* with other species was probably due to its infrequent occurrence in these samples.

Kendall and Dunn (1985) and Rugen[3] found a variety of recurrent groups and inter-species linkages among the neustonic fish larvae in the western Gulf of Alaska over four seasons. The species groups and affinities changed seasonally and were inconsistent among two-week sampling periods. Similar to the results presented here, *T. chalcogramma* did not occur among the recurrent groups or associated linkages of species identified in these studies.

Five species groups and eight sector groups (sectors= sampling sectors in Fig. 2) were identified from the agglomerative hierarchical classification of data combined for all the cruises (Table 5). The Bray-Curtis dissimilarity coefficient values at which these groups were formed were high (minimum value of 0.63), particularly among the sector groups. These indicated that the groupings were weak and that species were only loosely affiliated with each other in terms of density and distribution patterns.

The distribution of the eight sector groups seemed random (Fig. 8) but displayed certain geographical trends which reflected a variety of distribution pat-

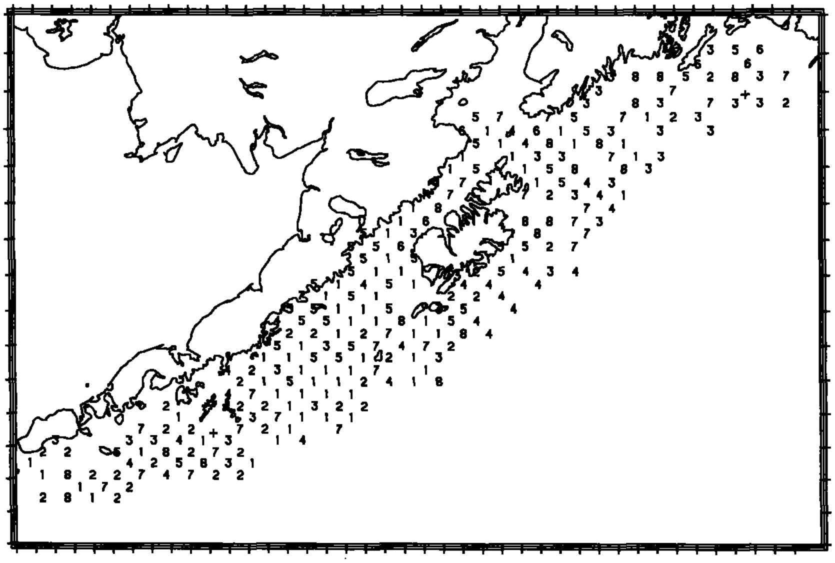

**Figure 8**

Distribution of sector groups resulting from numerical classification of density data for the dominant taxa of fish larvae in the neuston, based on all cruises (1981–86). A plus sign (+) indicates that no fish larvae were caught in that sector.

terns among the larval species. Groups 1 and 2 together were characterized by highest densities of most species (Table 5); these sectors were located primarily around Kodiak Island and particularly in the region between Kodiak Island and the Shumagin Islands to the southwest. Total larval abundance was very low in Group–3 sectors (Table 5) which were concentrated mainly to the northeast of Kodiak Island and to a lesser extent around the Shumagin Islands. Group–4 sectors displayed an offshore distributional trend, mainly seaward of Kodiak Island. Larval abundance was moderately high for this group, enhanced by highest mean density of *Hemilepidotus* spp. and *Pleurogrammus monopterygius* (Table 5). Most of the sectors in Group 5 were distributed close to Kodiak Island, and the coastal half of the region immediately southwest of Kodiak, along the Alaska Peninsula. Mean larval density was also moderately high for this group; *Theragra chalcogramma*, *Hexagrammos decagrammus*, and *Ammodytes hexapterus* were the predominant species. Group 6 included only eight sectors, five of which occurred close to Kodiak Island and three in the northeastern extremity of the sampling area. Mean densities of *T. chalcogramma* and *A. hexapterus* were highest for this group (Table 5) owing to their occurrence in extremely high numbers in one of the sectors (different one for each species) along the southern half of Kodiak Island (Fig. 5). *Hexagrammos decagrammus* was the only species to occur in sectors belonging to Groups 7 and 8 (Table 5) which were scattered randomly throughout the sampling area. This species was unusual in that its distribution was widespread in contrast with the other taxa that were confined primarily to two or three of the sector groups.

## Discussion

Our results indicated that species diversity and density of fish eggs in shelf waters in the western Gulf of Alaska were essentially the same in the surface and subsurface zone. *Theragra chalcogramma* eggs were exceptionally abundant and, along with eggs of several pleuronectid species, accounted for >90% of all eggs taken in both bongo and neuston samples. Except for *T. chalcogramma*, pelagic eggs tended to be scarce in the neuston where the predominant mode of spawning among fish species is demersal (Kendall

**Table 5**

Two-way coincidence table showing mean density (no./1000 m$^3$) of dominant larval species among sector groups. Numbers in parentheses are dissimilarity coefficient values at which the groups were formed. Values are >1 in certain instances owing to use of the flexible sorting strategy in combining the entities into groups.

| | | Sector groups | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species groups | | 1<br>(1.35) | 2<br>(1.05) | 3<br>(1.67) | 4<br>(1.40) | 5<br>(1.42) | 6<br>(1.29) | 7<br>(0.95) | 8<br>(0.79) |
| 1 | *Hexagrammos stelleri* | 2.9 | 0.8 | 1.8 | 4.1 | 0.8 | 1.4 | 0.0 | 0.0 |
| (0.63) | *Hemilepidotus jordani* | 3.7 | 14.6 | 0.8 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Bathymaster* spp. | 65.4 | 0.1 | 0.0 | 0.6 | 0.0 | 1.4 | 0.0 | 0.0 |
| | *Cryptacanthodes aleutensis* | 171.2 | 18.6 | 1.7 | 0.3 | 2.0 | 45.6 | 0.0 | 0.0 |
| 2 | *Anoplopoma fimbira* | 85.4 | 1.3 | 3.6 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| (0.76) | *Hemilepidotus* spp. | 1.9 | 14.2 | 0.2 | 48.7 | 0.8 | 0.1 | 0.0 | 0.0 |
| | *Hemilepidotus spinosus* | 2.2 | 7.6 | 6.7 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| 3 | *Mallotus villosus* | 18.6 | 15.0 | 0.0 | 6.3 | 1.0 | 0.0 | 0.0 | 0.0 |
| (0.79) | *Pleurogrammus monopterygius* | 1.3 | 2.5 | 0.0 | 13.6 | 0.1 | 0.0 | 0.0 | 0.0 |
| | *Theragra chalcogramma* | 22.3 | 0.6 | 0.2 | 0.8 | 53.3 | 298.1 | 0.0 | 0.0 |
| 4 | *Hexagrammos* spp. | 2.9 | 0.7 | 4.1 | 0.2 | 0.3 | 0.0 | 0.0 | 0.0 |
| (0.98) | *Hemilepidotus hemilepidotus* | 55.3 | 291.1 | 2.3 | 22.7 | 1.2 | 0.0 | 0.1 | 0.0 |
| | *Sebastes* spp. | 7.0 | 1.0 | 0.0 | 0.0 | 0.0 | 2.1 | 0.0 | 0.0 |
| 5 | *Hexagrammos decagrammus* | 233.3 | 303.8 | 32.6 | 105.7 | 91.4 | 0.0 | 93.0 | 6.5 |
| (0.90) | *Ammodytes hexapterus* | 411.5 | 3.2 | 0.5 | 0.2 | 19.8 | 441.1 | 0.0 | 0.0 |
| | Total (dominant taxa) | 1084.9 | 675.1 | 54.5 | 206.5 | 170.7 | 789.8 | 93.1 | 6.5 |

and Dunn, 1985). In this region, fish eggs in the neuston could be considered strays because their accumulation at the surface may be attributed to their positive buoyancy rather than to the deposition of eggs in this zone. A similar conclusion has been made regarding the occurrence of fish eggs in the neuston of shelf and oceanic waters off Washington, Oregon, and northern California (Doyle, 1992).

In contrast, a unique group of larval fish appeared to be associated with the neuston in the western Gulf of Alaska, and most of the dominant taxa were scarce or absent in the subsurface zone. The dominance of hexagrammids, cottids, an osmerid, *Anoplopoma fimbria*, bathymasterids, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus* in this group has also been documented for the larval fish component of the neuston in the California Current region along the U.S. west coast (Brodeur et al., 1987; Shenker, 1988; Doyle, 1992). The occurrence of *T. chalcogramma* larvae in high numbers in the neuston of the western Gulf of Alaska, however, is unique to this region and reflects the overall dominance of this species in the plankton of the study area (Kendall and Dunn, 1985; Schumacher and Kendall, 1991; Rugen[3]).

Among the dominant taxa of fish larvae in the neuston, most were obligate tenants of the surface, despite the predominance of demersal spawning among these taxa. The most important taxa in this group included the hexagrammids, cottids, *Anoplopoma fimbria*, and *Cryptacanthodes aleutensis*, and, according to the general classification scheme for neustonic organisms (Zaitsev, 1970; Hempel and Weikert, 1972; Peres, 1982), they may be considered obligate members of the neuston. The same taxa of larvae have been identified as obligate neustonic organisms in the plankton off the U.S. west coast (Doyle, 1992). Because of their scarcity in bongonet samples, the dramatic daytime reduction in density of these larvae in the neuston samples may have been attributed primarily to light-aided avoidance of the sampling gear. The generally large sizes documented (predominantly >10 mm SL) for these neustonic larvae also contributed to their ability to avoid the neuston net.

*Theragra chalcogramma*, *Ammodytes hexapterus*, and *Bathymaster* spp. larvae were unusual among the dominant neustonic taxa in that they were extremely abundant in bongo net samples also; therefore, their association with the neuston was considered facultative. Their nighttime presence in the neuston suggested a pattern of diel vertical migration with movement upward at dusk and a return to deeper layers during the day. This pattern has been observed for many species of fish larvae and zooplankton in many different regions (Zaitsev, 1970; Hempel and Weikert, 1972; Neilson and Perry, 1990). *Mallotus villosus*, *Myoxocephalus* spp., and *Zaprora silenus* larvae, which were well represented in bongo net samples, but abundant in the neuston at night, may also exhibit this pattern of vertical migration. However, with the limited data presented here, it was difficult to verify this migration pattern. Daytime sampler avoidance, particularly by the larger larvae and early juveniles, is likely to have had a confounding influence on the observation of such a pattern. In addition, it is necessary to consider in more detail the diel variation in the vertical distribution pattern of the larvae over the entire range of the water column in which they occurred.

Kendall et al. (1987, 1994) observed that within the upper 50 m of the water column, *T. chalcogramma* larvae (size range approximately 7–10 mm SL) undergo limited vertical migration on a diel cycle. These larvae were found to be deepest during the day, shallowest in the evening, sink slightly at night, and sink more in the morning. Under controlled laboratory conditions, Olla and Davis (1990) also observed similar diel periodicity in vertical distribution of *T. chalcogramma* larvae; larvae moved downward with daytime light intensity, upward during evening twilight conditions, remained close to the surface at night, and moved downward again in the morning. The *T. chalcogramma* larvae caught in the neuston, mainly at night, during the present study were predominantly 5–14 mm SL unlike their counterparts in the bongo net samples that were mostly <6 mm SL. This diel pattern of neustonic occurrence for the larger-sized larvae was likely due to the pattern of diel vertical migration observed by the above authors.

Observations on the vertical distribution of *Ammodytes hexapterus* larvae have also been made in the western Gulf of Alaska (Rogers et al., 1979; Brodeur and Rugen, 1994). Unlike *T. chalcogramma* larvae, *A. hexapterus* larvae were found to be deepest in the water column at night and shallowest at dawn and during the day. This apparent migration pattern of nocturnal descent has also been observed for *A. personatus* larvae off Japan and has been interpreted as advantageous in terms of diurnal feeding and predator avoidance (Yamashita et al., 1985). If this is the normal diel pattern of vertical migration for *Ammodytes* larvae, the occurrence of high densities of *A. hexapterus* larvae in the neuston at night, documented during the present study, seems unusual. On examination of length-frequency distributions for these larvae, however, it appears that the pattern of nocturnal descent was prevalent among larvae <20 mm SL (Yamashita et al., 1985; Brodeur and Rugen, 1994), whereas the nocturnal concentration of larvae at the surface was restricted to larger larvae and early juveniles (Doyle, 1992; this study). Perhaps these larger specimens undertake a nocturnal migration into the neuston as has been indicated by data collected off the U.S. west coast (Doyle, 1992). The length-frequency distributions documented for *A. hexapterus* larvae here, however, suggest that during spring in the western Gulf of Alaska, the well-developed larvae and early juveniles (>20 mm SL) almost exclusively occupied the neuston. Such specimens were rare in the bongo net samples where the predominant larval size range was 5–15 mm SL. The scarcity of the large *A. hexapterus* larvae in the daytime neuston samples in this instance could be attributed to light-enhanced sampler avoidance.

Brodeur and Rugen (1994) also found that *Bathymaster* spp. larvae (4–7 mm SL) were deepest in the water column at night in the western Gulf of Alaska and suggest a diel migration pattern of nocturnal descent similar to *A. hexapterus*. A similar pattern of downward migration at night has been observed for *Bathymaster* spp. larvae in the Bering Sea (Walline[6]). Their absence from daytime neuston samples during the present study seemed to contradict such a pattern of vertical migration. Whereas most of the young larvae may follow the above pattern, our data also suggest a facultative association with the neuston by some of these larvae and a nighttime occupation of the neuston as a result of migration upward to the surface. This seems feasible as it is apparent from observations by Kendall and Dunn (1985) and Rugen[3] in the Gulf of Alaska that *Bathymaster* spp. larvae become more neustonic with development. Most *Bathymaster* spp. larvae taken here, both in neuston net and bongo net samples, were <10 mm SL and would not be able to avoid the sampler as did the *A. hexapterus* larvae found in the neuston during the present study. The facultative nocturnal association with the neuston proposed here for *Mallotus villosus* larvae does not contradict what is already known concerning vertical distribution patterns for osmerids in the Gulf of Alaska. Haldorson et al. (1993) recorded that osmerid larvae in Auke Bay apparently spend most of their time in the mixed layer, rising to the surface at night and returning to relatively shallow depths during the day.

Recent investigations on the interaction between the early life history stages of *T. chalcogramma* and the oceanographic environment in the western Gulf of Alaska indicate that prevailing southwesterly currents transport larvae from the Shelikof Strait region to nursery grounds along the Alaska Peninsula (Kendall et al., 1987; Kim and Kendall, 1989; Hinckley et al., 1991; Schumacher and Kendall, 1991). Although the southwesterly flowing Alaska Coastal Current bifurcates southwest of Kodiak Island, most of this water remains on the shelf, thus potentially retaining the majority of fish larvae in the coastal region. Physical features such as plumes and eddies also serve to retain larvae on the continental shelf and transport them southwestward along the Alaska Peninsula (Vastano et al., 1992).

Given these current patterns, the distribution patterns observed for most taxa of fish larvae in the neuston during this study suggest that springtime spawning and emergence of larvae into the plankton (and subsequently the neuston) took place mainly around Kodiak Island (except along the seaward side) and along the Alaska Peninsula to the southwest. A high concentration of larvae over the shelf from Kodiak Island to the Shumagin Islands was the predominant pattern for most species. Despite their occurrence in the neuston, these larvae were likely retained over the shelf and in the coastal zone by the prevailing currents. In contrast, the more offshore distribution patterns observed for *A. fimbria*, *P. monopterygius*, and *H. hemilepidotus* indicate that a significant proportion of these larvae may have been entrained in the Alaskan Stream over the slope and in deep water.

Analysis of multispecies spatial patterns using recurrent group analysis and numerical classification did not reveal the existence of more than one neustonic assemblage of fish larvae in the study area. A unique and comparable assemblage of neustonic fish larvae has also been identified off the U.S. west coast and its geographical distribution is essentially confined to shelf and slope waters off Washington, Oregon, and northern California (Doyle, 1992; Doyle[7]). Apart from perhaps *P. monopterygius* larvae, which are known to occur throughout the Gulf of Alaska (Gorbunova, 1962), and to a lesser extent *A. fimbria* and *H. hemilepidotus*, members of the neustonic assemblage of fish larvae in the western Gulf of Alaska are likely to be scarce in the oceanic zone.

It has been postulated that the primary advantage of a neustonic existence as an early life history strategy for certain species of marine fish is the enhanced trophic conditions that prevail in this biotope (Moser, 1981; Tully and O'Ceidigh, 1989; Doyle, 1992). The suitability of the neuston as a feeding ground for larvae is, however, dependent on the ability of larvae to

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[6] Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June-July 1979. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA 98115. Proc. Rep. 81-05, 22 p.

[7] Doyle, M. J. 1992. Patterns in distribution and abundance of ichthyoplankton off Washington, Oregon, and northern California (1980 to 1987). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA, 98115. Proc. Rep. 92-14, 344 p.

seek and capture prey. Although surface aggregations of zooplankton are common at frontal and convergence zones, the neuston may in general have a reduced biota, at least during the daytime. The relatively large size and well-developed form that characterizes most fish larvae occurring in the neuston of the western Gulf of Alaska and elsewhere is possibly an adaptive advantage in terms of finding and consuming suitable quantities of food. The data of Kendall and Dunn (1985) and Rugen[3] indicate that hexagrammid and cottid larvae (obligate members of the neuston) are abundant in the study area during all seasons. Given that peak production of copepod nauplii, a dominant larval fish food, occurs during summer in this region (Cooney, 1986), the above larvae are likely to encounter a diminished biota in the neuston during fall and winter months in particular. Because of their relatively large size, however, a wide diversity of prey organisms are likely to be available to them in the neustonic layer and this diversity may compensate for the lower prey densities of copepod nauplii.

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