NEUSTONIC ICHTHYOPLANKTON IN THE NORTHERN REGION OF THE CALIFORNIA CURRENT ECOSYSTEM

MIRIAM J. DOYLE[1]
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331-3803

ABSTRACT

Analysis of ichthyoplankton data collected off Washington, Oregon, and northern California during the 1980s indicates a neustonic assemblage of fish eggs, larvae, and juveniles. This assemblage is most diverse over the shelf and continental slope. Diel variation in the occurrence and abundance of certain species of fish larvae in the neuston samples is striking. Three categories are apparent among the neustonic ichthyoplankton. Obligate members include larvae and early juveniles of nine species that occurred permanently and almost exclusively in the neuston but were scarce or absent in subsurface samples. Other taxa of larvae and juveniles were abundant at the surface only at night and are identified as facultative members of the neuston. Several taxa of fish eggs were abundant in the neuston; they seem to accumulate at the surface because of positive buoyancy. They are considered strays in the neuston.

Fish larvae in the neuston were larger overall than those deeper in the water column; this is advantageous in terms of seeking prey and avoiding predators. Juveniles were also common in the neuston, but recently hatched larvae were largely absent.

Several factors may limit the successful habitation of the neuston by fish eggs and larvae: high levels of damaging UV radiation, intensive wave action, a reduced biota, enhanced visibility to predators, and larval dispersal. However, adaptations to these potentially adverse factors are apparent among the species. Advantages to a neustonic existence may include enhanced growth, reduced levels of predation, and suitable concentrations of food. The main reason that larvae and juveniles of certain species select the neuston as a suitable ecological niche is probably the unique trophic conditions that prevail in this biotope.

RESUMEN

Análisis de datos de ictioplancton colectados en las costas de Washington, Oregon y en el norte de California durante la década del 80 señala la existencia de un grupo neustónico de huevos de peces, larvas y juveniles. Este grupo tiene máxima diversidad sobre la plataforma y el talúd continental. La variación diurna en la ocurrencia de algunas especies de peces en el neuston es sorprendente. El ictioplancton neustónico puede dividirse en tres categorías. Miembros obligados, que incluyen larvas y juveniles tempranos de nueve especies que ocurren permanente y casi exclusivamente en el neuston, pero escasos o ausentes en las muestras sub-superficiales. Otro grupo de taxa de larvas y juveniles fué abundante en la superficie sólo de noche y se identifican como miembros facultativos del neuston. Varios taxa de huevos de peces fueron abundantes en el neuston donde aparentemente se acumulan debido a que poseen flotación positiva; se considera que este es un grupo "extraviado" en el neuston.

Las larvas de peces en el neuston fueron mas grandes que las encontradas a mayor profundidad en la columna de agua; se considera que esto es ventajoso al buscar presas y evitar depredadores. Los juveniles también se encontraron a menudo en el neuston, contrastando con larvas de reciente eclosión, quienes estuvieron ausentes.

Varios factores podrían limitar al neuston como un hábitat exitoso para el ictioplancton: altos niveles de radiación ultravioleta, oleaje intenso, una biota disminuída, mayor visibilidad para los depredadores y dispersión larval. Sin embargo, las especies muestran adaptaciones a esos factores adversos. Las ventajas de una existencia neustónica incluirían mayor crecimiento, menores niveles de depredación y concentraciones de alimento adecuadas. La razón principal por la cual larvas y juveniles de algunas especies eligen al neuston como un nicho ecológico conveniente estriba probablemente en las condiciones tróficas únicas que prevalecen en este biotopo.

INTRODUCTION

A diverse assemblage of planktonic organisms occurs in the uppermost surface layer (10–20 cm) of the oceans and is collectively referred to as the neuston (Zaitsev 1970; Peres 1982). The composition and abundance of neustonic organisms vary consider-

[1]Present address: National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way, NE, Seattle, Washington 98115-0070

[Manuscript received February 10, 1992.]

ably, both geographically and temporally. In general, concentrations of neuston are higher in neritic areas than in the open ocean at the same latitudes (Hempel and Weikert 1972; Peres 1982). Holdway and Maddock (1983a) also showed that tropical and subtropical neritic and upwelling areas supported greater concentrations of neuston than oceanic and boreal zones. Diel variation in occurrence and abundance of organisms in the neuston is well documented. Although many members of the neuston are permanently present in the surface zone (obligate members), a diverse range of organisms concentrates at the surface only during certain hours (facultative members), mostly at night (Zaitsev 1970; Hempel and Weikert 1972; Peres 1982; Holdway and Maddock 1983a, b).

Fish eggs, larvae, and juveniles are abundant in the neuston, which is considered an important nursery ground for the early stages of many fish (Zaitsev 1970; Hempel and Weikert 1972; Moser 1981; Peres 1982). Although eggs of various fish species concentrate in the neuston, essentially because of their positive buoyancy, larvae and juveniles actively migrate to the surface zone and may be obligate or facultative members of the neuston. The importance of the neustonic realm in the ontogeny and ecology of larval fish populations varies with geographical area and local conditions. Factors such as latitude, surface water temperature, water depth, nutrient concentration, and upwelling all affect the diversity, age structure, and vertical migratory patterns of fish larvae in an area (Hempel and Weikert 1972; Tully and O'Ceidigh 1989a).

Several studies of planktonic neuston in the northeast Pacific were carried out during the 1970s and 1980s. Most were for the purpose of documenting fish larvae in the neuston. Richardson (1975) made a preliminary report on the occurrence and abundance of fish larvae and juveniles in the neuston along an east-west transect off the mid-Oregon coast. Ahlstrom and Stevens (1976) documented species composition and abundance of fish larvae in the neuston and in the water column over an extensive area of the northeast Pacific, including the coastal and oceanic zone from northern Washington to southern Baja California. In their account of the distribution of ichthyoplankton in the Southern California Bight, Gruber et al. (1982) compared the occurrence of larvae in neuston tows with their occurrence in oblique tows. These studies established that many species of fish larvae are abundant in the surface zone as well as deeper in the water column but that an additional group of species is almost exclusively neustonic. Brodeur et al. (1987) and Brodeur (1989) examined species composition and abundance of fish larvae and invertebrate components of the neuston in coastal waters of the northeast Pacific as part of a study of juvenile salmonids' feeding habits. Shenker (1985, 1988) was the first to carry out a biological and ecological investigation of neustonic larval and juvenile fishes in the northeast Pacific. That study, however, was restricted to a single transect of stations off the Oregon coast.

From 1980 to 1987, a series of cooperative U.S./U.S.S.R. ichthyoplankton surveys was conducted off the U.S. west coast from 48°N to 40°N (Dunn and Rugen 1989). These surveys were designed to determine spatial and temporal patterns in the ichthyoplankton. The neuston as well as the water column fauna was sampled, and hydrographic data were collected. Preliminary results from these surveys were given in Kendall and Clark 1982a, b; Clark 1984, 1986a, b; Bates 1984; Clark and Kendall 1985; Clark and Savage 1988; and Savage 1989a, b. These data made it possible to investigate the occurrence and ecology of fish eggs and larvae in the neuston over a large area and in comparison with their occurrence deeper in the water column.

In this investigation, species composition and relative abundance are documented, as are length-frequency distributions of larvae and diel variation in their occurrence and abundance in the neuston. Different categories of neustonic ichthyoplankton, such as obligate and facultative members, are identified. Horizontal patterns of distribution are described for the numerically dominant neustonic taxa. The ecological significance of a neustonic existence for early life stages of these fish is also discussed.

MATERIALS AND METHODS

The cooperative ichthyoplankton surveys conducted off the U.S. northwest coast during the 1980s involved the U.S. Northwest and Alaska Fisheries Center in Seattle, and the U.S.S.R. Pacific Research Institute in Vladivostok. Over a period of seven years, ten cruises were made. During each cruise, a maximum of 125 stations was occupied (table 1). Seasonal coverage was limited: six of the ten cruises were made in spring (March to early June); one cruise in summer (August 1980); one in winter (January 1987); and two in autumn (October–November 1981 and November–December 1983). The station grid covered an area of approximately 249,000 km^2 off Washington, Oregon, and northern California. Stations were more closely spaced over the shelf and slope than in deep water west of the 1,000-m isobath (figure 1).

TABLE 1
Sampling Schedule and Number of Stations Sampled for Ichthyoplankton

			Stations occupied	
Cruise	Vessel	Cruise dates	Neuston tows	Bongo tows
TK80	*Tikhookeanski* U.S.S.R.	Apr. 20–May 15, 1980	125	125
PO80	*Poseydon* U.S.S.R.	Aug. 1–20, 1980	91	91
PO81	*Poseydon* U.S.S.R.	May 9–June 2, 1981	123	123
DA81	*Mys Dalniy* U.S.S.R.	Oct. 24–Nov. 19, 1981	125	125
PO82	*Poseydon* U.S.S.R.	May 3–June 1, 1982	124	49
EQ83	*Equator* U.S.S.R.	Apr. 23–May 15, 1983	124	124
MF83	*Miller Freeman* U.S.A.	Nov. 11–Dec. 2, 1983	113	113
PO84	*Poseydon* U.S.S.R.	Mar. 11–Apr. 4, 1984	124	124
BA85	*Mys Babyshkina* U.S.S.R.	Apr. 19–May 11, 1985	124	124
MF87	*Miller Freeman* U.S.A.	Jan. 7–31, 1987	88	88
Total number of stations occupied			1161	1086

During each cruise, plankton was sampled for fish eggs and larvae, and hydrographic casts were made to determine temperature and salinity at all stations. Water samples were collected with Niskin bottles at nominal depths of 0, 5, 10, 15, 20, 25, 30, 35, 50, 75, 100, 200, 250, and 300 m, as depth permitted. For 10 minutes at each station, paired neuston tows were made with Sameoto samplers (Sameoto and Jaroszynski 1969) with 0.3-m-high-by-0.5-m-wide frames and 0.505-mm mesh netting. The samplers were towed at a speed of 2.0 knots and sampled approximately the upper 15 cm of the water column. Following standard procedures, oblique tows to 200-m depth, or 5 m from the bottom in water shallower than 200 m, were carried out at each station. For these tows, 60-cm-frame bongo samplers fitted with 0.505-mm-mesh nets were used (Smith and Richardson 1977). Flowmeters in the mouths of the samplers were used to determine the volume of water filtered by each net.

The plankton samples were preserved in a 5% buffered Formalin solution. One of each of the paired neuston and bongo samples was retained by the Americans and the other by the Soviets. The American plankton samples were processed by the Polish Plankton Sorting Center in Szczecin, Poland, and subsequently by the Northwest and Alaska Fisheries Center, Seattle. Fish eggs and larvae were removed from the samples, identified to the lowest taxonomic level possible, counted, and measured.

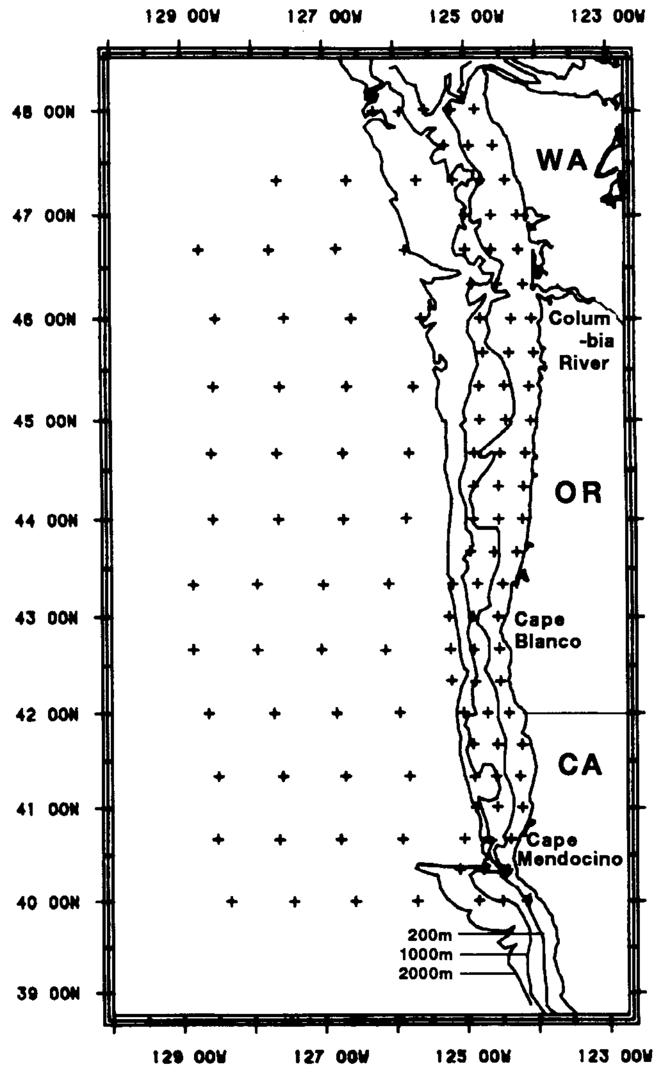


Figure 1. Survey area, sampling stations, and bathymetry off the U.S. west coast.

Counts of fish eggs and larvae were converted to numbers per 10 m^2 of sea-surface area for the bongo samples and numbers per 1000 m^3 for the neuston samples.

OCEANOGRAPHIC ENVIRONMENT

The oceanography of the survey area is characterized by the California Current system, a typical eastern boundary current regime (Hickey 1979, 1989). The main California Current is slow, meandering, broad, and indistinct, and it proceeds southwards along the U.S. west coast (figure 2). Subcomponents of the California Current include the northward-flowing California Undercurrent and Davidson Current (Hickey 1989). The California Undercurrent consists of a jetlike poleward flow with a subsurface maximum. Its core appears to be confined to

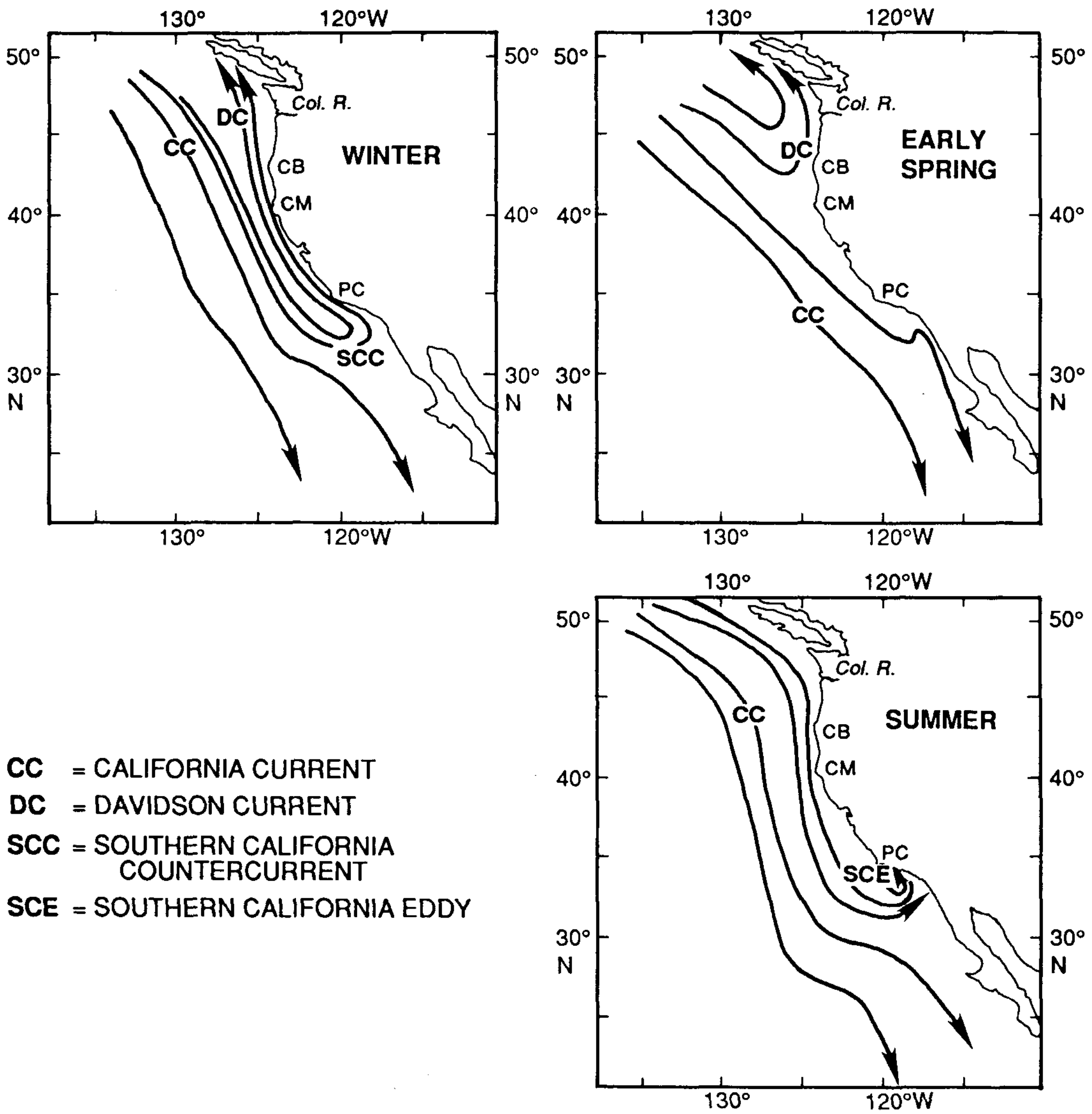


Figure 2. Seasonal variation in deep-ocean boundary currents off the U.S. west coast: Col. R. = Columbia River; CB = Cape Blanco; CM = Cape Mendocino; PC = Point Conception. From Hickey 1989.

the continental slope. The northward-flowing Davidson Current that prevails on the coastal side of the California Current during winter is a seasonal surface current (figure 2).

Coastal surface currents in this region are primarily wind-driven, with strong seasonal variability (Huyer et al. 1975; Hickey 1979; Strub et al. 1987). Spring and autumn transitions in prevailing winds and associated coastal currents are driven by large-scale changes in atmospheric pressure systems over the North Pacific. In winter, southerly winds result in the northward-flowing Davidson Current, onshore Ekman transport of surface water, and downwelling close to the coast. In spring the winds shift from southerly to northerly, and by summer the prevailing conditions include a southward-flowing coastal current, offshore Ekman transport, and upwelling of cold oceanic water close to the coast. The autumn transition from northerly to southerly winds leads back to the winter conditions.

The intensity of Ekman transport and associated upwelling varies along the coast. Mean monthly upwelling indices (derived from geostrophic wind stress; Bakun 1973) for four locations along the 125°W meridian—from northern Washington to northern California—show that the extent and intensity of upwelling increases from north to south (figure 3). Off Washington and northern Oregon, the upwelling season is confined largely to summer, whereas winter is characterized by vigorous downwelling. Along the northern California coast, winter downwelling is weaker and less extensive, and

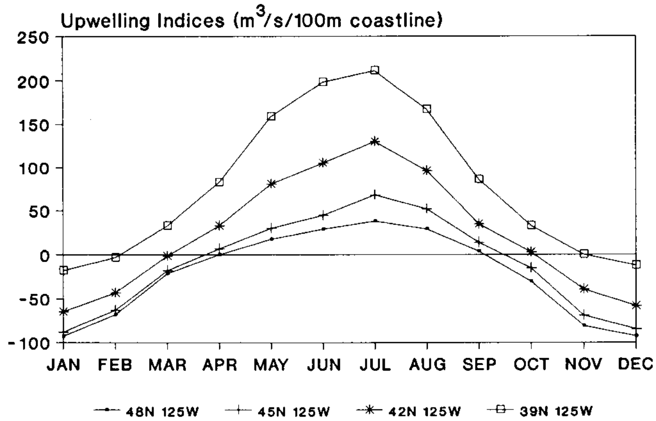


Figure 3. Monthly upwelling indices (Bakun 1973), mean of years 1946 to 1989, for four locations along the west coast. 48N = northern Washington; 45N = northern Oregon; 42N = Oregon/California border; 39N = northern California.

summer upwelling indices are considerably higher than off Washington and northern Oregon. The region of maximum upwelling along the U.S. west coast is between Cape Blanco in southern Oregon and Point Conception in southern California, with a local maximum at Cape Mendocino (Parrish et al. 1981).

The oceanography of waters off the U.S. northwest coast is modified significantly by the Columbia River, which divides the Washington and Oregon coastal regions (Hickey and Landry 1989). The Columbia River is the largest point source of freshwater flow into the eastern Pacific Ocean, and its water forms a low-salinity plume that extends outwards from the river mouth above a shallow halocline (<20 m; Fiedler and Laurs 1990). The extent and orientation of the plume is variable and subject to seasonal changes in runoff (peak period in June) and coastal circulation patterns.

RESULTS

Species Composition and Relative Abundance

Both fish eggs and larvae were abundant in neuston samples, but species diversity was lower than in the bongo samples. Twenty-five species of eggs representing 17 families were identified from neuston samples (table 2). In addition, three identifications were to generic level and five to family level. In terms of percentage occurrence and mean abundance in all samples, *Engraulis mordax*, *Trachipterus altivelis*, *Icichthys lockingtoni*, the paralichthyids, and the pleuronectids dominated. The paralichthyids (*Citharichthys* spp.) were outstandingly abundant, with a mean density of 389 eggs per 1000 m^3, even though they occurred in only 27% of neuston samples. The mesopelagic species *Chauliodus macouni* and *Icosteus aenigmaticus* were moderately abundant but occurred in approximately 10% of all samples.

Taxonomic diversity was higher for larvae in the neuston samples. Forty-six species were identified in a total of 24 families (table 3). Among the nine identifications to generic level, *Sebastes* spp., representing numerous rockfish, was most important. Species composition, and particularly relative abundance, differed greatly from that recorded for eggs in the neuston. *Engraulis mordax* was the only species for which both eggs and larvae were abundant. Although paralichthyid and pleuronectid larvae appeared in the neuston samples, occurrence and abundance were very low in comparison with their eggs. The numerically dominant taxa of larvae in the neuston included *Engraulis mordax*, *Cololabis saira*, *Sebastes* spp., *Anoplopoma fimbria*, *Hexagrammos decagrammus*, *Hemilepidotus spinosus*, and *Scorpaenichthys marmoratus*. Less abundant, but also well represented, were *Tarletonbeania crenularis*, *Hexagrammos lagocephalus*, *Ophiodon elongatus*, *Hemilepidotus hemilepidotus*, *Ronquilus jordani*, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus*.

Eggs of all species that were prominent in the neuston were also prominent in subsurface bongo samples (tables 4 and 5). Except for *Engraulis mordax*, larvae of the same species were absent or scarce in the neuston, but were generally prominent in the bongo collections. It seems, therefore, that species of fish eggs that are abundant in the neuston accumulate passively at the surface and on hatching into larvae migrate downwards into the subsurface zone.

In contrast, many of the larval species that were abundant in the neuston were absent or scarce in the bongo samples and therefore may be considered almost exclusively neustonic (obligate members of the neuston). These include *Cololabis saira*, *Anoplopoma fimbria*, the hexagrammids, the cottids, and *Cryptacanthodes aleutensis*. Because their eggs were absent from the neuston (table 2), these larvae must actively migrate to, and remain in the surface zone. *Ronquilus jordani* and *Ammodytes hexapterus* were recorded frequently in the bongo samples, although they were not abundant. Their incidence of occurrence in neuston samples was, however, higher than in the bongo samples. These larvae are considered to be more facultative than obligate neustonic types. The remaining taxa that were prominent in the neuston—including *Engraulis mordax*, *Tarletonbeania crenularis*, and *Sebastes* spp.—were also abundant, and had a higher incidence of occurrence, in the bongo samples, which indicates that they are essentially facultative in the neuston.

TABLE 2
Percentage Occurrence and Mean Abundance of All Taxa of Eggs in Neuston Samples Collected during All Cruises

Family	Species	% occurrence (all samples)	Mean no./1000 m³ (all samples)
Unidentified	—	2.83	3.10
Engraulidae	*Engraulis mordax*	2.74	32.28
Argentinidae	Unidentified	0.19	0.02
	Nansenia candida	0.28	0.04
	Nansenia crassa	0.38	0.07
Bathylagidae	Unidentified	1.51	0.60
	Bathylagus spp.	1.42	0.26
	Bathylagus ochotensis	0.28	0.04
Chauliodontidae	*Chauliodus macouni*	10.21	2.23
Melanostomidae	*Tactostoma macropus*	2.65	4.88
Myctophidae	Unidentified	0.09	0.02
Gadidae	*Merluccius productus*	0.09	0.01
	Theragra chalcogramma	0.19	0.07
Scomberesocidae	*Cololabis saira*	1.04	2.70
Trachipteridae	Unidentified	0.66	0.12
	Trachipterus altivelis	39.98	37.77
Scorpaenidae	*Sebastolobus* spp.	1.51	57.49
Carangidae	*Trachurus symmetricus*	0.19	0.08
Icosteidae	*Icosteus aenigmaticus*	10.21	5.54
Ammodytidae	*Ammodytes hexapterus*	0.09	0.02
Centrolophidae	*Icichthys lockingtoni*	30.15	43.48
Tetragonuridae	*Tetragonurus cuvieri*	0.47	0.13
Paralichthyidae	*Citharichthys* spp.	27.03	389.37
Pleuronectidae	Unidentified	10.40	76.18
	Errex zachirus	8.88	13.05
	Hippoglossoides elassodon	0.57	0.13
	Pleuronectes isolepis	1.80	0.55
	Eopsetta exilis	5.86	4.13
	Microstomus pacificus	14.75	42.19
	Pleuronectes vetulus	3.50	3.13
	Platichthys stellatus	1.13	0.81
	Pleuronichthys coenosus	0.76	0.17
	Pleuronichthys decurrens	3.02	1.15
	Psettichthys melanostictus	4.44	3.43

Diel Variation in Catches of Larvae

For larvae in the neuston, it is important to consider diel variation in catches, especially for the facultative members that are only occasionally abundant in the surface layer. The pattern of diel variation in total catches differs significantly between the two sampling gears (figure 4). There is very little variation over 24 hours for the bongo samples, whereas in the neuston, catches were considerably lower during daylight than at night. Between 0800 and 1900 hours, catches in the neuston were always <3% of total catch; from 2000 to 0600, catches per hour ranged from approximately 5% to 12% of the total larval fish catch (figure 4a). Two possible factors may contribute to this diel pattern: (1) vertical migration of larvae into the neuston at night causes an increase in catches during darkness, and (2) enhanced avoidance of the neuston sampler during daylight reduces catches during the day. One or both of these factors may operate among the individual species of larval fish in the neuston.

There was little variation in catches of *Cololabis saira* over 24 hours, with only a slight reduction during daylight (figure 5a). Given that it occurred almost negligibly in the bongo samples (table 6), this species appears to be a permanent resident in the neuston. *Anoplopoma fimbria* larvae were less abundant in neuston samples during the day than at night (figure 5b), and their occurrence in bongo samples was, although low, higher than for *Cololabis saira* (table 6). There may be some migration of these larvae out of the immediate surface zone during the day.

The incidence of occurrence of hexagrammid larvae in bongo samples was very low (<1%) or, in the case of *Hexagrammos lagocephalus*, zero (table 6), implying that they are obligate neustonic species. Diel variation in catches, however, indicates that these larvae were slightly more abundant at night than during daylight (figure 5c–e). The cottid *Hemilepidotus spinosus*, which accounted for approximately 25% of all larvae caught in the neuston (table 6), was considerably more abundant in nighttime neuston

TABLE 3
Percentage Occurrence and Mean Abundance of All Taxa of Larvae in Neuston Samples Collected during All Cruises

Family	Species	% occurrence (all samples)	Mean no./1000 m³ (all samples)
Clupeidae	*Clupea harengus pallasi*	0.58	0.19
Engraulidae	*Engraulis mordax*	3.88	9.99
Osmeridae	Unidentified	1.23	1.07
Argentinidae	*Nansenia candida*	0.09	0.01
Bathylagidae	Unidentified	0.09	0.02
	Bathylagus spp.	0.09	0.02
	Bathylagus ochotensis	1.13	0.25
Myctophidae	Unidentified	0.19	0.02
	Ceratoscopelus townsendi	0.09	0.02
	Diaphus theta	0.28	0.04
	Lampanyctus regalis	0.09	0.02
	Protomyctophum crockeri	0.19	0.05
	Protomyctophum thompsoni	0.09	0.01
	Stenobrachius leucopsarus	1.42	0.65
	Symbolophorus californiense	0.19	0.03
	Tarletonbeania crenularis	5.95	5.56
Merluccidae	*Merluccius productus*	0.09	0.02
Gadidae	*Microgadus proximus*	0.09	0.01
	Theragra chalcogramma	0.09	0.01
Scomberesocidae	*Cololabis saira*	31.29	16.71
Scorpaenidae	Unidentified	0.09	0.19
	Sebastes spp.	18.05	19.86
	Sebastolobus spp.	0.09	0.05
Anoplopomatidae	*Anoplopoma fimbria*	22.02	26.46
Hexagrammidae	Unidentified	0.19	0.14
	Ophiodon elongatus	4.16	3.39
	Pleurogrammus monopterygius	0.19	0.04
	Hexagrammos spp.	0.19	0.06
	Hexagrammos decagrammus	19.01	15.16
	Hexagrammos lagocephalus	5.01	1.61
	Hexagrammos stelleri	0.09	0.04
Cottidae	Unidentified	0.28	0.04
	Artedius fenestralis	0.28	0.08
	Artedius harringtoni	0.28	0.08
	Cottus asper	0.09	0.01
	Hemilepidotus hemilepidotus	3.02	1.24
	Hemilepidotus spinosus	13.14	40.84
	Leptocottus armatus	0.76	0.21
	Radulinus spp.	0.09	0.16
	Radulinus asprellus	0.09	0.01
	Scorpaenichthys marmoratus	16.54	8.38
Agonidae	Unidentified	0.09	0.01
Cyclopteridae	Unidentified	0.94	0.16
Carangidae	*Trachurus symmetricus*	0.09	0.09
Bathymasteridae	*Bathymaster* spp.	0.19	0.03
	Ronquilus jordani	3.49	1.75
Stichaeidae	Unidentified	0.09	0.22
Cryptacanthodidae	*Delolepis gigantea*	0.09	0.01
	Cryptacanthodes aleutensis	1.42	1.83
Pholidae	*Pholis* spp.	0.09	0.02
Ammodytidae	*Ammodytes hexapterus*	4.06	7.11
Centrolophidae	*Icichthys lockingtoni*	0.39	0.07
Paralichthyidae	*Citharichthys* spp.	0.57	0.44
	Citharichthys sordidus	0.19	0.03
	Citharichthys stigmaeus	1.51	0.24
Pleuronectidae	*Eopsetta jordani*	0.28	0.09
	Errex zachirus	0.09	0.43
	Pleuronectes isolepis	0.28	0.22
	Microstomus pacificus	0.19	0.03
	Pleuronectes vetulus	1.42	0.44
	Platichthys stellatus	0.19	0.02
	Pleuronichthys decurrens	0.28	0.35
	Psettichthys sp.	0.09	0.01
	Psettichthys melanostictus	0.28	0.06

TABLE 4
Dominant Ichthyoplankton Taxa in Neuston and Bongo Samples Collected during All Cruises

Family	Species	Neuston Eggs	Neuston Larvae	Bongo Eggs	Bongo Larvae
Engraulidae	*Engraulis mordax*	x	x	x	x
Osmeridae	Unidentified				x
Bathylagidae	Unidentified			x	
	Bathylagus spp.			x	
	Bathylagus ochotensis			x	x
	Bathylagus pacificus				x
Chauliodontidae	*Chauliodus macouni*	x		x	x
Melanostomidae	*Tactostoma macropus*	x			
Myctophidae	Unidentified			x	x
	Diaphus theta				x
	Protomyctophum crockeri				x
	Protomyctophum thompsoni				x
	Tarletonbeania crenularis		x		x
	Stenobrachius leucopsarus				x
Scomberesocidae	*Cololabis saira*		x		
Trachipteridae	*Trachipterus altivelis*	x		x	
Scorpaenidae	*Sebastes* spp.		x		x
	Sebastolobus spp.				x
Anoplopomatidae	*Anoplopoma fimbria*		x		
Hexagrammidae	*Hexagrammos decagrammus*		x		
	Hexagrammos lagocephalus		x		
	Ophiodon elongatus		x		
Cottidae	*Hemilepidotus hemilepidotus*		x		
	Hemilepidotus spinosus		x		
	Scorpaenichthys marmoratus		x		
Bathymasteridae	*Ronquilus jordani*		x		
Cryptacanthodidae	*Cryptacanthodes aleutensis*		x		
Icosteidae	*Icosteus aenigmaticus*	x		x	
Ammodytidae	*Ammodytes hexapterus*		x		
Centrolophidae	*Icichthys lockingtoni*	x		x	
Paralichthyidae	*Citharichthys* spp.	x		x	
	Citharichthys sordidus				x
	Citharichthys stigmaeus				x
Pleuronectidae	Unidentified	x		x	
	Errex zachirus	x		x	x
	Eopsetta exilis	x		x	x
	Microstomus pacificus	x		x	
	Pleuronectes vetulus	x		x	x
	Psettichthys melanostictus	x		x	x

TABLE 5
Relative Abundance of Dominant Taxa of Eggs in Neuston Samples

Family	Species	Common name	% total egg abundance	% occurrence (all samples) Neuston	Bongo
Engraulidae	*Engraulis mordax*	Northern anchovy	4.44	2.74	2.17
Chauliodontidae	*Chauliodus macouni*	Pacific viperfish	0.30	10.21	20.69
Melanostomidae	*Tactostoma macropus*	Longfin dragonfish	0.69	2.65	2.17
Scomberesocidae	*Cololabis saira*	Pacific saury	0.36	1.04	0.94
Trachipteridae	*Trachipterus altivelis*	King-of-the-salmon	5.19	39.98	32.61
Scorpaenidae	*Sebastolobus* spp.	Thornyheads	7.93	1.51	0.76
Icosteidae	*Icosteus aenigmaticus*	Ragfish	0.76	10.21	13.04
Centrolophidae	*Icichthys lockingtoni*	Medusafish	5.99	30.15	20.71
Paralichthyidae	*Citharichthys* spp.	Sanddabs	56.28	27.03	26.00
Pleuronectidae	Unidentified	Righteye flounders	10.48	10.40	11.91
	Eopsetta exilis	Slender sole	0.55	8.88	15.12
	Errex zachirus	Rex sole	1.79	5.86	21.83
	Microstomus pacificus	Dover sole	5.80	14.75	14.37
	Pleuronectes vetulus	English sole	0.93	3.50	3.59
	Psettichthys melanostictus	Sand sole	0.42	4.44	4.82

Based on data from all cruises.

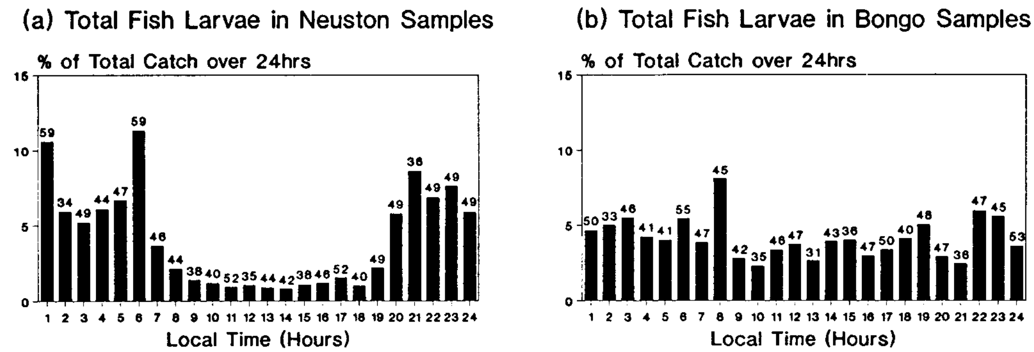


Figure 4. Diel variation in total catch of fish larvae in neuston (*a*) and bongo (*b*) samples. For each hourly interval over 24 hours, abundance was summed for all stations (10 cruises combined) where larvae were found. The percentage of total catch (24 hours combined) accounted for by each hourly interval was then calculated. Numbers above the bars are the total number of samples collected during each hourly interval.

samples than in daytime ones (figure 5f), indicating a possibly significant migration out of the surface layer. The incidence of occurrence of *H. spinosus* larvae in the bongo samples was still low (approximately 1.9%), however, but higher than for the obligate neustonic species (table 6). An unusual pattern of diel variation was apparent for the cottid *Scorpaenichthys marmoratus* (figure 6a). Its larvae were most abundant in the neuston after midnight until early afternoon (1400 hours); after that, hourly catches made up less than 3% of the total catch. These larvae may migrate out of the neuston during the latter period.

Diel variation in larval abundance was most dramatic for *Ronquilus jordani*, *Engraulis mordax*, *Tarletonbeania crenularis*, *Sebastes* spp., and *Ammodytes hexapterus* (figure 6b–f). Daytime catches of these larvae were usually insignificant. It seems that high numbers of these larvae migrate into the surface zone at night, which indicates a facultative association with the neuston. For *E. mordax*, *T. crenularis*, and *Sebastes* spp., this facultative association is further emphasized by the much higher occurrence and abundance of these larvae in the bongo samples than in the neuston collections (tables 4 and 6). *Ronquilus jordani* and *A. hexapterus* occurred in fewer bongo than neuston samples, and their overall abundance in the bongo samples was low (tables 4 and 6).

Categories of Neustonic Ichthyoplankton

The patterns of occurrence and abundance of eggs and larvae in the neuston collections, and the diel variation in catches indicate three categories of neustonic occurrence for west coast ichthyoplankton (table 7).

Obligate members of the neuston permanently live in the surface zone. Among the west coast ichthyoplankton, larvae and early juveniles of the species *Cololabis saira*, *Anoplopoma fimbria*, *Hexagrammos decagrammus*, *H. lagocephalus*, *Ophiodon elongatus*, *Hemilepidotus hemilepidotus*, *H. spinosus*, *Scorpaenichthys marmoratus*, and *Cryptacanthodes aleutensis* are assigned to this category (table 7).

Facultative members of the neuston are occasionally abundant in the surface layer. In the study area, larvae and early juveniles of *Engraulis mordax*, *Tarletonbeania crenularis*, *Sebastes* spp., *Ronquilus jordani*, and *Ammodytes hexapterus* belong to this category. They are abundant in the neuston only at night and migrate vertically in a diel pattern, remaining in the subsurface zone during daylight.

A third category of neustonic ichthyoplankton, "strays," includes a wide variety of fish eggs and larvae. Most of the species assigned to this category were most abundant in the subsurface zone of the water column, but some also appeared in the neuston. The species listed in tables 2 and 3 but not included in tables 4–6 (dominant neustonic taxa) are considered strays. In contrast, several species of eggs accumulate passively and abundantly in the surface zone. They float to the surface because they are positively buoyant. Eggs of the paralichthyids *Citharichthys* spp. are the most prominent members of this category, accounting for over 50% of all eggs in the neuston collections (table 5). Other species of eggs that were relatively abundant in the neuston included *Engraulis mordax*, *Trachipterus altivelis*, *Sebastolobus* spp., *Icichthys lockingtoni*, and various pleuronectids.

Horizontal Patterns of Distribution

Patterns of distribution described here for neustonic fish larvae are based on data combined for the ten sampling cruises; no adjustment is made for day-night differences in catches. The distribution maps represent general patterns of horizontal distribution

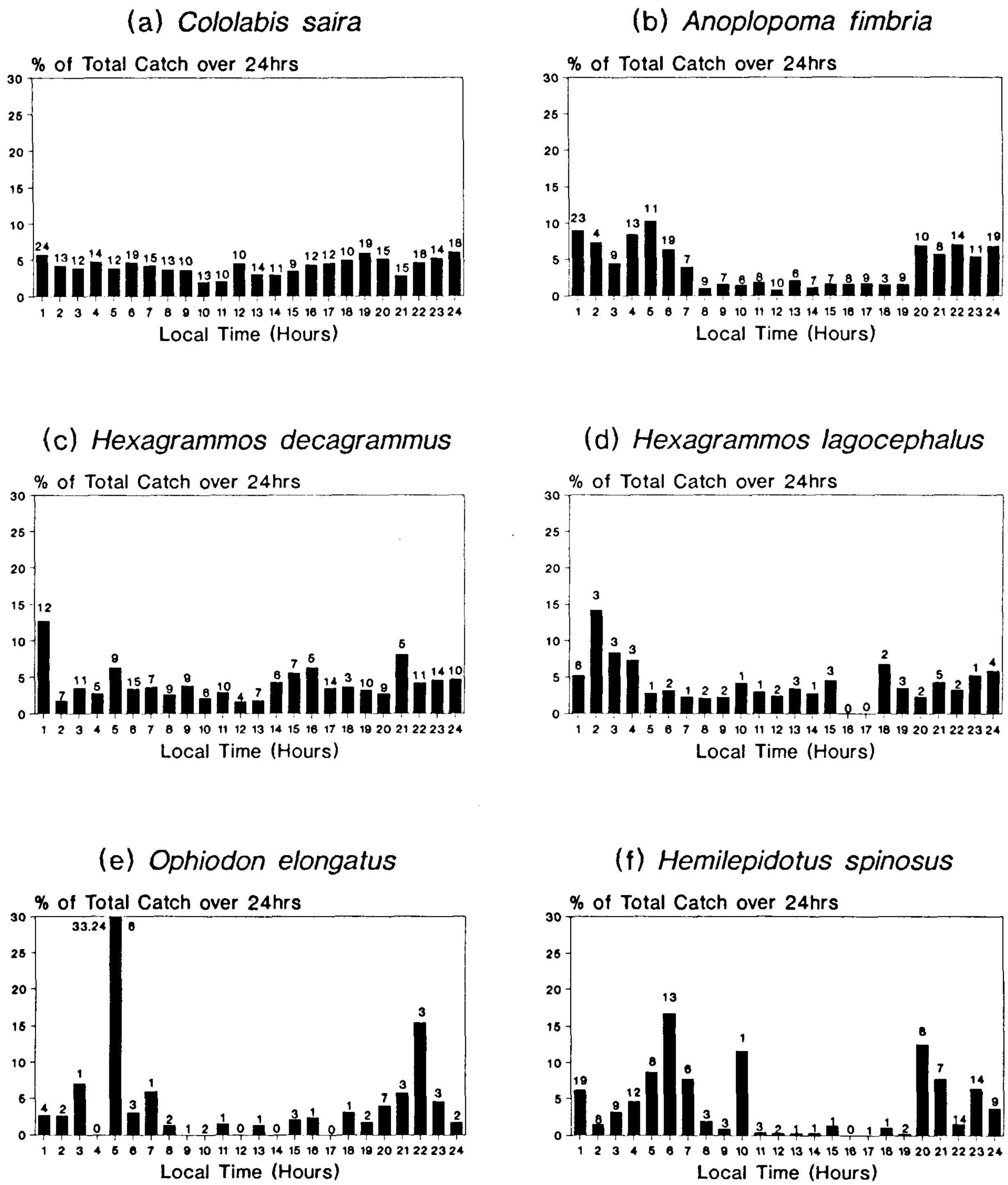


Figure 5. Diel variation in catches of fish larvae in neuston samples. For each hourly interval over 24 hours, abundance was summed for all stations (10 cruises combined) where larvae were found. Numbers above the bars are the total number of stations at which fish larvae were caught (with either gear) during each hourly interval. The total number of neuston samples collected during each hourly interval is given in figure 4a.

in the sampling area rather than accurate plots of mean larval abundance. Most taxa of fish larvae occurred close to the coast over the shelf and slope and were absent or scarce in the deepest part of the oceanic zone (figures 7 and 8). This is true of the pelagic *Engraulis mordax* and the demersal hexagrammids, cottids, *Ronquilus jordani*, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus*. Adult populations of these species are essentially coastal. Some, such as *Hexagrammos decagrammus*, *H. lagoce-*

TABLE 6
Relative Abundance of Dominant Taxa of Larvae in Neuston Samples

Family	Species	Common name	% total larval abundance	% occurrence (all samples)	
				Neuston	Bongo
Engraulidae	*Engraulis mordax*	Northern anchovy	5.96	3.88	5.67
Osmeridae	Unidentified	Smelts	0.26	1.23	4.91
Myctophidae	*Tarletonbeania crenularis*	Blue lanternfish	3.33	5.95	34.40
	Stenobrachius leucopsarus	Northern lampfish	0.26	1.42	56.33
Scomberesocidae	*Cololabis saira*	Pacific saury	10.08	31.29	0.47
Scorpaenidae	*Sebastes* spp.	Rockfish	11.99	18.05	43.57
Anoplopomatidae	*Anoplopoma fimbria*	Sablefish	15.97	22.02	1.23
Hexagrammidae	*Hexagrammos decagrammus*	Kelp greenling	9.15	19.01	0.66
	Hexagrammos lagocephalus	Rock greenling	0.91	5.01	0.00
	Ophiodon elongatus	Lingcod	1.95	4.16	0.47
Cottidae	*Hemilepidotus hemilepidotus*	Red Irish lord	0.74	3.02	0.28
	Hemilepidotus spinosus	Brown Irish lord	24.65	13.14	1.89
	Scorpaenichthys marmoratus	Cabezon	5.06	16.54	0.85
Bathymasteridae	*Ronquilus jordani*	Northern ronquil	1.05	3.49	2.08
Cryptacanthodidae	*Cryptacanthodes aleutensis*	Dwarf wrymouth	1.00	1.42	0.19
Ammodytidae	*Ammodytes hexapterus*	Pacific sandlance	4.16	4.06	1.80

Based on data from all cruises.

TABLE 7
Categories of Neustonic Ichthyoplankton

Obligate	Facultative	Strays
Permanently in the neuston—most abundant in the surface zone. Neustonic larval niche.	Occasionally abundant in the neuston because of diel vertical migration.	Accumulate passively in the neuston because of neutral or positive buoyancy, or because of occasional forays to the surface.
Larvae and juveniles of:	Larvae and juveniles of:	Eggs of:
Cololabis saira	*Engraulis mordax*	*Engraulis mordax*
Anoplopoma fimbria	*Tarletonbeania crenularis*	*Trachipterus altivelis*
Hexagrammos decagrammus	*Sebastes* spp.	*Sebastolobus* spp.
Hexagrammos lagocephalus	*Ronquilus jordani*	*Icichthys lockingtoni*
Ophiodon elongatus	*Ammodytes hexapterus*	*Citharichthys* spp.
Hemilepidotus hemilepidotus		Pleuronectidae
Hemilepidotus spinosus		
Scorpaenichthys marmoratus		Other less abundant eggs and larvae of
Cryptacanthodes aleutensis		various species.

phalus, *Hemilepidotus spinosus*, and *Scorpaenichthys marmoratus*, are most abundant close to shore, where they spawn from the intertidal zone to a maximum depth of 100 m (Hart 1973; Matarese et al. 1989). It seems unusual, then, that the larval distribution of *S. marmoratus* extends as far offshore as it does, with occurrences over the slope and adjacent deep water and sometimes over the deepest water of the sampling grid (figures 7f,g and 8b,c). Obviously larval drift is extensive; larvae in the neuston are subject to wind-generated transport as well as the prevailing patterns of water circulation. Because the station grid began three miles offshore, the highest larval densities of the shallow-water species were probably missed by this sampling program.

The occurrence of highest densities of *Engraulis mordax* larvae over the shelf, slope, and immediate deepwater zone off Washington and northern Oregon (figure 7a) reflects the known association of this species with the Columbia River plume. The northern subpopulation of *E. mordax* spawns in the near-surface waters of the Columbia River plume during summer (Richardson 1980).

Larvae that occurred extensively in the neuston of the shelf, slope, and oceanic zones include the myctophid *Tarletonbeania crenularis* (figure 7b), the Pacific saury (*Cololabis saira*; figure 7c), the rockfish complex (*Sebastes* spp.; figure 7d), and the sablefish (*Anoplopoma fimbria*; figure 7e). Larval distribution accurately reflected the distribution of adult popu-

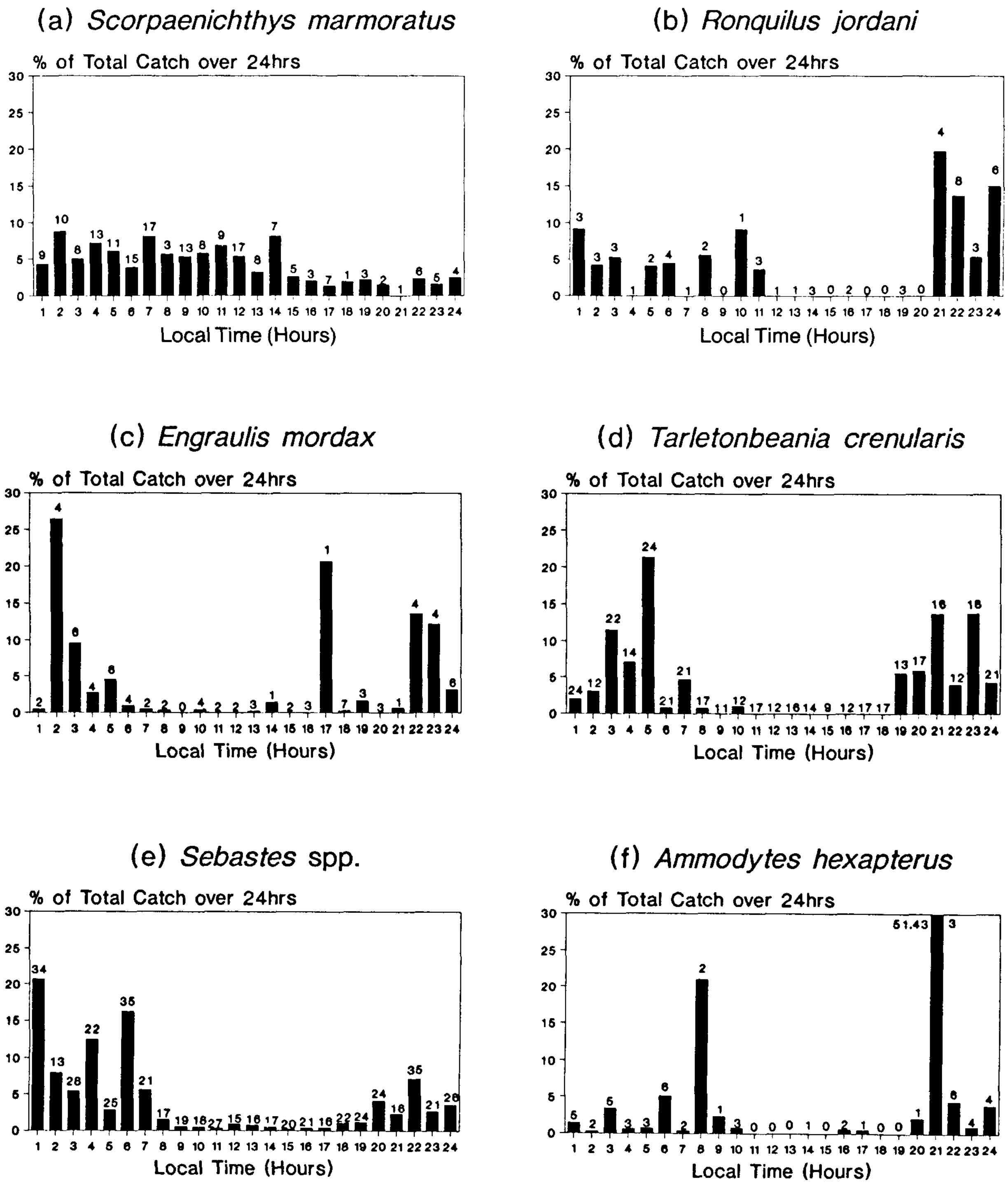


Figure 6. Diel variation in catches of fish larvae in neuston samples (continued). For each hourly interval over 24 hours, abundance was summed for all stations (10 cruises combined) where larvae were found. Numbers above the bars are the total number of stations at which fish larvae were caught (with either gear) during each hourly interval. The total number of neuston samples collected during each hourly interval is given in figure 4a.

lations only in the case of the mesopelagic *T. crenularis*, which is an oceanic species. *Sebastes* spp., *C. saira*, and *A. fimbria* are most abundant as adults along the outer shelf and over the slope, and their larvae are advected extensively into deep water.

Early Life-History Characteristics for Species with Neustonic Larvae

Larval length distributions are compared between the neuston and bongo collections for the facultative neustonic species with larvae abundant in the water

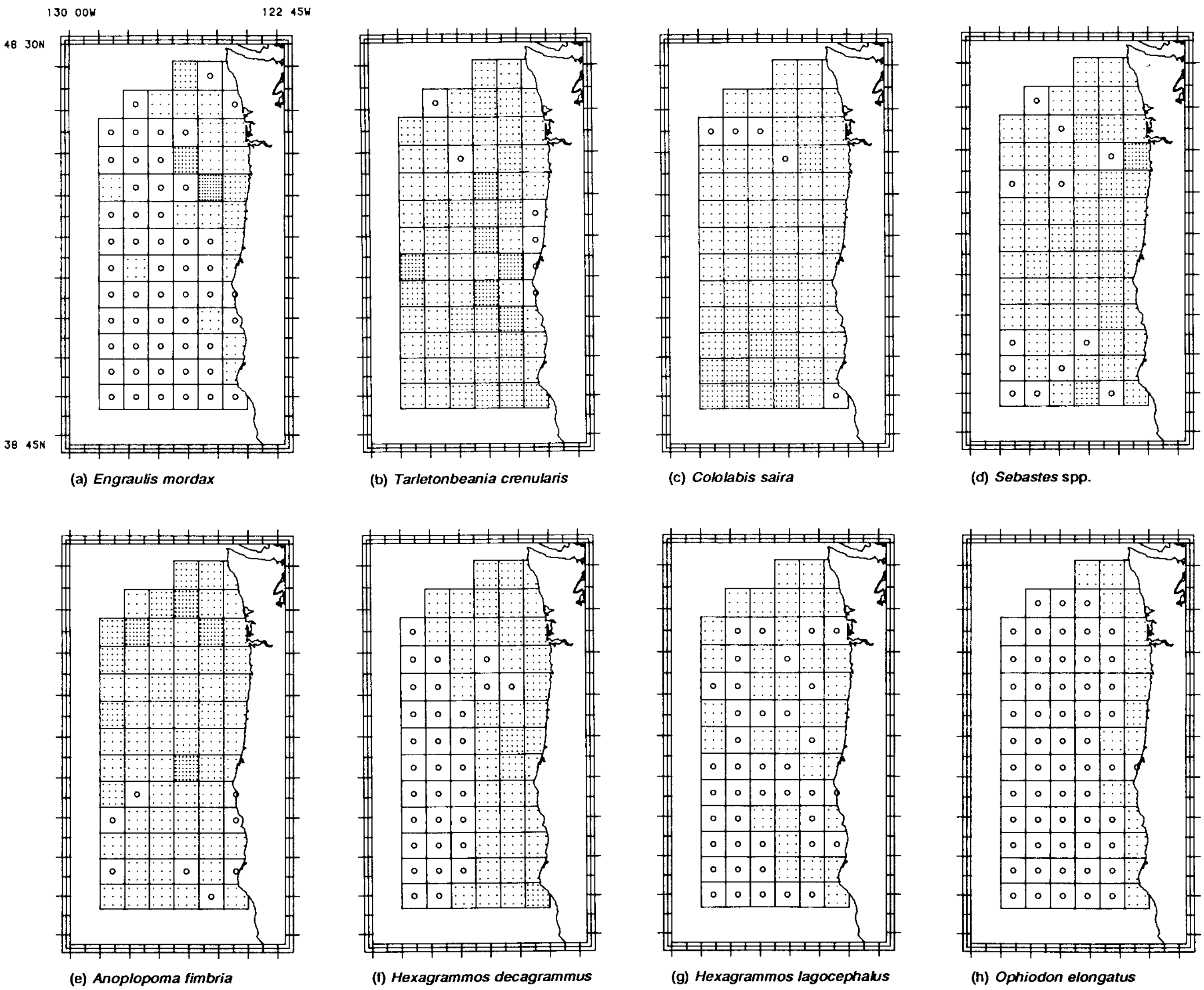
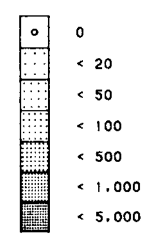


Figure 7. Patterns of distribution for dominant taxa of fish larvae in the neuston. Data are combined for 10 cruises, and mean abundance of larvae (no./1000 m³) is calculated for each grid square.



column (figure 9a–j). A broader size range of specimens was encountered in the neuston than in the bongo samples. Neustonic specimens were significantly larger, and many were juveniles. Most of the larvae taken in the bongo samples were less than 10 mm long, or in the case of *A. hexapterus* less than 15 mm, whereas neustonic larvae were mostly longer than 10 mm (figure 9). The difference was greatest for *Tarletonbeania crenularis*: its smallest neustonic specimens were 19 mm (figure 9c,d). Length at transformation for this species is given at 19–21 mm (Matarese et al. 1989). It seems, therefore, that among the facultative neustonic species, mainly the well-developed, large larvae and young juveniles migrate to the surface zone at night.

Among the obligate neustonic species, a wide size range of larvae and early juveniles was encountered, and most larvae were larger than 10 mm (figure 10a–i). Catches of early juveniles varied among species. Length at transformation to juvenile stage varies among these species. For some, such as the hexagrammids and cottids, the transition stage is prolonged, and a prejuvenile, neustonic stage is

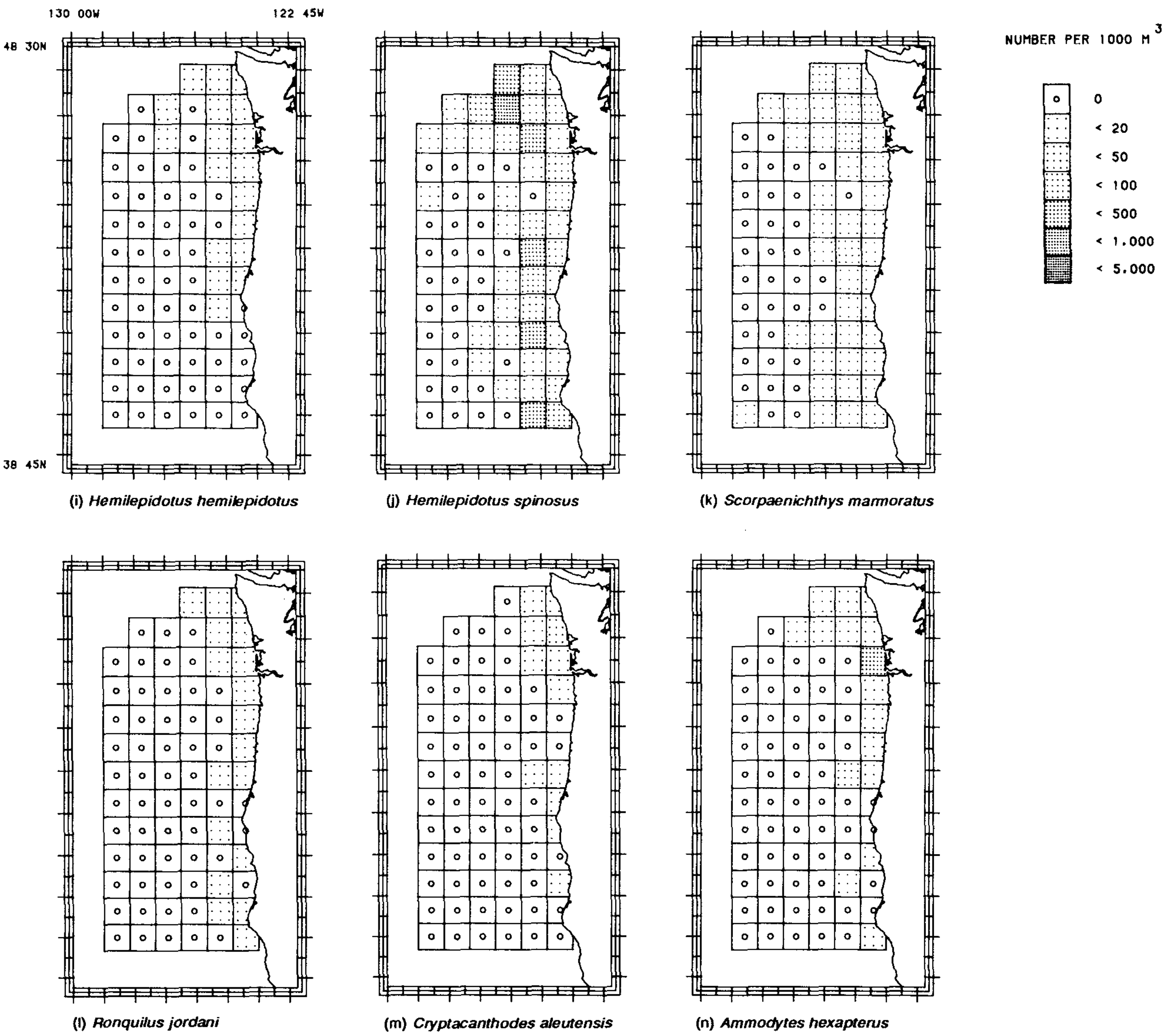
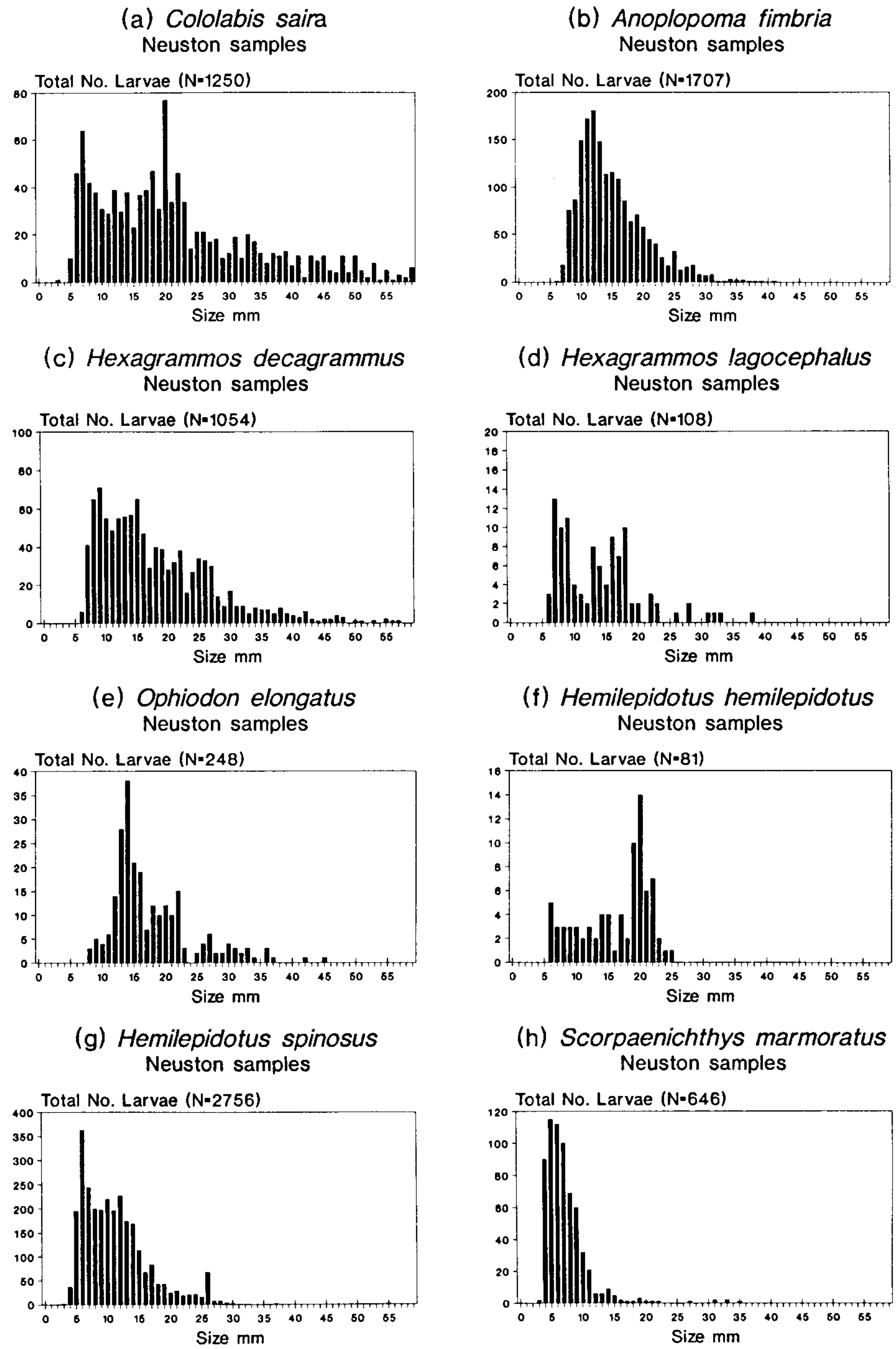


Figure 8. Patterns of distribution for dominant taxa of fish larvae in the neuston (continued). Data are combined for 10 cruises, and mean abundance of larvae (no./1000 m³) is calculated for each grid square.

recognized (Kendall et al. 1984). This prejuvenile stage differs from both the larval and the adult stage, and the morph resembles a herring, with silvery sides.

By the time *Cololabis saira* have reached a body length of 25 mm, most adult characters are present. These juveniles (>25 mm) were well represented in the catches, although less abundant than the larval stages (figure 10a). Large larvae and early juveniles (>30 mm) were scarce for *Anoplopoma fimbria* (figure 10b). Prejuvenile stages (>20–25 mm) for the hexagrammids *Hexagrammos decagrammus*, *H. lagocephalus*, and *Ophiodon elongatus* were present but in low concentrations, and specimens longer than 40 mm were rare. Lengths at transformation for the cottids *Hemilepidotus hemilepidotus* (19–23 mm), *H. spinosus* (19 mm), and *Scorpaenichthys marmoratus* (14 mm) are less than for the hexagrammids (Matarese et al. 1989). Prejuveniles of these species were scarce, and specimens longer than 40 mm were absent from the neuston samples (figure 10f–h).

Obligate neustonic larvae and larvae that are abundant deeper in the water column differ strikingly in their levels of pigmentation, particularly on the dorsal surface (Zaitsev 1970; Hempel and Weikert 1972; Moser 1981). The obligate neustonic larvae (*Cololabis saira*, *Anoplopoma fimbria*, hexagrammids, cottids, and *Cryptacanthodes aleutensis*) all have heavy melanistic pigmentation along the dorsal surface, particularly at the late larval and juvenile stage (Matarese et al. 1989). The intensity of pigmentation and beginning of its development, how-



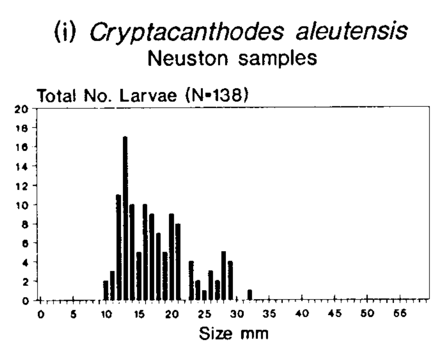


Figure 9. Length-frequency distributions among obligate neustonic fish larvae and juveniles in neuston samples. Catches combined for 10 cruises. N = total number of larvae caught for each species.

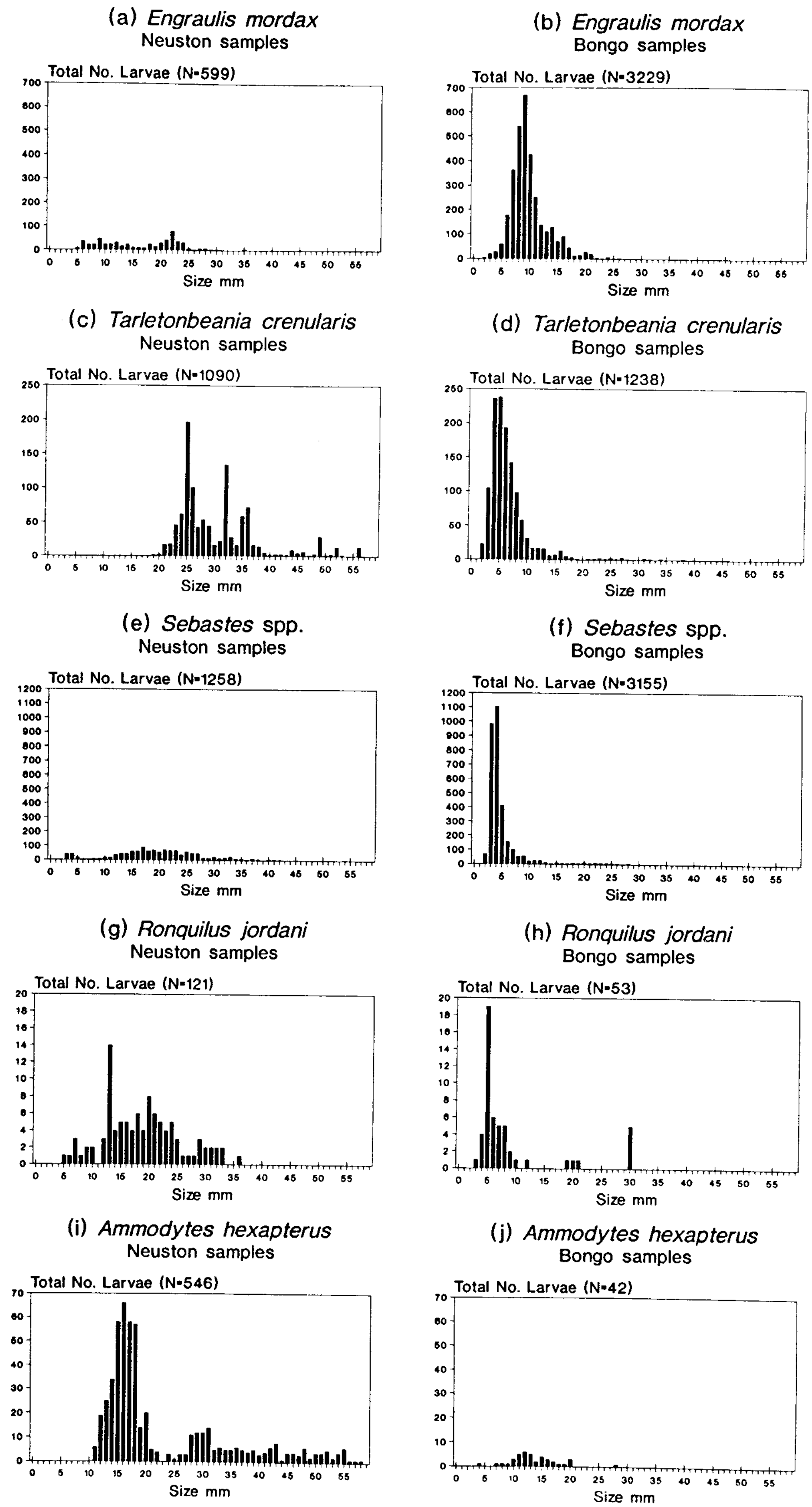


Figure 10. Length-frequency distributions among facultative neustonic fish larvae and juveniles in neuston and bongo samples. Catches combined for 10 cruises. N = total number of larvae caught for each species.

TABLE 8
Habitat and Spawning Strategies among Species with Obligate Neustonic Larvae

Species	Habitat	Spawning season	Spawning mode	Larval hatch size (mm)
Cololabis saira	Epipelagic Shelf and slope	Winter–autumn Peak: Feb.–July	Epipelagic, eggs attached to flotsam	6–8.5
Anoplopoma fimbria	Semidemersal Shelf and slope	Winter–spring Peak: Feb.–March	Bathypelagic	6
Hexagrammos decagrammus	Demersal Coastal–inshore	Autumn–spring Peak: Dec.	Demersal, shallow water, adhesive eggs	7–9
Hexagrammos lagocephalus	Demersal Coastal–inshore	Autumn–winter Peak: Dec.–Jan.	Demersal, shallow water, adhesive eggs	7–9
Ophiodon elongatus	Demersal Coastal and shelf	Winter–spring Peak: Dec.–Feb.	Demersal, shallow water, adhesive eggs	7–10
Hemilepidotus hemilepidotus	Demersal Coastal and shelf	Winter–spring Peak: Dec.–Jan.	Demersal, shallow water, adhesive eggs	5–6
Hemilepidotus spinosus	Demersal Coastal–inshore	Winter–spring Peak: Dec.–Feb.	Demersal, shallow to moderately deep water	5
Scorpaenichthys marmoratus	Demersal Coastal–inshore	All year Multiple spawning	Demersal, shallow water, adhesive eggs	4–6
Cryptacanthodes aleutensis	Epi/meso-benthal Shelf and slope	Winter–spring Peak: Jan.–March	Demersal, moderately deep water	10?

Life-history information from Matarese et al. 1989.

ever, varies among species. In contrast, in the facultative neustonic larvae identified here dorsal melanistic pigmentation is poorly developed.

Habitat and spawning strategies among the west coast species with obligate neustonic larvae are similar (table 8). Except for *Cololabis saira*, which is epipelagic, all live on or close to the bottom, mainly in coastal waters. *Cololabis saira*, *A. fimbria*, and *C. aleutensis* extend into deeper water than the other species, and they are common near the slope. The spawning season for most species is short, with a winter peak, usually from December to March. In contrast, *C. saira* has an extended spawning period from winter to autumn, with a peak from February to July, and *Scorpaenichthys marmoratus* is a multiple spawner throughout the year. *Cololabis saira* and *A. fimbria* are the only species that do not have demersal eggs. Eggs of *C. saira* are epipelagic and are usually attached to flotsam, whereas *A. fimbria* eggs are bathypelagic. Hexagrammids and cottids tend to have adhesive eggs that are attached to the substratum, either rocks or seaweed. Size at hatching among the obligate neustonic larvae is greater than 5 mm, and may be up to 10 mm, except for *S. marmoratus*, which hatches at a minimum size of about 4 mm. These sizes are relatively large in comparison with most species that hatch at sizes <5 mm. For instance, *E. mordax* hatches at 2.5–3 mm and *T. crenularis* at <3 mm (Matarese et al. 1989). Obligate neustonic larvae therefore tend to be relatively well developed at hatching.

DISCUSSION

Data from this study and from previous ichthyoplankton investigations indicate a neustonic assemblage of fish eggs and larvae off the coasts of Washington, Oregon, and northern California (Richardson[1]; Ahlstrom and Stevens 1976; Gruber et al. 1982; Brodeur et al. 1987; Shenker 1985, 1988). This assemblage is most diverse over the shelf and continental slope, but several species are also distributed throughout the oceanic zone.

The three categories of neustonic occurrence among the ichthyoplankton follow the general classification scheme for neustonic organisms (Zaitsev 1970; Hempel and Weikert 1972; Peres 1982). Obligate and facultative members of the neuston include larvae and early juveniles that actively seek out the surface zone.

The nine species of fish larvae assigned here to the obligate neustonic category appear to live permanently in the surface zone. These species occupy an exclusively neustonic niche during their larval and early juvenile or prejuvenile stages. Their larvae are scarce or absent in subsurface ichthyoplankton collections from coastal and oceanic waters off Washington, Oregon, and northern California (Richardson 1973; Richardson and Pearcy 1977; Richardson et al. 1980; Boehlert et al. 1985; Brodeur

[1]S. L. Richardson. 1975. Oregon's coastal ichthyoneuston: a preliminary report. Unpublished report presented at American Society of Ichthyologists and Herpetologists, Williamsburg, Virginia.

et al. 1985; Doyle et al. in press). The reduced abundance of some of these larvae in neuston samples collected during daylight is attributed primarily to their visual avoidance of the sampling gear. It is also possible, however, that some larvae migrate vertically out of the surface layer during the day.

The facultative members differ from the obligate members in that they do not remain permanently in the neuston but migrate vertically in a diel pattern, moving up to the surface around dusk and remaining there until the onset of daylight.

Fish eggs are present in the neuston as "strays," accumulating at the surface because of positive buoyancy. Also included in this category are many species of larvae that appear frequently in the neuston but are much more abundant in the subsurface zone. For these species, the neuston represents the upper extreme of their vertical range.

In their review of the neuston of the subtropical and boreal northeast Atlantic Ocean, Hempel and Weikert (1972) documented the scarcity of very young fish larvae in the surface zone. Their neuston net caught mainly late larval and juvenile stages. The same was true for Shenker's (1985, 1988) ichthyoneuston collections off the Oregon coast. Comparing the length-frequency distributions of larvae caught in the bongo samples with those of the neuston collections in this study, I found that neustonic larvae are generally larger than those in the subsurface zone. The difference was particularly striking among the facultative larvae, indicating that those that migrate to the surface at night are well-developed larvae and early juveniles. Tully and O'Ceidigh (1989a) made the same observation for facultatively neustonic species of fish larvae in Galway Bay on the west coast of Ireland.

The scarcity of larvae less than 10 mm long among the obligate ichthyoneuston can be related to the strategies displayed by these species. Except for *Cololabis saira*, which is an epipelagic spawner, these species either deposit their eggs on the bottom—frequently in gelatinous masses that adhere to rocks or weed—or spawn bathypelagic eggs, e.g., *Anoplopoma fimbria* (Matarese et al. 1989). After hatching, larvae migrate to the surface, and small yolk-sac larvae are therefore likely to be dispersed throughout the water column rather than concentrated in the neuston. Their scarcity in the bongo samples may be attributed to the inefficiency of the gear in sampling relatively low densities of larvae scattered throughout the water column, in comparison with neuston nets, which efficiently sample larvae that are concentrated at the surface. Fecundity is also relatively low among the species with obligate neustonic larvae, and the larval hatch size is correspondingly high (Matarese et al. 1989), further contributing to the larger larval sizes in the neuston.

The implication from these length-frequency observations is that it is advantageous for larvae in the neuston to be well developed. With increasing size, fish larvae become more agile at seeking food and avoiding predators, thus enhancing their chances of survival. The size range of available food organisms also expands with increasing larval size. Hempel and Weikert (1972) observed that because phytoplankton seems to be scarce in the immediate vicinity of the surface, neustonic fish larvae are carnivorous or omnivorous. On depletion of the yolk sac, small first-feeding larvae may therefore be more vulnerable to starvation than they would be deeper in the water column.

Eggs that adhere to the substratum help retain young fish close to the adult habitat. The commencement of a planktonic existence is postponed to the larval phase, considerably reducing the period of drift in the plankton. It therefore seems contradictory that the dominant hexagrammid and cottid species inhabiting the coastal and inshore zone off Washington, Oregon, and northern California have larvae that are essentially neustonic. Their presence in the neuston subjects them to wind transport as well as to surface currents. In the dynamic surface zone they are much more likely to be widely dispersed away from suitable habitats for settlement than if they were concentrated deeper in the water column. The distribution patterns documented for all the neustonic larval species during this study indicate that larval drift is generally extensive in the surface zone of this region. Even among some of the inshore species such as *Hexagrammos decagrammus*, *H. lagocephalus*, and *Hemilepidotus spinosus*, the distribution of neustonic larvae extends well into the slope and oceanic zone. Larvae of these species encountered over deep water probably are lost to the adult populations and do not survive to recruitment. The widespread dispersal of larvae in the neuston may be facilitated by various mesoscale oceanographic features as well as wind transport and prevailing patterns of circulation. Eddies, offshore jets, meanders in the alongshore currents, and surface slicks associated with internal waves may contribute significantly to the onshore-offshore dispersal of ichthyoplankton (Shanks 1983; Kingsford and Choat 1986; Shenker 1988).

The prevalent spawning season among species with obligate neustonic larvae, however, is such that the larvae are most abundant when Ekman surface transport is onshore, and downwelling is occurring along the coast. The peak period of spawning for most species is winter; for the coastal species this favors retention of their larvae in the coastal zone, in the vicinity of the adult habitats. In their review of reproductive strategies among fish species in the California Current system, Parrish et al. (1981) observe a correspondence to the major features of surface transport that minimizes larval advection out of suitable habitats. Richardson et al. (1980) and Doyle et al. (in press) document a coastal assemblage of fish larvae in the plankton along the Washington, Oregon, and northern California coasts. This assemblage is present during winter and spring and, for the most part, absent from summer to autumn, when upwelling and offshore Ekman transport prevail. The spawning seasons among species with exclusively neustonic larvae therefore reflect the general correspondence between spawning strategies in this region and the prevailing circulation patterns.

By the time the neustonic larvae have developed to the juvenile stage, the transition to offshore Ekman transport and upwelling of oceanic water may have taken place along the coast. If young juveniles are still present in the neuston, they are likely to be transported away from the coastal zone. Postlarvae and juveniles of *Cololabis saira* and *Anoplopoma fimbria* remain at the surface (Hart 1973; Kendall and Matarese 1987) and therefore are widely distributed in deep water as well as along the coast. Among coastal and inshore hexagrammids and cottids, there is some evidence to suggest that large prejuveniles and juveniles migrate out of the neuston with the onset of upwelling, thus largely avoiding offshore transport. Shenker (1985, 1988) documented the disappearance of hexagrammid and cottid juveniles from neuston collections off Oregon in association with the beginning of upwelling and offshore Ekman transport. He proposed that upwelling triggers these fishes' settlement to the demersal habitat used by older juveniles and adults and that a possible stimulus for this transition is the breakdown of the thermocline.

Several factors that may limit the successful habitation of the neuston by fish eggs and larvae characterize the surface layer (Zaitsev 1970; Hempel and Weikert 1972). They include high levels of UV radiation, which may cause physiological stress or genetic damage; intensive wave action, which may cause mechanical damage to organisms; and a reduced biota, which may mean a diminished availability of prey. In addition, the high light intensity at the surface during the day is likely to make neustonic fish eggs and larvae more visible to predators. Surface transport mechanisms that disperse larvae away from a suitable adult habitat are another disadvantage associated with the neuston.

Adaptations to these potentially adverse factors are, however, apparent among neustonic ichthyoplankton in general (Zaitsev 1970; Hempel and Weikert 1972; Moser 1981) and specific to the U.S. west coast. For instance, the heavy melanistic pigmentation on the dorsal surface of larvae and early juveniles in the obligate neustonic category is considered to be a protective adaptation in response to high light intensity and associated UV radiation. Mechanical resistance of fish eggs is high, and eggs are believed to be endangered by wave action only during the first few hours after spawning (Hempel 1979), when they are deeper in the water column. Recently hatched larvae are likely to be much more vulnerable to mechanical damage, but—as observed off the U.S. west coast and elsewhere (Hempel and Weikert 1972)—in most species these larvae are absent from the neuston. The well-developed nature of neustonic larvae may be adaptive both in terms of seeking prey—which may be scarce in the neuston—and avoiding predators, to which they may be more visible than if they were deeper in the water column. As mentioned previously, the detrimental effects of surface transport along the west coast are reduced by the synchrony of spawning seasons. The demersal spawning mode is also an adaptive feature in this respect.

Given the hazardous conditions that may prevail in the sea-surface layer, it is interesting that certain species of fish along the U.S. west coast use this biotope as the ecological niche for their young. Advantages to a neustonic existence for ichthyoplankton may include enhanced growth and reduced levels of predation. For instance, accelerated embryogenesis is characteristic of fish eggs in the neuston, where temperatures are higher because of the intensive absorption of solar radiation in the upper 10 cm of the water column (Zaitsev 1970; Peres 1982). Positive buoyancy among certain species of fish eggs, resulting in their concentration in the neuston, may therefore be considered adaptive. Larval growth is also likely to be enhanced at the surface, shortening the most vulnerable early stage. For example, *Anoplopoma fimbria* larvae are known to grow rapidly (up to 2 mm per day) during spring off the U.S. west coast (Kendall and Matarese 1987). Hempel and Weikert (1972) propose that the surface layer of the ocean serves as a refuge from predators, particularly during the daytime, because of the relative scarcity of invertebrates and fishes, making it a less attractive hunting area for large predators. Hempel and Weikert suggest that the few enduring neustonic metazoa, including fish larvae, encounter relatively little predatory pressure during the daytime.

Based on their investigations of feeding among fish larvae and juveniles in the neuston of Galway Bay (west coast of Ireland), Tully and O'Ceidigh (1989b) conclude that feeding conditions at the surface are unique and that neustonic species are adapted to feed more successfully in this environment. It is likely that the most important advantage to a neustonic existence for fish larvae is the suitability of the surface layer as a trophic niche. Evidence that facultatively neustonic species of fish larvae migrate to the surface with the onset of darkness and return to deeper layers in the morning supports this hypothesis. A feature common to all investigated regions in the world ocean is that many plankton organisms migrate into the surface zone as daylight fades, thus making the neuston a much richer biotope at night, with higher concentrations of food suitable for fish larvae (Zaitsev 1970; Hempel and Weikert 1972; Peres 1982; Holdway and Maddock 1983a, b).

Apart from the high densities of zooplankton that may occur in the neuston at night, mesoscale physical features such as fronts, convergence zones, and surface slicks can cause aggregations of plankton at the surface, bringing high concentrations of fish larvae together with high concentrations of suitable prey. Kingsford and Choat (1986) found that small fish and zooplankton from surface waters off New Zealand were denser in slicks than in the rippled waters adjacent to them. Off Oregon, Shenker (1988) documented aggregations of Dungeness crab megalopae and fish larvae and juveniles in association with nearshore surface convergence zones and the periphery of the Columbia River plume. High concentrations of neustonic ichthyoplankton and zooplankton have also been found in association with the frontal structure around the discharge plume of the Mississippi River (Grimes and Finucane 1991). Clearly, the neuston biotope offers unique trophic conditions for young fish, and Moser (1981) proposes that the neustonic zone may be a permanent food patch available to larval fish. The feeding habits of the neustonic fish larvae described in the present study need to be investigated thoroughly, however, for a more complete understanding of the neustonic realm's importance in the early life history of fishes off the U.S. west coast.

ACKNOWLEDGMENTS

Suggestions and comments by three anonymous reviewers and by Art Kendall and Ann Matarese of the Alaska Fisheries Science Center in Seattle are gratefully acknowledged; they helped considerably with the final draft of this manuscript.

LITERATURE CITED

Ahlstrom, E. H., and E. Stevens. 1976. Report of neuston (surface) collections made on an extended CalCOFI cruise during May 1972. Calif. Coop. Oceanic Fish. Invest. Rep. 18:167–180.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. NOAA Tech. Rep. NMFS, SSRF-671, 103 pp.

Bates, R. D. 1984. Ichthyoplankton off Washington, Oregon and northern California, October–November 1981. NOAA, NMFS, NWAFC Proc. Rep. 84-12, 41 pp.

Boehlert, G. W., D. M. Gadomski, and B. C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83:611–621.

Brodeur, R. D. 1989. Neustonic feeding by juvenile salmonids in coastal waters of the northeast Pacific. Can. J. Zool. 67:1995-2007.

Brodeur, R. D., D. M. Gadomski, W. G. Pearcy, H. P. Batchelder, and C. B. Miller. 1985. Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. Estuarine Coastal Shelf Sci. 21:365–378.

Brodeur, R. D., W. G. Pearcy, B. C. Mundy, and R. W. Wisseman. 1987. The neustonic fauna in coastal waters of the northeast Pacific: abundance, distribution and utilization by juvenile salmonids. Oregon Sea Grant publ. ORESU-T-87-001, 61 pp.

Clark, J. B. 1984. Ichthyoplankton off Washington, Oregon and northern California, May–June 1981. NOAA, NMFS, NWAFC Proc. Rep. 84-11, 45 pp.

———. 1986a. Ichthyoplankton off Washington, Oregon and northern California, November–December 1983. NOAA, NMFS, NWAFC Proc. Rep. 86-14, 43 pp.

———. 1986b. Ichthyoplankton off Washington, Oregon and northern California, May–June 1982. NOAA, NMFS, NWAFC Proc. Rep. 87-01, 44 pp.

Clark, J. B., and A. W. Kendall, Jr. 1985. Ichthyoplankton off Washington, Oregon and northern California, April–May 1983. NOAA, NMFS, NWAFC Proc. Rep. 85-10, 48 pp.

Clark, J. B., and D. S. Savage. 1988. Ichthyoplankton off Washington, Oregon and northern California, March–April 1984. NOAA, NMFS, NWAFC Proc. Rep. 88-09, 57 pp.

Doyle, M. J., W. W. Morse, and A. W. Kendall, Jr. In press. A comparison of larval fish assemblages in the temperate zone of the northeast Pacific and northwest Atlantic. Contributions in Science. Natural History Museum of Los Angeles County. Proceedings of American Fisheries Society, Annual Larval Fish Conference, Special Symposium: Larval Fish Assemblages in Relation to Oceanographic Boundaries. Los Angeles, June 1991.

Dunn, J. R., and W. C. Rugen. 1989. A catalog of Northwest and Alaska Fisheries Center ichthyoplankton cruises, 1965–1988. NOAA, NMFS, NWAFC Proc. Rep. 89-04, 197 pp.

Fiedler, P. C., and R. M. Laurs. 1990. Variability of the Columbia River plume observed in visible and infrared satellite imagery. Int. J. Remote Sensing 11(6):999–1010.

Grimes, C. B., and J. H. Finucane. 1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75:109–119.

Gruber, D., E. H. Ahlstrom, and M. M. Mullin. 1982. Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23:172–179.

Hart, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180, 740 pp.

Hempel, G. 1979. Early life history of marine fish. The egg stage. Washington Sea Grant Publication. Seattle: Univ. Wash. Press, 70 pp.

Hempel, G., and H. Weikert. 1972. The neuston of the subtropical and boreal northeastern Atlantic Ocean. A review. Mar. Biol. 76:70–88.

Hickey, B. M. 1979. The California Current system — hypothesis and facts. Prog. Oceanogr. 8:191–279.

———. 1989. Patterns and processes in circulation over the shelf and slope. *In* Coastal oceanography of Washington and Oregon, M. R. Landry and B. M. Hickey, eds. Amsterdam: Elsevier, pp. 41–116.

Hickey, B. M., and M. R. Landry. 1989. Coastal oceanography of Washington and Oregon: a summary and a prospectus for future studies. *In* Coastal oceanography of Washington and Oregon, M. R. Landry and B. M. Hickey, eds. Amsterdam: Elsevier, pp. 595–599.

Holdway, P., and L. Maddock. 1983a. A comparative survey of neuston: geographical and temporal distribution patterns. Mar. Biol. 76: 263–270.

———. 1983b. Neustonic distributions. Mar. Biol. 77:207–214.

Huyer, A., R. D. Pilsbury, and R. L. Smith. 1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20(1):90–95.

Kendall, A. W., Jr., and J. Clark. 1982a. Ichthyoplankton off Washington, Oregon and northern California, April–May 1980. NOAA, NMFS, NWAFC Proc. Rep. 82-11: 44 pp.

———. 1982b. Ichthyoplankton off Washington, Oregon and northern California, August 1980. NOAA, NMFS, NWAFC Proc. Rep. 82-12: 43 pp.

Kendall, A. W., Jr., and A. C. Matarese. 1987. Biology of eggs, larvae and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. Mar. Fish. Rev. 49(1):1–13.

Kendall, A. W., Jr., E. H. Ahlstrom, and H. G. Moser. 1984. Early life history stages of fishes and their characters. *In* Ontogeny and systematics of fishes, H. G. Moser et al., eds. Special Publication No. 1, American Society of Ichthyologists and Herpetologists. Lawrence, Kans.: Allen Press, pp. 11–22.

Kingsford, M. J., and J. H. Choat. 1986. Influence of surface slicks on the distribution and onshore movements of small fish. Mar. Biol. 91:161–171.

Matarese, A. C., A. W. Kendall, Jr., D. M. Blood, and B. M. Vinter. 1989. Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Tech. Rep. NMFS-80, 625 pp.

Moser, H. G. 1981. Morphological and functional aspects of marine fish larvae. *In* Marine fish larvae. Morphology, ecology and relation to fisheries, R. Lasker, ed. Seattle: Univ. Wash. Press, pp. 90–131.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Peres, J. M. 1982. Specific pelagic assemblages: 1. Assemblages at the air-ocean interface. *In* Marine ecology, O. Kinne, ed. 5(1):313–372.

Richardson, S. L. 1973. Abundance and distribution of larval fishes in waters off Oregon, May–October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. U.S. Fish. Bull. 71(3):697–711.

———. 1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855–876.

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull. 75:125–146.

Richardson, S. L., J. L. Laroche, and M. D. Richardson. 1980. Larval fish assemblages and associations in the northeast Pacific Ocean along the Oregon coast, winter–spring 1972–1975. Estuarine Coastal Mar. Sci. 11:671–699.

Sameoto, D. D., and L. O. Jaroszynski. 1969. Otter surface trawl: a new neuston net. J. Fish. Res. Board Can. 26:2240–2244.

Savage, D. S. 1989a. Ichthyoplankton off Washington, Oregon and northern California, April–May 1985. NOAA, NMFS, NWAFC Proc. Rep. 89-06, 55 pp.

———. 1989b. Ichthyoplankton off Washington, Oregon and northern California, January 1987. NOAA, NMFS, NWAFC Proc. Rep. 89-08, 68 pp.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311–315.

Shenker, J. M. 1985. Biology of neustonic larval juvenile fishes and crabs off Oregon, 1984. Ph.D. thesis, Oregon State University, Corvallis, 156 pp.

———. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. Fish. Bull. 86:299–317.

Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fish. Tech. Paper No. 175, 100 pp.

Strub, P. T., J. S. Allen, R. L. Smith, and R. C. Beardsley. 1987. Seasonal cycles of currents, temperatures, winds and sea level over the northeast Pacific continental shelf. J. Geophys. Res. 92(C2): 1507–1526.

Tully, O., and P. O'Ceidigh. 1989a. The ichthyoneuston of Galway Bay (Ireland). I. The seasonal, diel and spatial distribution of larval, post-larval and juvenile fish. Mar. Biol. 101:27–41.

———. 1989b. The ichthyonesuton of Galway Bay (west of Ireland). II. Food of post-larval and juvenile neustonic and pseudoneustonic fish. Mar. Ecol. Prog. Ser. 51:301–310.

Zaitsev, Y. P. 1970. Marine neustonology. Naukova Dumka, Kiev. Translated from Russian by Israel Program for Scientific Translations, Jerusalem, 207 pp.