

AN ABSTRACT OF THE THESIS OF

Helena Molina Ureña for the degree of Master of Science in
Oceanography presented on December 5, 1989.

TITLE: Distribution of the Eggs and Larvae of Some Flatfishes (Pleuronectiformes)
off Washington, Oregon and Northern California, 1980-1983.

Redacted for Privacy

Abstract approved: _____

William G. Pearcy



Seasonal and geographic distributions of egg and larval abundances of eight species of flatfishes (Pleuronectiformes: Pleuronectidae, Paralichthyidae) were analyzed from seven cruises during 1980 to 1983, between 40 and 48°N (Cape Mendocino, California, to Juan de Fuca Strait, Washington). Temporal and spatial patterns were related to physical conditions of the study area.

A prolonged spawning season was found for *Parophrys vetulus*, *Citharichthys sordidus* and *C. stigmaeus* (fall spawners) and for *Psettichthys melanostictus* (spring spawner). *Isopsetta isolepis*, *Glyptocephalus zachirus* and *Lyopsetta exilis* were other spring spawners and *Microstomus pacificus* was a winter spawner.

Three pleuronectids (*I. isolepis*, *P. vetulus* and *P. melanostictus*) had coastal distributions. Several mechanisms of larval retention in nearshore waters were suggested: spawning during downwelling season, spawning close to shore, vertical migration or avoidance of the upper few meters of the water column and avoidance of regions of intense upwelling. The two coastal-transitional types appeared to be differentially affected by offshore Ekman transport; e.g., early stages of *G. zachirus*

occurred farther offshore than those of *L. exilis* during a given period of intense upwelling. *M. pacificus* was considered an offshore-transitional species. Geographic distributions of both parichthyids (*Citharichthys* spp.) were highly dependent upon the direction and intensity of the Ekman transport.

During the 1982-1983 El Niño Norte the changes in egg and larval distributions of most taxa were consistent with increased poleward advection from regions south of the study area, reduced upwelling activity and higher temperatures.

DISTRIBUTION OF THE EGGS AND LARVAE OF SOME FLATFISHES
(PLEURONECTIFORMES) OFF WASHINGTON, OREGON AND
NORTHERN CALIFORNIA, 1980-1983.

by

Helena Molina Ureña

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed December 5, 1989

Commencement June 1990

APPROVED

Redacted for Privacy

Professor of Oceanography in charge of major

Redacted for Privacy

Dean of School of Oceanography

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 5, 1989

A Tatica y mi Negrita de los Angeles,
a quienes debo lo que soy y lo que tengo.

A Papi, Mami, Silvia y Ronald,
cuyo amor me ha impulsado cada paso del camino.

A Tita, Tito, Abuela y Abuelo,
modelo de amor, entrega, honestidad,
deseo de superación y responsabilidad.

ACKNOWLEDGEMENTS

First and foremost, my deepest gratitude goes to my mentor and advisor, Dr. William G. Percy. His endless patience, encouraging guidance and critical reviews made the successful completion of this study possible. I am also particularly indebted to Dr. Art Kendall Jr. (Northwest and Alaska Fisheries Center, NWAFC, Seattle), for supplying the data and larval specimens from the NWAFC collection. Likewise, I am grateful to Jay B. Clark, Richard Bates, and the staff of Resource Assessment and Conservation Engineering (RACE) division of NWAFC, particularly Ann Matarese, Debbie Blood and Bev Vinter.

I wish to thank Dr. Douglas Markle, Dr. Roger Petersen, Dr. Tim Cowles and Dr. Norman Bishop for serving on my committee and for their critical comments on the thesis. Joe Fisher and Dr. Amy Schoener also reviewed the manuscript. I am particularly very grateful to Dr. Douglas Markle, Dr. Jane Huyer and Dr. Bob Smith for their invaluable help through the various stages of my study.

Countless introductory courses to the world of computers were kindly given to me by officemates Alton Chung and Joe Fisher. I thank them and Beth Hacker and Matt Wilson for their guidance and support through my coursework and during the first steps of my research. To them all my gratitude for their patience, perseverance and moral support. Many people also helped me in many different ways during my stay in Corvallis. Dr. Jeff Gonor, Dr. Dave Stein, Dr. Steve Neshyba, Donna Obert, Joy Burke, Susan Clements and Joyce Weathers were always ready to give me a hand whenever I needed it.

The Fulbright Scholarship made possible my graduate studies in the United States. My gratitude goes specially to my field representative through the Institute

of International Education (IIE), Ms. Paula Carter, whose kindness and reassurance brightened even the darkest day.

I would like to give the most special thanks to Dr. Lawrence Small and Consuelo Carbonell, for believing in me even when I had almost given up, and showing me the light at the end of the tunnel.

There will not be enough words to thank the support provided by my dearest friends from the most diverse parts of the world. Among the Costa Rican colony, special thanks to Roberto, Patricia, Enrique and Alejandro, who were my family in Corvallis. Other wonderful friends with whom I shared dreams, joys and tears were Sherri & Ralph, Susanne & Ferran, Heide-Rose, Wei, Tom, John Saturnino, Satoko & Masa, Christian & Jutta, Sharon, Consuelo & Sandy and the Peasley and Groshong families, as well as the volleyball gang. Thanks to all of you for the constant support and friendship during the hard times, and mostly, for being just the way you are.

Finalmente, el apoyo moral incondicional de mi familia y amigos en Costa Rica fue la fuerza principal que me impulsó durante todo el tiempo que estuve lejos de casa. Este trabajo no habría sido posible sin tenerlos a ellos conmigo a cada paso del camino. Dios los bendiga.

This research was partially supported by the National Oceanographic and Atmospheric Administration and the Mineral Management Service (Interagency Agreement No. 14-12-0001-30429), Grant NA-88-ABH-00051.

TABLE OF CONTENTS

INTRODUCTION	1
Ichthyoplankton studies off Washington, Oregon and northern California.	3
Review of biology of flatfishes	3
MATERIALS AND METHODS	10
Staging of larvae	12
Taxonomic limitations	15
Hydrographic data and region definitions	16
Data analysis	17
RESULTS	19
Physical conditions of the study area	19
Upwelling indices	19
Circulation patterns	21
The Columbia Plume	22
Temperature (T), Salinity (S) and Density (σ_t)	23
Biological data	24
Egg abundances	24
Frequency of occurrence of eggs (F.O.)	26
Larval abundances	28
Frequency of occurrence of larvae (F.O.)	29
Seasonality of early stages	31
Description of larval stages	34
Seasonal variation of larval lengths and developmental stages	40
Geographic distribution	45
DISCUSSION	58
Spawning seasons	58
Fall spawners (<i>Parophrys vetulus</i> , <i>Citharichthys sordidus</i> , <i>C. stigmaeus</i>).	58
Winter spawners (<i>Microstomus pacificus</i>).	61
Spring spawners (<i>Isopsetta isolepis</i> , <i>Psettichthys melanostictus</i> , <i>Glyptocephalus zachirus</i> , <i>Lyopsetta exilis</i>).	62
Spawning strategies	64
Geographic distribution	67
Onshore-offshore	67
Latitudinal trends	76
The 1982-1983 El Niño	79
SUMMARY AND CONCLUSIONS	85
REFERENCES	88
APPENDICES	96

LIST OF APPENDIX FIGURES

<u>FIGURE</u>	<u>PAGE</u>
1. General sampling locations of bongo and neuston stations off Washington, Oregon and northern California for seven cruises during the 1980-1983 period. The eight geographical regions considered in this study are also shown.	96
2. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1980.	97
3. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1981.	98
4. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1982.	100
5. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1983.	101
6. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during mid-spring, 1980.	102
7. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during summer, 1980.	104
8. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during late-spring, 1981.	106
9. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during mid-fall, 1981.	108
10. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during late-spring, 1982.	110
11. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during mid-spring, 1983.	112

LIST OF APPENDIX FIGURES (Continued)

- | | | |
|-----|---|-----|
| 12. | Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during late-fall, 1983. | 114 |
| 13. | Standard length (mm) distribution by developmental stage of larval Pacific sanddab (<i>Citharichthys sordidus</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 116 |
| 14. | Standard length (mm) distribution by developmental stage of larval speckled sanddab (<i>Citharichthys stigmaeus</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 117 |
| 15. | Standard length (mm) distribution by developmental stage of larval rex sole (<i>Glyptocephalus zachirus</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 118 |
| 16. | Standard length (mm) distribution by developmental stage of larval butter sole (<i>Isopsetta isolepis</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 119 |
| 17. | Standard length (mm) distribution by developmental stage of larval slender sole (<i>Lyopsetta exilis</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 120 |
| 18. | Standard length (mm) distribution by developmental stage of larval Dover sole (<i>Microstomus pacificus</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 121 |
| 19. | Standard length (mm) distribution by developmental stage of larval English sole (<i>Parophrys vetulus</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 122 |
| 20. | Standard length (mm) distribution by developmental stage of larval sand sole (<i>Psettichthys melanostictus</i>) caught off Washington, Oregon and northern California in the period between 1980 and 1983. | 123 |
| 21. | Standard length frequency distribution of Pacific sanddab (<i>C. sordidus</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983. | 124 |

LIST OF APPENDIX FIGURES (Continued)

22.	Standard length frequency distribution of speckled sanddab (<i>C. stigmaeus</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	126
23.	Standard length frequency distribution of rex sole (<i>G. zachirus</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	128
24.	Standard length frequency distribution of butter sole (<i>I. isolepis</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	130
25.	Standard length frequency distribution of slender sole (<i>L. exilis</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	132
26.	Standard length frequency distribution of Dover sole (<i>M. pacificus</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	134
27.	Standard length frequency distribution of English sole (<i>P. vetulus</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	136
	(a) Bongo tows	137
	(b) Neuston tows	138
28.	Standard length frequency distribution of sand sole (<i>P. melanostictus</i>) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.	139
29.	Distribution of egg abundances of <i>Citharichthys</i> spp. off Washington, Oregon and northern Washington between 1980 and 1983.	141
30.	Distribution of larval abundances of <i>C. sordidus</i> off Washington, Oregon and northern California, between 1980 and 1983.	143
31.	Distribution of larval abundances of <i>C. stigmaeus</i> off Washington, Oregon and northern California, between 1980 and 1983.	145
32.	Distribution of egg abundances of <i>G. zachirus</i> off Washington, Oregon and northern California, between 1980 and 1983.	147
33.	Distribution of larval abundances of <i>G. zachirus</i> off Washington, Oregon and northern California, between 1980 and 1983.	149

LIST OF APPENDIX FIGURES (Continued)

- | | | |
|-----|---|-----|
| 34. | Distribution of egg abundances of <i>I. isolepis</i> off Washington, Oregon and northern California, between 1980 and 1983. | 151 |
| 35. | Distribution of larval abundances of <i>I. isolepis</i> off Washington, Oregon and northern California, between 1980 and 1983. | 153 |
| 36. | Distribution of egg abundances of <i>L. exilis</i> off Washington, Oregon and northern California, between 1980 and 1983. | 154 |
| 37. | Distribution of larval abundances of <i>L. exilis</i> off Washington, Oregon and northern California, between 1980 and 1983. | 156 |
| 38. | Distribution of egg abundances of <i>M. pacificus</i> off Washington, Oregon and northern California, between 1980 and 1983. | 158 |
| 39. | Distribution of larval abundances of <i>M. pacificus</i> off Washington, Oregon and northern California, between 1980 and 1983. | 160 |
| 40. | Distribution of egg abundances of <i>P. vetulus</i> off Washington, Oregon and northern California, between 1980 and 1983. | 162 |
| 41. | Distribution of larval abundances of <i>P. vetulus</i> off Washington, Oregon and northern California, between 1980 and 1983. | 163 |
| 42. | Distribution of egg abundances of <i>P. melanostictus</i> off Washington, Oregon and northern California, between 1980 and 1983. | 165 |
| 43. | Distribution of larval abundances of <i>P. melanostictus</i> off Washington, Oregon and northern California, between 1980 and 1983. | 167 |
| 44. | Distribution of larval abundances by stage of some flatfishes off the Washington, Oregon and northern California coasts during: (a) late-spring 1981; (b) late-spring 1982; (c) mid-fall 1981 and (d) late-fall 1983. | 169 |

LIST OF APPENDIX TABLES

<u>TABLE</u>	<u>PAGE</u>
1. Summary of U.S.-U.S.S.R. cruises used for ichthyoplankton surveys in waters off Washington, Oregon and northern California, between 40 and 48°N lat and 3 to 200 miles offshore.	174
2a. Egg densities (number of eggs under 1000 m ² of sea surface) of seven taxa of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.	175
2b. Egg densities (number of eggs per 10 ⁵ m ³ of sea water) of seven taxa of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.	176
3. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on abundance of eggs of seven taxa of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. (P value=probability that rankings are not concordant. $\alpha=0.05$) m = number of cruises compared.	177
4. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on frequency of occurrence of eggs of seven taxa of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. (P value=probability that rankings are not concordant. $\alpha=0.05$) m = number of cruises compared.	178
5a. Egg frequency of occurrences (in percentages) of seven taxa of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.	179
5b. Egg frequency of occurrences (in percentages) of seven taxa of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.	180
6a. Larval densities (individuals under 1000 m ² of sea surface) of eight species of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.	181
6b. Larval densities (individuals per 10 ⁵ m ³ of sea surface) of eight species of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.	182

LIST OF APPENDIX TABLES (Continued)

7. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on larval abundance of eight species of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. (P value=probability that rankings are not concordant. $\alpha=0.05$) m = number of cruises compared. 183
- 8a. Larval frequency of occurrences (in percentages) of eight species of flatfishes collected off Washington, Oregon and northern California, during 1980-1983. 184
- 8b. Larval frequency of occurrences (in percentages) of eight species of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983. 185
9. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on larval frequency of occurrence of eight species of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. (P value=probability that rankings are not concordant. $\alpha=0.05$) m = number of cruises compared. 186
10. Summary of the F tests for differences in egg and larval abundances among cruises in bongo and neuston collections for eight species of flatfishes off Washington, Oregon and northern California, in the period 1980-1983. 187
11. Means \pm (standard deviations) and ranges (in parenthesis) of the standard length, and number of specimens in five developmental stages of larval flatfishes of eight species collected off Washington, Oregon and northern California during the 1980-1983 period. 188
12. Boundaries of the (a) latitudinal, (b) on/offshore and (c) geographic regions of the study area. 189
13. Summary of the F tests for differences in abundances of eggs and larvae in bongo (B) and neuston (N) tows (a) among four latitudinal regions, (b) between onshore/offshore stations and (c) among eight geographic regions, for eight species of flatfishes off Washington, Oregon and northern California, in the period 1980-1983. 191

DISTRIBUTION OF THE EGGS AND LARVAE OF SOME FLATFISHES (PLEURONECTIFORMES) OFF WASHINGTON, OREGON AND NORTHERN CALIFORNIA, 1980-1983.

INTRODUCTION

Ichthyoplankton surveys of pelagic fish eggs and larvae are useful for: a) appraising spawning biomass of fishery resources; b) studying the biology and systematics of fishes and c) assessing the population dynamics of fishes (Smith and Richardson, 1977; Smith, 1981). Two major projects have assessed the abundances and distributions of early stages of fishes in the California Current System. The first is the California Cooperative Oceanic Fisheries Investigations program (CalCOFI), a long-time series study off California and Baja California that was started in 1951 and has continued over 30 years. CalCOFI has monitored the spawning biomass of fishes and studied the causes of the fluctuations of fish stocks in the California Current System (Lasker and Smith, 1977; Smith, 1981). The second extensive project is the cooperative U.S.-U.S.S.R. study to survey ichthyoplankton from Washington to northern California in different seasons between 1980 and 1985. Its major objectives were to determine seasonal and spatial distribution of early stages of fish in this area (Dunn, 1986). The present work is based on data gathered by that second project, and it focuses on eight species of flatfishes.

Flatfishes (Order Pleuronectiformes) of families Pleuronectidae, Bothidae and Paralichthyidae are very common species of the northeastern Pacific Ocean (Miller and Lea, 1972; Weinberg *et al.*, 1984). Furthermore, some of them are commercially important in Oregon and were top-ranked in trawl catches in the past decade (Krygier and Pearcy, 1986; Pearcy *et al.*, 1977). The present study will analyze the early developmental stages of six species of the family Pleuronectidae (righteye flounders) and two species of the family Paralichthyidae (lefteye sanddabs):

Fam. Pleuronectidae

Rex sole (*Glyptocephalus zachirus*)

Butter sole (*Isopsetta isolepis*)

Slender sole (*Lyopsetta exilis*)

Dover sole (*Microstomus pacificus*)

English sole (*Parophrys vetulus*)

Sand sole (*Psettichthys melanostictus*)

Fam. Paralichthyidae

Pacific sanddab (*Citharichthys sordidus*)

Speckled sanddab (*C. stigmaeus*)

The objectives of this study are to:

- 1- Determine temporal variation of egg and larval abundances on a seasonal and interannual basis.
- 2- Determine spatial distribution of eggs and larvae in two directions:
 - (a) onshore-offshore zones (based on bottom depth) and
 - (b) alongshore (i.e., latitude)
- 3- Relate temporal and spatial variation with variation of selected environmental parameters (e.g., upwelling intensity, salinity, temperature, density).
- 4- Develop standard criteria to stage all available larval specimens of the eight species and use that classification with standard length as an indicator of a chronological order of development.

Ichthyoplankton Studies off Washington, Oregon and Northern California

Many studies of the early stages of flatfishes from the Northeast Pacific have been published in the recent years. Descriptive, non-quantitative studies of ichthyoplankton off the Oregon coast were started by Aron between 1958-1960 (Mundy, 1984). Quantitative analyses were initiated in 1972, when surveys designed for ichthyoplankton sampled with neuston or bongo nets (Richardson and Pearcy, 1977; Laroche and Richardson, 1979; Laroche *et al.*, 1982; Boehlert *et al.*, 1985; Brodeur *et al.*, 1985; Dunn, 1986). Richardson and Pearcy's (1977) work off Yaquina Bay, Oregon, was a major study of early stages of fishes in the Northeast Pacific Ocean north of California for several reasons. First, it gave the first quantitative information on coastal and offshore assemblages of larval fishes in this area. Secondly, it yielded the greatest number of species recorded from a larval fish study for this region to that time, reflecting both increased sampling effort and improved larval fish identification. Thirdly, it was also the first survey conducted for one complete year of sampling, which permitted the analysis of some seasonal trends.

The most recent extensive studies of larval fishes off Washington, Oregon and northern California are the series of cooperative U.S.- U.S.S.R. surveys conducted from 48-40°N for the years 1980-85, at different times of the year. (See Kendall and Clark, 1982a-b; Clark, 1984; Bates, 1984; Clark, 1986a-b; Clark and Kendall, 1985 for individual cruise reports, and a summary by Dunn, 1986).

Review of Biology of Flatfishes

The following section is a review of some aspects of the biology and distribution of the six species of the family Pleuronectidae and two species of

Paralichthyidae that I studied.

English sole, *Parophrys vetulus*. Although this species often ranked second in annual landing of trawl catches off Oregon in the past decade (Barss, 1976, cited by Krygier and Percy, 1986), it ranked 19th in the Pacific West coast bottom trawl survey in 1983 (Weinberg et al., 1984). It is found in the Northeast Pacific, from south of Point Conception to the Bering Sea (Matarese et al., 1986). The English sole spawns pelagic eggs (≤ 1 mm diameter) in coastal waters during a protracted spawning season, during winter and spring, as well as fall (Richardson and Percy, 1977; Laroche and Richardson, 1979; Hewitt, 1980; Gadomski and Boehlert, 1984; Matarese et al., 1986). Hewitt (1980) suggested the central Oregon coast as an important spawning ground for this species. A minimum threshold bottom temperature of 7.8°C for spawning has been suggested by Kruse and Tyler (1983), a temperature which occurs during onshore convergence (Mundy, 1984). Fecundity may range from 1.5×10^5 to 1.95×10^6 ova (Matarese et al., 1986).

A planktonic larva (2.8 mm notochord length, NL) hatches in 4 days at 10°C (Laroche and Richardson, 1979). Its pelagic life lasts 8-10 weeks (Laroche et al., 1982); transformation occurs between 15 mm and 22 mm standard length (SL) (Laroche and Richardson, 1979; Hogue and Carey, 1982; Laroche et al., 1982). A protracted benthic recruitment spans November through July (Richardson and Percy, 1977; Hogue and Carey, 1982). Unlike earlier stages, metamorphosing larvae and early juveniles are common in estuaries (Krygier and Percy, 1986). While pelagic stages feed primarily on appendicularians (Gadomski and Boehlert, 1984), juveniles and adults are benthic feeders, opportunistically exploiting different prey which are densely aggregated (Hogue and Carey, 1982). Their generalist diet is mostly based on polychaetes and amphipods, and to a lesser degree molluscs, ophiurids and

crustaceans (Kravitz et al., 1977).

Dover sole, *Microstomus pacificus*. It was the first-ranked in annual flatfish landing of catches off Oregon in the decade of 1970 (Pearcy et al., 1977; Gabriel and Percy, 1981; Krygier and Percy, 1986), and third-ranked among the west coast groundfish landings in 1983 (Weinberg et al., 1984). This species is distributed from San Cristóbal Bay, Baja California to the Bering Sea (Miller and Lea, 1972), and larvae have been collected as far as 280 miles offshore (Hagerman, 1952). It spawns relatively low numbers of large pelagic eggs (2.05-2.57 mm diameter) (Ahlstrom et al., 1984) in specific sites offshore in depths >400 m during winter, from November through March (Pearcy et al., 1977). Fecundity ranges from 37,188 to 260,000 ova/female (Matarese et al., 1986).

A planktonic, 6-mm SL larva hatches in 27 days at 10°C (Matarese et al., 1986). The Dover sole is characterized by its long-duration giant larva: although eye migration begins at 20 mm SL, the larva remains pelagic for about one year (Pearcy et al., 1977), reaching >45 mm SL before settling (Matarese et al., 1986). Adult *M. pacificus* is a selective feeder, preying mainly upon polychaetes and ophiuroids (Gabriel and Percy, 1981), although it is usually less selective during the summer than during the winter (Pearcy and Hancock, 1978). The diet of one-year olds seem very similar to that of the adults. Small burrowing invertebrates (bivalves, gastropods and scaphopods, as well as sipunculids, polychaetes, echinoids and some crustacean forms) and demersal eggs have been found in stomach contents (Hagerman, 1952).

Butter sole, *Isopsetta isolepis*. This species is of minor importance in commercial fisheries due to its small size and slender body (Laroche and Richardson,

1979; Richardson et al., 1980); adults ranked 11th and 7th in flatfish biomass in 1971-72 and 1973-74 trawl surveys off Oregon. Its geographic range includes from Ventura, California, to the Bering Sea (Miller and Lea, 1972). It spawns in coastal waters during winter and spring months (Laroche and Richardson, 1979), from February through April (Matarese et al., 1986). Although it has small eggs (ca. 1 mm diameter) (Richardson et al., 1980), fecundity is moderate ($3.5-6.5 \times 10^5$ ova) (Matarese et al., 1986).

The larva hatches at 2.7-2.9 mm SL, after a 6-day incubation at 9-10°C (Richardson et al., 1980). Eye migration begins at 12-13 mm SL, and the juveniles settle between May and August (Hogue and Carey, 1982), after reaching 18.5 mm SL (Richardson et al., 1980). Diet of larval butter sole changes with increasing size. While small larvae (<15 mm SL) feed mostly on tintinnids, invertebrate eggs and nauplii, large larvae (15-21 mm SL) consume more copepodite stages and adult copepods (Gadomski and Boehlert, 1984). The diet of recently settled butter sole is similar to that of the English sole, although it feeds to a greater extent on mysids and decapods (Hogue and Carey, 1982).

Rex sole, *Glyptocephalus zachirus*. It was the fourth-ranked in the 1973 Oregon flatfish landings (Pearcy et al., 1977), and third-ranked flatfish in 1983 Pacific West coast (Weinberg et al., 1984). Rex sole is distributed from the San Diego Trough to the Bering Sea (Miller and Lea, 1972). A winter-spring spawner (Matarese et al., 1986), it spawns in non-specific sites between 100 and 300-m depth contours (Pearcy et al., 1977). It produces 3,900-238,000 eggs (Hosie, 1975, 1977), which are large (1.80-2.05 mm diameter) (Matarese et al., 1986).

A planktonic larva hatches at 4-6 mm SL, undergoing transformation at 59-69

mm SL (Matarese et al., 1986; Pearcy et al., 1977), and settling to the bottom during winter (at >50 mm SL), mainly on the outer continental shelf (Pearcy, 1978). However, the pelagic life may last about one year and the record size of this "giant larva" was 89 mm SL (Richardson, 1973 cited by Pearcy et al., 1977). Rex sole juveniles are benthic feeders whose main prey are polychaetes and crustaceans (euphausiids, cumaceans, amphipods) (Pearcy and Hancock, 1978; Krygier and Pearcy, 1985).

Slender sole, *Lyopsetta exilis*. Although a relatively abundant flatfish in trawl catches on the central continental shelf off Oregon (Pearcy and Hancock, 1978), it is not very important in the commercial fisheries of this region, probably due to its small maximum size of 33.6 cm (see Miller and Lea, 1972). Its geographic range extends from Cedros Is., Baja California, to Alsek Canyon, Alaska (Miller and Lea, 1972). The pelagic eggs (1.47-1.71 mm diameter) are spawned in spring (Matarese et al., 1986), apparently from March through June (Richardson and Pearcy, 1977).

A pelagic larva hatches at 5.6 mm SL, transforming at 16-24 mm SL (Matarese et al., 1986). Crustaceans are the main prey of juveniles within 100-300 mm SL while annelids and "other taxa" were also important in the diet of 101-200 mm SL (Pearcy and Hancock, 1978).

Sand sole, *Psettichthys melanostictus*. Although it is a relatively common species in trawl catches off Oregon, it is only of minor commercial importance (Laroche and Richardson, 1979). It was not among the 20 most abundant groundfish in the Pacific west coast bottom trawl survey (Weinberg et al., 1984). It is found from Port Hueneme, California to the northern Gulf of Alaska (Miller and Lea, 1972). Sand sole spawn in coastal waters during late winter and spring (Laroche and

Richardson, 1979; Matarese et al., 1986), although Mundy (1984) found recently hatched larvae as late as August in 1969. This flatfish produces small (0.83-1.04 mm diameter), pelagic eggs (Matarese et al., 1986).

A pelagic larva hatches at 2.8 mm SL, undergoing metamorphosis at 22-28 mm SL (Hickman, 1959; Matarese et al., 1986). Juvenile stages feed almost exclusively on mysids (Hogue and Carey, 1982). The existence of "two readily distinguishable types of *Psetichthys* larvae" (based on morphology and pigmentation patterns) has been reported (Matarese et al., 1986).

Pacific sanddab, *Citharichthys sordidus*. It was the fourth most abundant flatfish in the shallow strata (55-183 m) of the 1983 Pacific west coast bottom trawl survey (Weinberg et al., 1984), although it is not important in commercial landings of this area. It is distributed from Cape San Lucas (Baja California) to the Bering Sea (Miller and Lea, 1972). This sanddab spawns in late winter and spring in Puget Sound, Washington, and during summer in California, producing small (0.51-0.79 mm diameter), pelagic eggs.

A planktonic larva hatches at 2 mm SL and later undergoes transformation at 20 to >39 mm SL (Matarese et al., 1986). Juveniles and adults feed on pelagic preys (Pearcy and Hancock, 1978), such as crustaceans (Pearcy and Vanderploeg, 1973 cited by Kravitz et al., 1977) and fishes (e.g., northern anchovy, *Engraulis mordax*) (Kravitz et al., 1977).

Speckled sanddab, *C. stigmaeus*. Although relatively common flatfish in the Northeast Pacific region, it is not commercially important in the fisheries of this area because of its small maximum size of 17 cm. It is found from Magdalena Bay, Baja

California, to Montague Is., Alaska (Miller and Lea, 1972). A spring-summer spawner in California, speckled sanddab produces small (0.75-0.83 mm diameter), pelagic eggs.

The planktonic larva hatches at 2 mm SL and transforms at 24-35.5 mm SL (Matarese et al., 1986). Unlike earlier stages, juveniles of speckled sanddab may abound in abundant environments (Pearcy and Myers, 1974). Juveniles feed equally on epibenthic crustaceans and pelagic prey (Hogue and Carey, 1982).

Planktonic larvae of these eight species belong to either (a) a coastal assemblage that includes *P. vetulus*, *I. isolepis*, *P. melanostictus* (see Richardson and Pearcy, 1977; Richardson, Laroche and Richardson, 1980; Mundy, 1984; Brodeur et al., 1985) and *C. stigmaeus* (Brodeur et al., 1985), or (b) an offshore assemblage that includes *M. pacificus*, *G. zachirus* (see Richardson, Laroche and Richardson, 1980; Brodeur et al., 1985) and *L. exilis* and *C. sordidus* (Richardson and Pearcy, 1977; Brodeur et al., 1985). Rex and slender soles are considered to be transitional-coastal, and Dover sole are considered to be transitional-offshore species (Richardson and Pearcy, 1977; Richardson, Laroche and Richardson, 1980; Mundy, 1984).

MATERIALS AND METHODS

Samples for this study, provided by the Northwest and Alaska Fisheries Center (NWAFC) of the National Marine Fisheries Service, were collected during cooperative U.S.- U.S.S.R. ichthyoplankton surveys from the Strait Juan de Fuca (Washington) to northern California, between 40-48°N lat and 3-200 miles (4.8 to 322 Km) offshore, 1980-1985. Reports on the ichthyoplankton collected have been published for the 1980-1983 cruises (Table 1). The two letters representing the initials of the season and the year of the survey will be used in this thesis to designate cruises (e.g., MS80 is the survey made by the R/V Tikhookaenskiy in Mid-Spring 1980).

Most cruises occupied 113 to 125 stations from north to south. The exceptions were SU80, which sampled only 91 stations (Table 1), and LF83 that occupied the southernmost stations first and continued northward. For all cruises except LF83 in November-December 1983, temperature, dissolved oxygen, phosphate and silicate were determined for each station using hydrographic casts at the following depths: 0, 10, 20, 30, 50, 75, 100, 150, 200, 300, 400, 500 and 600 m (depth permitting) (Bates, 1984; Clark, 1984, 1986a, 1986b; Clark and Kendall, 1985; Dunn, 1986; Kendall and Clark, 1982a, 1982b). In the LF83 cruise, the physico-chemical properties were determined with a CTD (conductivity, temperature, depth device) to near bottom or to a maximum depth of 500 m, or with XBT's (expandable bathythermograph).

Ichthyoplankton were sampled by using paired neuston nets (0.3-m high by 0.5-m wide Sameoto samplers. See Sameoto and Jaroszynski, 1969) of 505- μ mesh

towed at 2.0 knots (1.03 m/s) for 10 minutes at each station. Immediately after these, standard MARMAP bongo nets (505- μ mesh, 0.6-m mouth diameter) were towed obliquely to and from approximately 200 m depth at 1.8 knots (.93 m/s) (Bates, 1984; Clark, 1984, 1986a, 1986b; Clark and Kendall, 1985; Dunn, 1986; Kendall and Clark, 1982a, 1982b). General Oceanics flowmeters (Model 2040) were suspended in the mouths of both nets to determine the volume of water filtered. The cruise LS82 has only 49 bongo samples out of 124 stations, because two previous cruises (MS80 and LS81) had surveyed the same area at the same time of the year (Clark, 1986a). Most samples were preserved in 3% formalin solution. LS82 neuston samples were preserved in 80% ethanol, which permitted the use of otolith for aging of larvae.

Double sets of bongo and neuston collections were taken so that the scientific teams of each country could work with one complete set of samples from every survey. The U.S.A. samples were sorted at the Polish Sorting Center (Szczecin, Poland). Fish eggs and larvae were removed and counted, and larvae were identified "to the lowest taxonomic level possible" (Bates, 1984; Clark, 1984, 1986a, 1986b; Clark and Kendall, 1985; Kendall and Clark, 1982a, 1982b). Fish eggs were identified at NWAFC (Seattle). Relative abundances of both eggs and larvae of each taxon for both bongo and neuston tows were estimated by means of different indices (see NWAFC reports):

- a) Total number caught.
- b) Percentage of occurrence.
- c) Mean number per 1000 m³ and 10 m².

Geographic distributions of eggs and larvae and length frequencies of the most abundant taxa of larvae have been published for each cruise (Bates, 1984; Clark, 1984, 1986a, 1986b; Clark and Kendall, 1985; Dunn, 1986; Kendall and Clark, 1982a, 1982b) for bongo and neuston collections. In addition, most reports include a recurrent group analysis for either neuston or bongo catches (both fish eggs and larvae) based on presence or absence of species.

All of the methodology mentioned above was conducted by the National Marine Fisheries Service in Seattle, Washington. I performed the following research at Oregon State University.

Staging of Larvae

Based upon previous descriptions of developmental stages of flatfishes belonging to Pleuronectidae, Paralichthyidae and Bothidae (Hickman, 1959; Shelbourne *et al.*, 1963; Smith and Fahay, 1970; Leonard, 1971; Richardson and Joseph, 1973; Russell, 1976; Pearcy *et al.*, 1977; Chiu, 1987), the following characteristics were selected to stage larvae:

1) **Notochord flexion.** Three events were recognized: preflexion, postflexion before the formation of the hypural bones, and postflexion with caudal fin fully formed. Both the angle of the notochord tip relative to the longitudinal axis and the extent of its reabsorption increase in later stage larvae (Chiu, 1987).

2) **Fin rays.** Developmental stages of dorsal, anal and caudal rays were categorized as follows: (a) Unformed, (finfold surrounds the larva; some traces of

actinotrichia might be present); (b) Incomplete, (fin bases were apparent and some or many rays were formed); (c) Complete (all fin rays were fully formed in number and extent).

3) **Color asymmetry.** Pigmentation was considered symmetrical when patterns (melanophore distribution and intensity) were equal on both sides of an individual. Asymmetrical gut pigmentation of *Citharichthys* larvae will be discussed later.

4) **Eye migration.** Three stages of this process, considered the most obvious feature of the metamorphosis by most authors, have been described (Chiu, 1987; Pearcy *et al.*, 1977): (a) initiation of eye migration until the eye reaches the middorsal ridge, (b) migrating eye positioned on middorsal ridge (when a straight line along the middorsal ridge drawn forward from the dorsal fin transects any part of the eyeball), and (c) migrating eye fully on the pigmented side (when the middorsal line drawn forward from the dorsal fin does not intersect any part of the eyeball) (Pearcy *et al.*, 1977).

I recognized five stages of larval development that could be applied to all eight species considered in this study, and which do not necessarily coincide with the stages assigned by previous authors. These five stages are as follows:

STAGE I: Yolk absorbed; notochord straight; symmetrical, slim body; finfolds present, symmetrical caudal bud (Hickman, 1959) and pectoral buds; eyes unpigmented or pigmented; myomeres either V- or W-shaped. Some authors call this stage 'larva' (Leonard, 1971; Chiu, 1987), or 'early post-larva' (Russell, 1976), or 'Stage 2' (Shelbourne *et al.*, 1963).

STAGE II: Eyes and body symmetrical. Notochord flexed; ossification of dorsal, anal, caudal and pelvic rays; pelvic fins may appear only as buds (Richardson and Joseph, 1973); the caudal fin is incomplete (Hickman, 1959; Smith and Fahay, 1970; Leonard, 1971; Richardson and Joseph, 1973). This is equivalent to Pearcy *et al.*'s (1977) 'Stage I', Shelbourne *et al.*'s (1963) 'Stage 3', Russell's (1976) 'late post-larva' and the late stages of Chiu's (1987) 'larva'.

STAGE III: Eye migration in progress but not at the middorsal position; notochord is resorbed; caudal fin complete (Hickman, 1959; Leonard, 1971; Richardson and Joseph, 1973); development of dorsal and anal fins highly variable, from finfolds with actinotrichia (Smith and Fahay, 1970) to completely developed fins (Richardson and Joseph, 1973). This stage corresponds with the first part of Chiu's (1987) "metamorphic period", Pearcy and co-workers' (1977) "Stage II", Shelbourne and co-workers' (1963) "Stage 4".

STAGE IV: Migrating eye on the middorsal ridge; the color pattern slightly asymmetrical; all fins complete or almost complete. This stage coincides with Pearcy *et al.*'s Stage III (1977), Hickman's postlarva (1959) and part of Chiu's 'metamorphic larva' (1987).

STAGE V: Eye migration complete or almost complete; color asymmetry pronounced. This is considered the last stage, either the fourth (Pearcy *et al.*, 1977) or the fifth (Shelbourne *et al.*, 1963).

Once the eyes are located in their final position and pigmentation is complete, the individual is classified as a 'juvenile'. Because neither yolk-sac larvae (equivalent to STAGE 0) nor juveniles were caught in any of the surveys, only stages I-V are considered in this study.

All staged larvae were re-measured to the nearest tenth of millimeter. Body shrinkage of specimens preserved in formalin (5.1% of standard length after four months of preservation, Laroche et al., 1982) may cause small differences between the standard length distributions (based on data from NWAFC) and the description of stage-standard length relation.

Taxonomic Limitations

The larvae of both sanddabs (*Citharichthys sordidus* and *C. stigmaeus*) smaller than 7 mm, previously identified to genus level by NWAFC staff, were fully identified with the advice of Dr. H.G. Moser and co-workers (Pearcy, W. 1988. pers. comm.). This further identification is yet to be checked by NWAFC qualified staff.

At present, sanddab eggs are not distinguishable to the species level because of their similarity to those of *Paralichthys* (Matarese et al., 1986). Eggs of three co-occurring species, *Parophrys vetulus* (English sole), *Psettichthys melanostictus* (sand sole) and *Platichthys stellatus* (starry flounder) are very difficult to distinguish (Matarese et al., 1986), although these identifications have been checked.

Hydrographic Data and Region Definitions

Weekly and monthly upwelling index values at 39°N, 42°N, 45°N and 48°N latitude for the period 1980-1983 were taken from Mason and Bakun's (1986) Upwelling Index Update, U.S. West Coast, 33°N-48°N Latitude.

Sea water density was described in terms of sigma-t (σ_t), the specific gravity anomaly multiplied by a thousand (Huyer and Smith, 1985). Sigma-t was computed with the equation of state by Millero and Poisson (UNESCO, 1981), as a function of temperature and salinity. Contour maps based on Kriging-octant method (SURFER program) of temperature and salinity at three depths (0, 75 and 200 m) and sigma-t at 200 m, as well as circulation patterns from literature, were used to describe the physical properties of the study area.

The study area was arbitrarily divided into four latitudinal regions of two degrees each numbered from south to north (e.g., region 1 = 40 to 42°N, region 2 = 42 to 44°N and so forth). The study area was also divided into onshore and offshore regions based on bottom depth rather than distance from shore; the 200-m isobath was chosen as an arbitrary borderline between these two regions and as the average depth of the continental platform break¹. The combination of both divisions

¹The bottom depth of the outer edge of the continental shelf break off Oregon usually occurs from 146 to 183 m (85-100 fathoms), and the shelf varies in width from 16 to 72 km (9-40 n.m.) (Byrne, 1962, 1963).

resulted in eight geographic regions (I-VIII) (Fig. 1).

Data Analysis

The information was processed using DBASE™ III PLUS, LOTUS™ 1-2-3 and Number Crunching™ programs. Because the maximum depths of the oblique bongo tows varied with bottom depth nearshore, the abundances in bongo collections were standardized in terms of individuals under unit of sea surface ($\text{ind}/10 \text{ m}^2$) (Smith and Richardson, 1977). However, because neuston nets only sample the upper 20-30 cm of the water column, the numbers in terms of $\text{ind}/10 \text{ m}^2$ were very low in these collections. Consequently, neuston catches are expressed in terms of individuals per unit volume ($\text{ind}/1000 \text{ m}^3$).

Non-parametric Kendall's Coefficient of Concordance Tests (Tate and Clelland, 1959; Zar, 1984) were performed to compare the agreement among the rankings of egg and larval abundances and among rankings of frequency of occurrence by gear of each species for all cruises combined and by season. The ranking of the species abundances in bongo collections was based upon the values of total standardized abundances ($\text{ind}/10 \text{ m}^2$) divided by the total bongo stations sampled in each cruise. For neuston collections, the catch divided by the total volume filtered in each cruise was used. The ranking of species' frequency of occurrence was based upon the amount of positive stations (i.e., where specimens were caught).

Because of the low percentages of positive stations for each species per cruise,

the square root transformation ($\sqrt{[x+1]}$) of ind/10 m², ind/1000 m³ was applied to reduce skewness (Snedecor and Cochran, 1974) when parametric statistical tests were performed. Larval distributions among gears, cruises, latitudinal regions and onshore/offshore abundances were compared with independent Analyses of Variance (ANOVA) followed by Multiple Comparisons Tests: Duncan's New Multiple Range Test and Newman-Keuls Multiple Range Test (Zar, 1984).

Ecological and multifactorial analyses were conducted by AID1, AIDN and CLUSB4 programs developed by David McIntyre and co-workers at Oregon State University. CLUSB4 is a divisive, non-hierarchical clustering algorithm which minimizes the within-cluster sum-of-squares, and the number of clusters are specified by the user (Smith, 1987). However, neither analysis yielded valuable information for biological interpretation of the data.

RESULTS

Physical Conditions of the Study Area

Upwelling indices

Upwelling/downwelling seasons varied among years and with latitude off the coasts of northern California, Oregon and Washington (125° long W, 40-48°N) between 1980 and 1983 (Figs. 2-5). In the southern regions the upwelling season was longer and stronger, while the downwelling season was shorter and weaker than in the northern areas. Both the spring and fall transition periods² between seasons shortened with decreasing latitude. Huyer (1983) gives two reasons for this pattern of stronger coastal upwelling at lower latitudes in the eastern North Pacific: first, wind stress (τ) is equatorward (i.e., upwelling-favorable) all year south of about 40°N, while in the study area (40-48°N) the winds are poleward (upwelling-unfavorable) during winter. The closer to that boundary, the longer the upwelling season and the stronger the offshore Ekman transport. Second, because the Coriolis force parameter (f) increases with latitude, the net offshore transport in the surface Ekman layer (τ/f) for a favorable wind of the same magnitude (τ) is greater off northern California than off Washington.

Figures 2-5 show that during the 1980-1983 period, the upwelling season

²Defined as the period between the end of consistent up/downwelling and the onset of consistent down/upwelling. It is characterized by highly variable and/or near-zero of upwelling index values.

extended from the third week of April (from mid-March off northern California) through mid-August off Washington (48°N ; Figs. 2a-5a), through early-September off Oregon (45 and 42°N ; Figs. 2b,c-5b,c) and through early-October off northern California (39°N ; Figs. 2d-5d), and the indices were higher in the southern regions than in the northern regions. The onset of the downwelling season was delayed about ten to fifteen days for every three degrees of latitude equatorward: it started in late-September off Washington (48°N ; Figs. 2a-5a)³, in mid- and late-October off Oregon (45 and 42°N ; Figs. 2b-5b and 2c-5c, respectively) and in early-November off northern California (39°N ; Figs. 2d-5d). Downwelling appeared stronger in the northern regions than in the southern regions. The transitional phase varied from 7-12 weeks at 48°N to 5-6 weeks at 39°N .

Temperature and salinity contours at three different depths (0, 75 and 200 m) indicate the influence of upwelling usually as deep as 75 m but not at 200 m depth (Figs. 6-12). Water upwells from depths >30 m along the entire west coast of the United States. According to Huyer (1983), the depth from which water upwells is correlated with the magnitude of the offshore Ekman transport. The coastal upwelling zone is 20-30 km over the shelf along the west coast, but when favorable wind stress is persistent the effects of the coastal upwelling can extend more than 100 km seaward (Huyer, 1983). However, the Columbia Plume provides an offshore limit off northern Oregon, and the surface effects of upwelling are restricted to a narrow band between the coast and the nearshore edge of the Columbia Plume (Huyer, 1983).

³Although the maximum values of the downwelling index occur from mid-October to late-February of the following year.

In the 1983 El Niño year, upwelling indices were different from the three previous years. Although off Washington (48°N) no major differences were observed (Fig. 5a), off Oregon (45 and 42°N) the downwelling season remained strong until the third week of March (four weeks after the normal time), and the upwelling season was two weeks later than in the previous years, from early May through late September (Fig. 5b,c). Off northern California, the downwelling season that began in 1982 is more consistent than before, while the upwelling season also seemed to shift two weeks later than usual (early-May through mid-October) (Fig. 5d). Also, upwelling appeared confined to the layers above the thermocline, as suggested by the absence of its normal influence upon the 75-m temperature, salinity and sigma-t (σ) contours.

Circulation patterns

The California Current, an eastern boundary current off the west coast of the United States, is about 1000 km wide and flows southward at an average of 10 cm s⁻¹ (8.6 km d⁻¹) (Landry *et al.*, 1989). It brings subarctic waters, characterized by low temperature, low salinity, and high oxygen and phosphate levels, to lower latitudes (Landry *et al.*, 1989). The velocity maximum of the California Current occurs seaward of the continental slope, 250-350 km off the Washington and Oregon coasts and 850 km off Cape Mendocino (Hickey, 1979). The current over the continental shelf between 25 and 40 m depth flows at about 8.5-10 cm s⁻¹ (7-9 km d⁻¹) off central Oregon (Huyer and Smith, 1985). There is also a northward undercurrent at 200-300 m depth very near the continental slope, whose influence

on water properties decreases with distance from shore. Its presence had been verified off Washington in fall and summer, and off Oregon in spring and early summer (Huyer and Smith, 1985).

The nearshore component of the California Current (within 256 km from the coast) is more variable than the offshore branch (Hickey, 1979) and the flow changes seasonally. In spring the current is equatorward at all depths with strong vertical shear in the lower half of the water column (Huyer and Smith, 1985). In summer, a southward mean flow of about 10 km d^{-1} (Huyer, 1983) of the surface layers overlays a northward flowing of deeper waters with a strong vertical shear (Huyer *et al.*, 1979). In winter, however, there are northward currents at all depths with little or no vertical shear (Huyer and Smith, 1985).

The Columbia plume

The runoff of the Columbia River (which enters the ocean at $46^{\circ}15'$ lat N) is the dominant freshwater discharge in the study area during summer. After the onset of the upwelling season with the associated equatorward flow nearshore and offshore Ekman transport (late-spring and summer), the plume extends southward of the river's mouth in nearshore waters, often extends far offshore, and a strong salinity gradient is developed (Figs. 7b, 8b, 10b). The Columbia Plume ranges from 2 to 0.5 m thick (Huyer, 1983), and its inshore boundary represents an offshore limit to the offshore Ekman transport during upwelling season.

During and shortly after the downwelling season (fall and mid-spring cruises),

a low-salinity core occurs northward of the river's mouth. This core may be due to a combination of local runoff (Willapa Bay discharge) and a small input of the Columbia River that is shifted northward by the poleward mean flow (Figs. 6a, 9a, 11a, 12a).

Temperature (T), salinity (S) and density (σ_t)

Detailed description and comparison of temperature and salinity data in the study area and particularly between 1980 and 1987 are given elsewhere (Landry *et al.*, 1989; Savage, 1989). In general, waters were progressively warmer at lower latitudes, while the main salinity gradients were parallel to the shore (Figs. 6-12).

Upwelling activity in late spring and summer was reflected in strong gradients of surface temperature (T_{surf}) parallel to the shore with colder water onshore (Figs. 8a, 10a, 7a), while the mid-spring and fall contours showed transitional patterns (Figs. 6a, 11a, 9a, 12a). The distribution of surface salinity (S_{surf}) was an indicator of the Columbia Plume (described above); during summer (1980) the gradient indicated the boundary between the recently upwelled high-salinity waters inshore and the plume (Fig. 7a).

At 75 m depth, temperature and salinity gradients were not as strong as at the sea surface, although both variables showed the influence of upwelling (Figs. 6b-12b). Inshore temperature and salinity gradients suggested the influence of the upwelling activity, with colder and more saline waters inshore during upwelling season (Figs. 6b, 7b, 8b, 10b, 11b) and relatively homogeneous temperatures and

salinities during downwelling season (Figs. 9b, 12b). A warm core of water extended from the south to about 46°N during mid-spring, towards the end of the downwelling season (Figs. 6b, 8b, 11b), reflecting the northward flow typical of winter (Huyer and Smith, 1985). Late-spring and summer showed a transitional pattern between the poleward and equatorward mean flow (Figs. 8b, 10b, 7b). By mid-fall 1981 a cool water mass extended from the north (Fig. 9b), indicating the southward flow of the previous months.

At 200 m depth, temperature (T_{200}), salinity (S_{200}) and sigma-t (σ_t) contours did not reflect any upwelling activity (Figs. 6c-12c). The 200-m isotherms, isohalines and isopycnals suggested the spring northward tongue of warm water except in 1983 (Figs. 6c, 8c, 10c, 11c), while during late-summer (1980) the flow seemed to start reversing (Fig. 7c), and by fall it had become a cool tongue of water extending south (Figs. 9c, 12c).

Biological Data

Egg abundances

A grand total of 6071 eggs was collected (all cruises, taxa and gears combined), 3353 (55.2%) in neuston tows and 2718 (44.8%) in bongo collections. Bongo and neuston results are treated separately. Eggs of each of the six soles (Pleuronectidae) were identified to the species level, but eggs of sanddabs (Paralichthyidae) were identified to genus.

In bongo tows, slender sole (*Lyopsetta exilis*) eggs were the most common, followed by rex sole (*Glyptocephalus zachirus*), Dover sole (*Microstomus pacificus*) and the sanddabs (*Citharichthys* spp.) (Table 2a). These taxa comprised 94.6% of the total abundances, all taxa and cruises combined.

Neuston collections were dominated by eggs of sanddabs (*Citharichthys* spp.) and Dover sole (*M. pacificus*), which accounted for 77.2% of the total egg abundances. Rex sole (*G. zachirus*) and sand sole (*Psettichthys melanostictus*) ranked third and fourth, respectively (Table 2b). Eggs of butter sole (*Isopsetta isolepis*) and English sole (*Parophrys vetulus*) were the least abundant in both bongo and neuston collections.

Seasonal variation: The rank order of abundance of the eggs of seven flatfishes in bongo tows varied among cruises (Kendall's Coefficient of Rank Concordance, $W=0.21$, $P>0.1$; Table 3), indicating seasonal changes in species composition. However, concordance was high ($W>0.92$) within seasons (Table 3), suggesting relatively low interannual variation and consistent seasonal spawning patterns. In the spring, slender sole (*L. exilis*) eggs were always the most numerous, and rex sole (*G. zachirus*) or Dover sole (*M. pacificus*) were the second or third in abundance (Table 2a). Sanddabs (*Citharichthys* spp.) were the most abundant in summer. In the two fall cruises the two sanddabs, English sole (*P. vetulus*) and sand sole (*P. melanostictus*) accounted for most of the bongo catches (Table 2a).

In neuston collections of eggs, high concordance of ranks of the seven taxa

among cruises suggested a lack of pronounced seasonal variation at the sea surface (Table 3). The high concordance in spring, mid-spring and fall of different years ($W > 0.90$) indicated the absence of major interannual variation within these seasons. However, because no eggs were caught by neuston nets in late-spring of 1982, the W value was low for this season. Neuston tows were dominated by sanddab eggs (*Citharichthys* spp.) in three of the cruises. Eggs of Dover sole, rex sole and the two sanddabs were usually the most abundant in spring (Table 2b). In summer, eggs of sanddabs and sand sole were most abundant in neuston collections. As in bongo collections, eggs of sanddabs dominated the neuston samples in fall, while English sole and sand sole were present in lower numbers (Table 2b).

Frequency of Occurrence of eggs (F.O.)

In bongo collections, ranks of F.O.'s were concordant ($P=0.05$) among all cruises (Table 4). Although these results suggest a low seasonal variation in the ranks, the three most frequent taxa during the spring were different from those most frequently occurring during fall (Table 5a). As expected, concordance of ranks was higher within seasons (Table 4), with W values greater than 0.90. The high concordance within a season for different years suggests relatively low interannual variation in relative egg abundances among the seven taxa.

In the bongo catches during the spring, slender sole had the highest or second highest frequency of occurrence (27 to 59%), while rex sole and Dover sole usually ranked second or third in relatively similar proportions (15 to 29%). The exception was in late-spring of 1982, when occurrence of rex sole was higher than that of

Dover sole (Table 5a). *Citharichthys* spp. was the most frequently occurring taxon in summer of 1980, while eggs of the six pleuronectids occurred infrequently (Table 5a). In fall, eggs of the two sanddabs were the most frequent (12-10% of the bongo tows) and accounted for 57% and 41% of the total standardized catch of fall of 1981 and 1983, respectively (Table 5a).

Ranks of frequency of occurrence of taxa in neuston catches were concordant among cruises, but not for spring (Table 4), probably because of the absence of eggs in late-spring of 1982 (Table 5b), as only 49 stations were sampled. Within-season rankings had a higher concordance ($W=0.96$ in mid-spring, and fall; Table 4) suggesting a low interannual variation among years 1980-83.

Among neuston collections, Dover sole frequency of occurrence was the highest throughout the spring (20% to 25% of the stations in each cruise). Rex sole had its maximum frequency in mid-spring and a reduced occurrence in late-spring. *L. exilis* egg frequency also decreased from mid- to late-spring, although in mid-spring of 1983 it was unusually low (3.2%). Samples during mid-fall of 1981 were dominated by *Citharichthys* spp. eggs, with *P. vetulus* and *P. melanostictus* in second and third place. However, in late-fall 1983 frequencies of occurrence of these three taxa were low and very similar (Table 5b). In neuston collections of the summer of 1980, sanddab eggs were the most frequent taxon, and sand and rex soles occurred infrequently.

Larval abundances

A total of 1273 larvae was caught (all cruises, species and gears combined). While 1198 larvae (94.1%) were collected in bongo tows, only 75 larvae (5.9%) in neuston nets. Larval slender sole (*L. exilis*) was the most abundant species, comprising 40% of the total standardized abundances of bongo tows (all species and cruises combined) (Table 6a). Pacific sanddab (*C. sordidus*) ranked second, accounting for ca. 20% of the total bongo catches. Rex sole and butter sole, third- and fourth-ranked, respectively, had similar total larval abundances.

In neuston catches, larvae of English sole, butter sole and speckled sanddab (*C. stigmaeus*) were the most abundant, comprising 75.3% of the total standardized abundances in neuston collections (Table 6b). Interestingly, slender and rex sole were not caught in any neuston tows.

Seasonal variation: Although ranked abundances of the species of larvae in bongo catches varied among cruises ($W=0.19$, $P>0.20$; Table 7), concordance was high within the spring ($P<0.01$) and in the fall. However, W values in mid- and late-spring were considerably lower than their counterparts for egg abundances (Table 3 and 7), suggesting a higher within-season variability for larval than for egg abundances. In spring, slender sole was the most abundant species in bongo tows while rex sole and Pacific sanddab usually were the second or third (Table 6a). This ranking was also consistent through summer of 1980. The high concordance in fall (Table 7) coincided with high abundances of *C. sordidus*, *C. stigmaeus* and *P. vetulus* in the bongo tows of both 1981 and 1983 fall cruises (Table 6a).

Although the rankings in neuston collections were significantly concordant among cruises (Table 7), concordance was not significant during the spring. The large number of ties (caused by the total absence of some species in each cruise) might have increased the values of W when all cruises were considered together, despite the use of the correction factor (Tate and Clelland, 1959). In neuston collections, English sole and speckled sanddab were the most abundant flatfish larvae in spring (Table 6b). While no larvae were caught during the summer cruise (1980), the only species caught in fall were larval Pacific and speckled sanddab, and English sole.

Frequency of occurrence of larvae (F.O.)

Ranks of larval flatfishes by F.O. were similar to ranks by abundance, except in mid-spring 1983 (Table 8a,b). In bongo collections, seasonal variability was indicated by a non-significant concordance value in frequency of occurrence of larvae among all cruises (Table 9). Concordance was high, however, in the spring, and was moderately high in fall, suggesting consistent trends in the relative frequency of occurrence of larvae of certain species during some seasons. However, a higher W value in fall (0.93) than in mid- and late-spring (0.52 and 0.67, respectively), indicated that frequency of occurrence was more variable for spring spawners than fall spawners.

In spring, slender sole larvae were the most frequently occurring species and were caught in 25-50% of the bongo hauls (Table 8a), while rex sole, Dover sole

and butter sole usually ranked second, third or fourth with lower frequencies (less than 10% each). In summer, the most frequently caught species (i.e., larval slender sole) was present in less than 10% of the stations. In fall, Pacific and speckled sanddabs ranked first or second, and were caught at 16-30% of the bongo stations (Table 8a).

Although ranks of neuston catches were significantly concordant among cruises, they were not so in spring (Table 9). This apparent paradox may be explained by the lack of positive stations in summer of 1980 (the presence of tied ranks increases the value of W ; cf. Tate and Clelland (1959)). The low frequencies of occurrence in neuston collections (less than 5%, Table 8b) also might obscure some trends.

In summary, the rankings of eggs and larvae by abundances and frequency of occurrence are relatively consistent among years within seasons. At bongo stations, eggs and larvae of slender, rex and Dover soles were the most abundant (Tables 2a, 6a) and most frequently caught in spring (Tables 5a, 8a), suggesting that this is the main spawning season of these species⁴. Sanddab eggs were abundant in bongo tows during summer of 1980, but low numbers of larval sanddabs (*C. sordidus* and *C. stigmaeus*) were caught during this cruise (Tables 2a, 6a). Eggs and larvae of sanddabs and English sole dominated the fall collections in terms of abundance (Tables 2a, 6a) and frequency of occurrence (Tables 5a, 8a), indicating that they spawn in the fall.

⁴This is not necessarily true for species with long pelagic life (i.e., rex and Dover sole). See "Spawning seasons" section in the Discussion.

Seasonality of early stages

Results of analyses of variance (ANOVA's) among cruises for eggs and larvae of each taxon (Table 10) followed by Multiple Comparisons Tests confirm the observations mentioned in the previous paragraph. Egg and larval total abundances of the eight species were significantly different among cruises in bongo and neuston tows, except when abundances were low. The following discussion of the ANOVA results will emphasize seasonality of egg and larval abundances and seasonality of spawning of the eight species.

Although sanddab eggs were collected in all cruises (Table 2a,b), both bongo and neuston catches of sanddab eggs varied among surveys (Table 10). Both were significantly more abundant during summer 1980 and mid-fall 1981 than in other seasons (Duncan and Newman-Keuls Multiple Comparison Tests $p < 0.05$), with moderately high abundances during late-fall and mid-spring 1983. This suggested a protracted spawning season from late summer through late-spring, with a major peak between August and November. However, in addition to the temporal discontinuity of the sampling, the inability to identify sanddab eggs to the species level detracted from determining the duration of the intense spawning of each species separately.

The presence of larvae of Pacific sanddab in all surveys except during late-spring 1982 (Table 6a,b) and the highest abundance during mid-fall (1981) ($p < 0.01$; Table 10) coincided with the observations on egg abundances.

Significant variation among cruises in larval abundances of speckled sanddab in both bongo and neuston tows ($p < 0.01$ and $p < 0.05$, respectively; Table 10) showed the highest catches to occur during fall (1981 and 1983), although the standard length and developmental stage distribution (described below) also supported the idea of prolonged spawning for this species.

Egg abundances of rex sole varied among cruises ($p < 0.01$; Table 10). Although egg numbers were high during mid-spring (1980, 1983) and late-spring 1981, and were lowest in summer (1980) and fall (1981, 1983) in both gears, bongo catches were highest during late-spring 1982. This suggested a restricted spawning season through spring and part of the summer. Larval rex sole occurred only in bongo catches (Table 6a), and highest standardized abundances were found during mid-spring 1983 and late-spring 1982 ($p < 0.01$), coinciding with bongo catches of eggs.

The highest abundances of butter sole eggs occurred during mid-spring 1980 ($p < 0.05$ and $p < 0.01$ in bongo and neuston catches, respectively; Table 10), although few to no eggs were collected during the same season in 1983 (Table 2a,b). Small numbers were also present in spring of other years. Bongo catches of larvae of butter sole were more numerous in late-spring 1982 than in any other season ($p < 0.01$; Table 10), although they occurred during all the spring surveys (Table 6a).

In bongo and neuston catches, eggs of slender sole occurred in high numbers during mid- and late-spring ($p < 0.01$; Table 10), decreasing in summer (1980) and none being caught during fall (1981, 1983) (Table 2a,b). This suggested a restricted

spawning season during spring that ends by late summer. The same pattern of larval abundances was observed (Tables 6a,b and 10) and supported the idea of a restricted spring spawning.

Eggs of Dover sole seemed to be more abundant during mid-spring (1980, 1983) and late-spring (1981, 1982) than during other times of the year (Tables 2a,b and 10). Low numbers of eggs were collected in summer (1980) and none during fall (1981, 1983). Few Dover sole larvae were caught, however. Therefore elucidation of seasonal and year-to-year variability of standard length distributions was difficult. However, some general trends were observed. Although no significant differences among cruises were found in neuston tows ($p=0.07$), bongo catches of larvae were moderately high throughout the spring (Table 6a,b) ($p<0.01$).

English sole eggs were most abundant during mid-fall 1981 in both gears ($p<0.01$), but they also occurred in late-fall 1983 and late-spring 1982. This suggests a restricted spawning season through fall. Larval *P. vetulus*, however, were most abundant in bongo tows of mid-spring (Table 6a,b), and also occurred in late-spring 1982. This suggested spawning through winter in most years, and through early spring in 1982.

The occurrence of sand sole eggs during all the surveys indicated a prolonged spawning season. Significant differences among cruises were found only in neuston tows ($p<0.01$), when abundances in summer collections (1980) were higher than in any other of the seasons surveyed (Table 2b). Larval abundances showed significant

trends in bongo catches ($p < 0.01$), where the highest numbers were collected in mid- and late-spring (Table 6a). Sand sole larvae also occurred in summer (1980) and mid-fall (1981).

Description of larval stages

A progressive increase in larval body length was observed with increasing developmental stages of most larvae (Figs. 13-20). Length range at each stage varied within and among species (Table 11). A wide length range of a stage suggested slow morphological change or a fast body growth rate at that given developmental stage. A given stage does not necessarily have the same duration for all species. It may also be due, however, to differential shrinkage during preservation. The staging was intended to show chronological order of development, because the standard length by itself is not a good indicator of age in the very early stages of development (see Pearcy *et al.*, 1977; (Markle, 1989. Unpubl. manuscript.).

For some species, criteria for staging varied within a stage. For example, the early asymmetry in gut pigmentation found in some specimens of the two sanddab species (*C. sordidus* and *C. stigmaeus*) was unrelated to the normal symmetry change of flatfishes. Also, the order of the developmental events in rex sole was very flexible: e.g., eye migration sometimes began before the onset of flexion or fin formation, or color asymmetry was sometimes evident before notochord flexion was completed. Hence they were staged as closely as possible upon the standard criteria to allow comparisons with the development in the other species.

Citharichthys sordidus (Pacific sanddab). Asymmetry in gut pigmentation was found in some small specimens of larval Pacific sanddab. Because it was unrelated to the normal symmetry change of flatfishes, this feature was not considered an indicator of transformation. Stage I larval Pacific sanddab accounted for 74.3% of total larvae caught of this species (Table 11). The minimum size of these larvae (2.3 mm SL), which had already absorbed their yolk-sac, coincided with the size at hatching reported by Matarese et al. (1986). However, body shrinkage due to preservation might account for this difference. Shrinkage of larvae preserved in 10% seawater-diluted formalin was reported to be 5.1% of the original size after four months (Laroche et al., 1982).

Notochord flexion started at 6.8-9.5 mm SL (stage II). The first steps of eye migration (stage III) occurred over a remarkably wide range of standard lengths (Table 11; Fig. 13). Although eyes were usually asymmetric after caudal fin was complete, sometimes eye migration started almost simultaneously with notochord flexion. Matarese et al. (1986) reported this species to undergo metamorphosis (in which eye migration is the major event observed) at 20 to >39 mm SL. The migrating eye reached the middorsal ridge (stage IV) at 33.2 to 43.7 mm SL. Because no stage V specimens were caught, Pacific sanddab might settle to the bottom at sizes greater than 44 mm SL. Alternative explanations are net avoidance, insufficient volumes of water sampled, or the absence of those stages within the volumes sampled for a reason other than settling.

Citharichthys stigmaeus (Speckled sanddab). Larval development of speckled

sanddab closely resembled that of Pacific sanddab. Hatching at 2 mm SL (Matarese et al., 1986), the yolk-sac was absorbed by 3.3 mm SL. Notochord flexion usually started at 9.2-9.5 mm SL.

Eye migration occurred from 10.4 to 36.5 mm SL (Table 11). The two stage IV specimens caught in these surveys were smaller than larval Pacific sanddab at the same stage (25.0 and 34.3 mm SL) (Fig. 14), coinciding with the metamorphosing standard lengths reported by Matarese et al. (1986). No older stages were caught, due to either net avoidance or to their absence within sampled depths.

Glyptocephalus zachirus (Rex sole). The order of the developmental events in rex sole was very flexible: e.g., eye migration sometimes began before the onset of flexion or fin formation, or color asymmetry was sometimes evident before notochord flexion was completed.

Giant larvae of rex sole have been previously reported by Pearcy et al. (1977), and were also captured in this study (the largest specimen of rex sole found was a stage III larva of 65.5 mm SL). Preflexion larvae (stage I) were as large as 21.1 mm SL. Notochord flexion in symmetrical specimens (stage II) occurred over a 37.6 mm SL range, while the first part of the eye migration (stage III) occurred over a 53 mm SL range (Table 11, Fig. 15). Evidence suggests that rex sole has an extended larval period of about a year (Pearcy et al., 1977). The wide length ranges of the stages may be due to the variable development rates. Rex sole was the only species in this study whose larval stages were premetamorphic (stage II) at lengths ≥ 20 mm SL.

(Table 11) during different seasons. None of the older stages (IV and V) were collected in the surveys (Table 11), probably due to the increase of net avoidance or the absence of those stages in the sampled volumes. However, the capture of some large specimens indicated that not all large individuals avoided the net.

The findings of this study support the previous observations that rex sole can delay the onset of metamorphosis to extend their pelagic life (Pearcy et al., 1977). Very few physiological studies on metamorphosis of flounders have been conducted to determine the mechanisms of transformation in fishes. Hoar et al. (1951) found histological evidence of high thyroïdal activity in metamorphic starry flounder (*Platichthys stellatus*) (roughly corresponding to stage III larvae in the present work), similar to that of metamorphosing salamander and tadpole. However, they emphasized that thyroïdal activation is not related exclusively to the metamorphic period. Inui and Miwa (1985), however, experimentally accelerated metamorphosis in small larval specimens and produced giant larvae of the flounder *Paralichthys olivaceus* (Paralichthyidae). They found that thyroxine induced metamorphosis in this species, while the antithyroïdal agent, thiourea, produced "metamorphic stasis", thus confirming the role of the thyroid gland in transformation of pleuronectiforms. Nevertheless, it is yet unknown how "unfavorable conditions" (Pearcy et al., 1977) affect the balance of thyroxine and thiourea activity.

Isopsetta isolepis (Butter sole). The smallest specimens collected were smaller than the reported hatching size of ca. 2.8 mm SL (Richardson et al., 1980). This can be explained by the shrinkage due to preservation (Laroche et al., 1982). This was

the only species in which stage V specimens (smaller than 22 mm SL) were found (Table 11; Fig. 16). This may have two explanations: (a) larval development takes place over a small size range, and plankton nets are adequate gear to catch these older stages (e.g., net avoidance is not as developed in older stages of larval butter sole as in the other species), or (b) this species might settle out of the water column later (in terms of developmental stage) than the other flatfishes.

I. isolepis showed standard length means and ranges comparable to those of the other species at stages I, II and III (i.e., from yolk-sac absorption to the beginning of eye migration), except that of rex sole (Table 11). However, means and minimum and maximum lengths of stages IV and V (completing transformation) larvae were smaller than those of the other flatfishes of this study. This suggests that either butter sole metamorphosed at a smaller size than the other species, or that body growth was slow during eye migration.

Lyopsetta exilis (Slender sole). Twenty specimens were collected smaller than 4.5 mm SL (Fig. 17), considerably smaller than the hatching size of 5.6 mm SL reported by Matarese *et al.* (1986). Preflexion (Stage I) larvae accounted for the greatest portion of the total catch of slender sole larvae (77.4%). Flexion could start as early as 7.2 mm SL, or be delayed until the larva reached ca. 14 mm SL (Table 11). The left eye started migrating at 11.2 mm SL (stage III), and it reached the middorsal ridge at 19 mm SL. No Stage V specimens of slender sole were collected.

Microstomus pacificus (Dover sole). This species has also been reported to

have a "giant larva" of about one-year long pelagic life (Pearcy et al., 1977). Another unique trait of this species is the presence of a pair of otic spines that are evident after flexion (pers. observ.) and disappear before metamorphosis (Hagerman, 1952).

A few specimens smaller than the reported hatching size (6 mm SL, Matarese et al., 1986) were collected (Table 11). However, body shrinkage due to preservation might account for this difference (Laroche et al., 1982). Length ranges of preflexion (stage I) larvae were similar to those of the other stages.

Because eye migration usually began while the larva was undergoing notochord flexion, stage II had a small length range and relatively few specimens (Fig. 18). Stage III showed the widest length range (12 mm SL). This supports the observation that this species begins metamorphosis normally, but then it stops the process and the transforming larva remains pelagic reaching a size >45 mm SL (Pearcy et al., 1977; Matarese et al., 1986). No giant larvae of this species were captured, however. The largest specimens were <27 mm SL, at stages III and IV (Table 11).

Parophrys vetulus (English sole). Stage distribution of English sole is very different from the rest of the species. Many (63.0%) specimens collected were at stages III and IV. Notochord flexion began with little variation at 7.2 mm SL (stage II; Table 11). Eye migration started after completion of notochord flexion (roughly at 13 mm SL). The migrating eye reached the middorsal ridge (stage IV) between 18.9 and 21.8 mm SL, with almost negligible body length growth (Fig. 19). The

dominance of older stages in the stage distribution of larval English sole may be due to a sampling artifact caused by the absence of a continuous sampling throughout the year.

Psettichthys melanostictus (Sand sole). Most of the sand sole larvae (72.7%) were at stage I within the length range for preflexion of other species in this study (Table 11; Fig. 20). Notochord flexion occurred within a very narrow length interval (Stage II; Table 11), suggesting either a fast flexion, or little length growth during the process. Eye migration started when flexion was well advanced, and a considerable length increase during this third stage is apparent. Stage IV larval sand sole were found over a range of ca. 14 mm SL (Table 11), although color asymmetry appeared evident only after the larva reached 18 mm SL. The great overlap between the size ranges of stages III and IV suggested a rapid rate of eye migration (Fig. 20).

Seasonal variation of larval lengths and developmental stages

This section is based on distributions of standard length (Figs. 21-28) and stage (Table 11). These distributions will be useful to aid the elucidation of spawning seasons of the eight species in this study. Two precautions, however, must be made. First, because bongo tows accounted for 95% of total larvae caught in the seven surveys, analyses of larval lengths will be confined to bongo collections. Second, conclusions on seasonal and interannual trends are severely limited since only one or two cruises were made in each of the four years.

Citharichthys sordidus (Pacific sanddab). The largest catches of recently

hatched (<7 mm SL), stage I larvae occurred during mid-fall 1981 (921.4 ind/10 m² of 4-5 mm SL; Fig. 21)⁵. This indicated that a major pulse of spawning occurred in the late summer or early fall of 1981. High catches of stage I larvae were not found in late-fall 1983 however, when larval catches were lower and dominated by stage II specimens in bongo tows. This suggested that spawning ended by mid-fall of this year or that 1983 was an aberrant year. Spawning of Pacific sanddab earlier in the year is indicated by the few (5.9-8.3 ind/10 m²) stage I larvae collected during mid-spring and summer of 1980 and late-spring of 1981 (Fig. 21). Mid-spring of 1983 showed a moderately high catch dominated by recently hatched larvae (85.7 ind/10 m² at 4 mm SL), while moderate numbers during late-spring 1981, with peak catches of 12 mm SL larvae (29.3 ind/10 m²) suggested a minor spawning peak from early- to mid-spring of those years. Because larval Pacific sanddab is not known to have a long pelagic life (Richardson and Pearcy, 1977), the presence of later stages (III and IV) at different seasons (e.g., mid-spring 1980, late-spring and mid-fall 1981 and late-fall 1983) supports the idea of prolonged spawning.

Citharichthys stigmaeus (Speckled sanddab). Abundances of recently hatched, stage I larvae (< 9 mm SL; Table 11) were highest during mid-fall 1981 (104.9 ind/10 m² at 5-7 mm SL) (Fig. 22). Stage II and III larvae were also common during this cruise, indicating spawning activity earlier in the year. During late-fall 1983, a distinct mode of 10-11 mm SL larvae (mostly stage II) occurred, but few recently hatched (3-5 mm SL) were caught, suggesting that spawning activity subsided

⁵Note that the vertical scales differ among cruises in these figures.

later in the fall. Few speckled sanddab larvae were caught during mid-spring 1980 or late-spring 1982, and none was caught during summer 1980 and late-spring 1981. However, moderate abundances of stage I individuals during mid-spring 1983 (42.9 ind/10 m² at 7 mm SL) suggested spring spawning in that year.

Glyptocephalus zachirus (Rex sole). Stage I larvae were most abundant during mid-spring 1983, when a distinct mode of 67.6 ind/10 m² occurred at 8 mm SL (Fig. 23). Larvae between 5-13 mm SL were moderately abundant during mid-spring 1980 and late-spring 1981 and 1982. Few recently hatched specimens were caught during summer 1980 (4.3 ind/10 m²) and none during fall (1981 and 1983). This suggested a spring-early summer spawning season for rex sole. During the fall cruises (1981, 1983), only one specimen, a 'giant' larva (stage III, 68 mm SL) was caught, suggesting little spawning activity during fall. However, large (≥ 25 mm SL) pre-metamorphic and beginning metamorphosis specimens (stages II and III) were present during most cruises, suggesting prolonged spawning and long larval life.

Isopsetta isolepis (Butter sole). This flatfish appeared to spawn through late winter and spring and settle to the bottom before summer and fall. In bongo tows, recently hatched (≤ 5 mm SL) butter sole were most abundant during mid-spring 1980 and late-spring 1982 (28.1 and 30.9 ind/10 m², respectively, at 4 mm SL) (Fig. 24), suggesting spring spawning activity. Catches of stage III and IV specimens during spring cruises suggests spawning earlier in the year (e.g., winter), while the absence of larvae during summer 1980 and fall (1981, 1983) may indicate that settlement of metamorphosing larvae (stages IV, V) ended by July-August.

Lyopsetta exilis (Slender sole). Abundances of recently hatched (5-7 mm SL) larvae of this species were highest during mid-spring (645.4 ind/10 m² in 1980 and 374.8 ind/10 m² in 1983, and were moderately high during late-spring (293.3 ind/10 m² in 1981 and 172.5 ind/10 m² in 1982) (Fig. 25). Catches of later stages (III and IV) collected during late-spring (1981) and summer 1980 suggested early-spring spawning, while their presence during mid-spring 1983 suggested spawning since mid- or late-winter in that particular year. Despite the large catches during spring, no slender sole larvae were caught during fall (1981, 1983). Settlement to the bottom probably occurred in August-September.

Microstomus pacificus (Dover sole). The largest catches of stage I (<10 mm SL) larvae occurred during mid-spring 1983 (66.7 ind/10 m² at 6-7 mm SL), although during the same season in 1980 larval catches were much lower (Fig. 26). Recently hatched specimens also occurred during late-spring (21.5 ind/10 m² at 7 mm SL in 1981 and 15.3 ind/10 m² at 6 mm SL in 1982), which may suggest spawning activity during early spring that subsided later in the season. In addition to the absence of larval catches during fall (1981, 1983), collection of later stages (III and IV) during late-spring 1981 (58.8 ind/10 m² at a distinct modal length of 12-13 mm SL) and summer 1980 supported the observation of early spring spawning. However, stage III larvae were also caught during mid-spring 1983, which suggested that spawning started earlier in 1983 than in the previous years.

Absence of giant Dover sole larvae (i.e., >50 mm SL, sensu Pearcy et al.,

1977) in the 1980-1983 period may be the result of small volumes of water filtered, net avoidance or other processes (e.g., settling, high mortality rates, or advection out of the region).

Parophrys vetulus (English sole). The spawning cycle of English sole appeared to begin in September-October and continue through spring months. In bongo tows, recently hatched larvae (≤ 7 mm SL) occurred in most of the cruises, although they were most abundant during mid-fall 1981 (48.7 ind/10 m²) and were common during mid-spring (31.3 ind/10 m²) and late-fall of 1983 (21.2 ind/10 m²) (Fig. 27a). Stage III and IV (16-23 mm SL) were caught at both bongo and neuston stations of most of the spring cruises, but they were most abundant during mid-spring in bongo (42.5 and 38.7 ind/10 m² in 1980 and 1983, respectively; Fig. 27a) and neuston catches (88.4 and 26.6 ind/1000 m³ in 1980 and 1983, respectively; Fig. 27b). This suggested early spawning (e.g., the previous fall and winter), and the absence of those later stages during summer (1980) and fall (1981, 1983) indicated that settlement ended by July-August.

The unusually high proportion of large (13-22 mm SL) stage III and IV specimens (Table 11) of *P. vetulus* in bongo and neuston collections during all cruises except those in fall (beginning of the spawning season) (Fig. 27a,b) suggests that most spawning ended prior to the spring surveys.

Psettichthys melanostictus (Sand sole). This species appeared to spawn mainly from winter through mid-spring. The highest abundances of stage I larvae occurred

during mid-spring, when there was a distinct modal length of 4-5 mm SL (80.8 and 60.8 ind/10 m² in 1980 and 1983, respectively) (Fig. 28). However, numbers of recently hatched larvae were lower during late-spring 1981 and 1982 (0 and 30.4 ind/10 m², respectively). Later stages (III and IV) occurred during mid-spring and summer 1980 and during late-spring and mid-fall 1981. The absence of larvae >13 mm SL during mid-spring 1983 and late-spring 1982 suggests either a delayed spawning in those years, high mortality of larvae hatched earlier in the year, or slower body growth rate. Although the low numbers of later stages after summer indicated that most larvae settled to the bottom by August, some stage IV specimens were pelagic as late as October (Fig. 28). Larval sand sole were absent only during the late-fall 1983 survey.

Geographic distribution

Three different distributional trends were analyzed. (1) On/offshore and (2) latitudinal patterns were tested separately among and within cruises with ANOVA's and Multiple Comparisons. The boundaries of the regions are given in Table 12a,b. (3) Within-cruise variations among the eight geographic regions (Fig. 1 and Table 12c) were also analyzed separately with one-way ANOVA and subsequent Multiple Comparisons. These three analyses will be discussed sequentially for each species. Some discrepancies between among- and within-cruise analyses arose due to interaction between the effects of bottom depth and latitude on egg/larval abundances. When latitude/depth interaction was significant⁶, only differences among the eight

⁶When interaction is present, the response to changes of levels of factor A (e.g., bottom depth) depends upon the level of factor B (e.g., latitude).

geographic regions shown in Fig. 1 were considered, as recommended by Devore and Peck (1986). When discrepancies arose between the conclusions of ANOVA and Multiple Comparisons, ANOVA results were considered to be a more robust test (Snedecor and Cochran, 1974; Devore and Peck, 1986).

Eggs of *Citharichthys* spp. (Sanddabs). Significant interaction between latitude and bottom depth among cruises ($p < 0.01$) and within most cruises ($p < 0.05$) detracted from analyzing latitudinal and on/offshore trends separately in both bongo and neuston tows of many surveys (Table 13a,b). For those cruises in which depth/latitude interaction was non-significant, no latitudinal trends were observed (Table 13a). However, egg abundances were highest onshore ($p < 0.05$) (Table 13b; Fig. 29a-g).

In a separate analysis of distribution, within-cruise differences among the eight regions in both bongo and neuston tows were significant in all cruises except late-spring 1982 (Table 13c), indicating that eggs and larvae were more abundant in certain regions than in others. The low numbers of eggs caught during late-spring 1982 may explain why significant differences were not found for this cruise. Spawning seemed to occur mainly on the continental shelf (bottom depth ≤ 200 m) off the Oregon and Washington coasts. In bongo and neuston collections, sanddab eggs were most abundant in region V (onshore, 44-46°N) and were very common in region VII (onshore, 46-48°N) during most of the cruises (Fig. 29). High numbers of eggs also occurred in region I (onshore, 40-42°N) during summer 1980 and mid-

spring and late-fall 1983 ($p < 0.05$). Significant egg catches with both gears in regions III, V (onshore, 42-46°N) occurred during mid-spring 1980, late-spring and mid-fall 1981. Interestingly, sanddab eggs occurred at far-offshore stations at various latitudes only in summer 1980 (Fig. 29b), although usually in small numbers.

Citharichthys sordidus (Pacific sanddab) larvae. Latitudinal differences among cruises were significant in both bongo and neuston collections (Table 13a), indicating that their latitudinal distribution changed with the season and the year. However, in only one cruise, mid-fall 1981, were larval Pacific sanddab more abundant ($p < 0.01$) in bongo catches between 44-46°N (northern Oregon coast) than in other regions (Fig. 30d). Although on/offshore distributions were not statistically significant among or within other cruises in bongo and neuston tows ($p > 0.05$) (Table 13b), more larval Pacific sanddabs occurred further offshore in the fall surveys (1981, 1983) than in other cruises (Fig. 30).

Pacific sanddab larvae occurred in bongo and neuston catches of all cruises except in neuston tows of late-spring 1982. However, differences in catches among the eight geographic regions were significant only at bongo stations of a few cruises (Table 13c). This suggests that larvae of this species were dispersed both offshore and onshore from northern California to Washington.

In bongo collections, *C. sordidus* larvae were most abundant onshore off the Oregon coast (regions III and V, 42-46°N) during mid-spring 1983 ($p < 0.01$), reflecting the onshore spawning of the sanddab eggs discussed above (Fig. 29f), and possible

onshore advection of the larvae during that season of the 1983 El Niño year. Pacific sanddab larvae were also more abundant beyond the continental shelf off the northern coast of Oregon (region VI, 44-46°N) during fall 1981 than any other region or cruise ($p < 0.01$) (Fig. 30d). They were also abundant at offshore stations off northern California and southern Oregon coasts (40-44°N) during late-fall 1983 (Fig. 30f), although no statistically significant differences were detected. Considering that most of the sanddab eggs collected during fall (1981, 1983) occurred at onshore stations (Fig. 29d,g), the large numbers of larvae found beyond the continental break suggested a strong offshore advection during fall of those years.

Citharichthys stigmaeus (Speckled sanddab) larvae. Latitudinal distributions were significantly different among cruises in bongo catches only ($p < 0.05$) (Table 13a). However, significant within-cruise trends were found only during mid-fall 1981, when larvae of this species were most abundant between 44-46°N (northern Oregon coast) in both onshore and offshore waters (regions V, VI) (Fig. 31c). Because of the absence of sanddab eggs at offshore stations during this season (Fig. 29d), the peculiar distribution of larval speckled sanddab shown in Fig. 31c suggested offshore advection along the California and southern Oregon coasts. Neither latitudinal differences in neuston collections (Table 13a) nor on/offshore trends in bongo and neuston tows were observed among and within cruises (Table 13b). However, larval abundances appeared closer onshore during mid-spring (1980, 1983) (Fig. 31a,e) than during fall (1981, 1983) (Fig. 31c,f), i.e., before or after upwelling season. Like Pacific sanddab, *C. stigmaeus* was not found far offshore during the 1983 El Niño year (Fig. 31e).

Separate ANOVA's comparing distributions among the eight regions yielded significant differences for bongo catches of two cruises (Table 13c). During mid-fall 1981 and mid-spring 1983, larval speckled sanddab were most abundant in region V (on the continental shelf off the northern Oregon coast, 44-46°N) (Fig. 31c,e). Also, although no statistical significance was detected during late-fall 1983, this species also appeared most abundant between 41 and 45°N (Fig. 31f).

Glyptocephalus zachirus (Rex sole). Significant interaction of latitude and bottom depth ($p < 0.02$) was found in the distribution of eggs and larvae of this species among and within most cruises in both bongo and neuston tows (Table 13a,b). Thus, most of the analyses focused on geographic regions. Egg abundances showed significant latitudinal trends during mid-spring 1983, when numbers were highest off Washington (46-48°N) in bongo and neuston tows ($p < 0.01$) (Fig. 32e). During the rest of the surveys, eggs seemed to occur evenly across the four latitudinal regions (Fig. 32a-d). Larval densities did not show significant latitudinal trends (Table 13a), probably because of their low numbers. During the season that they were most abundant, mid-spring 1983, larvae appeared evenly distributed along the west coast (Fig. 33f).

Onshore-offshore analyses showed that the highest catches of eggs occurred onshore at bongo and neuston stations during mid-spring 1983 ($p < 0.01$) and at bongo stations during late-spring 1982 ($p < 0.05$) (Table 13b). However, eggs were usually found not too far offshore from the continental shelf (Fig. 32a-e). Only during mid-

spring 1980 were larval catches of rex sole significantly higher onshore than offshore ($p < 0.05$) in bongo tows (Table 13b). Although no significant differences were detected during mid-spring 1983, rex sole larvae were caught farther offshore than during any other season (Fig. 33a-f), suggesting offshore advection. This is opposite to the onshore advection for *C. sordidus* during mid-spring of the 1983 El Niño year mentioned above.

Table 13c shows significant differences among geographic regions of rex sole eggs caught in most cruises, while larval abundances differed significantly in only one cruise (probably because of the low catches in the other surveys). During mid-spring 1980, *G. zachirus* eggs were most abundant onshore off northern Oregon and Washington coasts (regions V, VII within 44-48°N) in bongo collections, while in neuston tows they were most abundant onshore the northern California coast (region I, 40-42°N) (Fig. 32a). As the season progressed (summer 1980), the spawning activity decreased and was more concentrated in region V (northern Oregon coast) than in the other regions ($p \leq 0.01$) for both gears (Fig. 32b). During late-spring 1981, egg densities were highest onshore off the northern coast of California (region I) in bongo and neuston tows. Eggs were also common farther north, i.e., off Oregon (42-46°N) in bongo collections but not off Washington (Duncan's New Multiple Range Test $p < 0.05$) (Fig. 32c). Nevertheless, during late-spring 1982 eggs of rex sole appeared to be evenly distributed across all four latitudinal regions (Fig. 32d). Finally, during mid-spring 1983 rex sole appeared to spawn farther offshore and to the north than during previous seasons, as indicated by the significantly high concentrations of eggs ($p < 0.01$) in region VIII (off Washington, 46-48°N) (Fig. 32e).

This suggested a northward shift from the normal occurrence of eggs during this 1983 El Niño year.

Patterns of larval distribution were significant only during mid-spring 1980 ($p < 0.05$) when larvae were most abundant onshore along the Oregon and Washington coasts ($42-48^{\circ}\text{N}$) and offshore at 45°N at the continental break (310-650 m depth), reflecting the egg distribution in bongo tows of the same cruise (Fig. 33a). Unlike the northern distribution of eggs, larvae were found in high numbers in all latitudinal regions during mid-spring of the 1983 El Niño year.

Isopsetta isolepis (Butter sole). No latitudinal trends were observed among or within cruises for egg and larval abundances of this species (Table 13a). Although no on/offshore trends in egg and larval distributions were observed among cruises (Table 13b), eggs occurred at stations where the bottom depths were less than 112 m (Fig. 34) and most larvae were collected inshore of the 160 m isobath (Fig. 35). This suggests that this flatfish spawns along the inner continental shelf.

Within cruises, eggs occurred mainly onshore in bongo tows of late-spring 1981 (Fig. 34c) and in neuston tows of mid-spring 1980 and 1983 (Fig. 34a,f). Larvae also occurred more onshore than offshore during mid-spring 1980, 1983 and late-spring 1981, 1982 ($p < 0.05$; Fig. 35a-d).

Among the eight geographic regions, egg and larval catches of butter sole were highest onshore off Washington (region VII, $46-48^{\circ}\text{N}$) during mid-spring 1980 (Fig.

34a, Wa). Egg catches were also high at bongo stations onshore at 44° 40' lat N (region V) (Fig. 34a), while high numbers of metamorphosing larvae (stage IV, 18-22 mm SL) occurred at neuston stations onshore between 41-42°N (region I) (Fig. 35a). This suggests that even though spawning occurred in the northern part of the sampled area during that season, larvae were settling to the bottom in the southern part of the sampling range. During late-fall 1983, eggs occurred on the continental shelf off the Oregon coast (Fig. 34f). High numbers of larval butter sole occurred along the northern Oregon and Washington coasts (regions V, VII) during late-spring 1981 (Fig. 35b), while they occurred onshore off northern California and southern Oregon coasts (regions I, III) during mid-spring 1983 (Fig. 35d).

Lyopsetta exilis (Slender sole). Ichthyoplankton of this species were very common at all latitudes, usually over the continental shelf. The absence of latitudinal differences among cruises in egg abundances (Table 13a) indicated that they were evenly distributed across the four latitudinal regions (Figs. 36a-d). However, during mid-spring 1980, bongo catches of eggs were significantly higher off the Oregon coast (42-46°N), while neuston catches were higher farther south off the northern California and southern Oregon coasts (40-44°N) (Fig. 36a) than other latitudes (Table 13a), suggesting southward advection of eggs at the top 30-cm of the water column. Nevertheless, during mid-spring of the 1983 El Niño, it was precisely at bongo stations in the region between 40 and 44°N where egg numbers were lower than at other latitudes (Fig. 36e) ($p=0.05$), suggesting that either spawning was not common so far south or northerly advection of eggs in the 1983 El Niño year. Larval abundances showed no latitudinal trends among or within cruises, suggesting an even

latitudinal distribution throughout the sampled area (Table 13a; Fig. 37a-e).

On/offshore distribution of eggs and larvae did not vary significantly among cruises (Table 13b); early stages of slender sole were most abundant on the continental shelf in most of the surveys (Figs. 36, 37a-d) ($p < 0.05$ for egg catches), except for larval abundances during mid-spring of the 1983 El Niño year (Fig. 37e), suggesting an unusual offshore advection in that season.

Eggs and larvae of slender sole occurred in all the eight geographic regions in most of the spring surveys (none was caught during fall) (Figs. 36, 37). Eggs were usually most abundant onshore off the northern California and southern Oregon coasts (regions I and III, 40-44°N) and were very common off northern Oregon (region V, 44-46°N) (Table 13c; Fig. 36), except in late-spring 1982 when they were evenly distributed. Highest larval abundances ($p < 0.01$) were more restricted to onshore waters off Oregon (regions III and V, 42-46°N) (Figs. 37a,c,e), suggesting northerly advection from southern spawning grounds or earlier hatching in that particular area.

Microstomus pacificus (Dover sole). Latitudinal distributions of eggs and larvae of this flatfish did not vary significantly among cruises (Table 13a), suggesting a latitudinal pattern consistent through the seasons. Eggs seemed evenly distributed across the four latitudinal regions during the surveys (Figs. 38a-d), although during mid-spring the catches with both gears were highest off Washington (46-48°N) in 1980 (Fig. 38a) and 1983 ($p < 0.05$) (Fig. 38e). Due to the low larval numbers, no significant latitudinal differences were detected among cruises, although they tended

to be more abundant off Washington (46-48°N).

On/offshore distributions of egg and larval catches were not usually significantly different among cruises, except for bongo tows of eggs in two cruises (Table 13b) and larvae in one cruise ($p < 0.05$). Dover sole eggs occurred on- and offshore along the coast, but they were most abundant at bongo stations just beyond the continental shelf during late-spring 1981 and 1982 (Fig. 38c,d). Most larvae appeared to occur farther offshore (Fig. 39a-e), but the low numbers did not yield significant results in the ANOVA tests, except in late-spring 1981 (Table 13b).

Egg collections showed within-cruise differences among the eight geographic regions during mid-spring 1980 and 1983 (Table 13c), when catches were highest onshore off Washington (46-48°N; region VII) in bongo tows (Fig. 38a) and offshore with both gears (region VIII) (Fig. 38e). During late-spring 1981, they were evenly distributed at all latitudes not too far from the continental shelf. Larvae, however, were more abundant farther beyond the continental break off Washington and northern Oregon during late-spring 1981 ($p < 0.05$) (Fig. 39c) than eggs were in the same season, suggesting offshore advection in that year.

Parophrys vetulus (English sole). Significant depth/latitude interactions among and within cruises (Table 13a,b) detracted from analyzing separate latitudinal and on/offshore trends of distribution of eggs and neuston catches of larval English sole. No significant differences were found with either latitude or distance from shore, possibly because of the low numbers of eggs and larvae caught.

Among the eight geographic regions, the main spawning activity seemed to occur onshore along the northern Oregon coast (region V, 44-46°N) (Fig. 40a,c), and larval distributions reflected the spawning activity of previous months (Figs. 41a-d). During mid- and late-fall 1981 and 1983, bongo catches of *P. vetulus* eggs and larvae and neuston catches of eggs were higher (Table 13c) in region V than elsewhere ($p < 0.01$). Eggs were also common near the Washington coast (region VII, 46-48°N). Larval abundances were highest in bongo and neuston tows of region V during mid-spring 1980 (Fig. 41a). Larval English sole also occurred in large numbers at onshore neuston stations along the Washington coast (region VII) during late-spring 1982, suggesting a northerly advection from the spawning grounds of that season (Fig. 41c). An unusual offshore advection off the Washington coast was suggested by the occurrence of larval *P. vetulus* in region VIII during mid-spring of the 1983 El Niño year.

Psettichthys melanostictus (Sand sole). No latitudinal trends for egg and larval abundances of this pleuronectid were observed among and within most cruises (Table 13a). Although sand sole eggs appeared evenly distributed across the four latitudinal regions during most cruises, spawning seemed to occur only north of 43°N (i.e., off northern Oregon and Washington coasts) during fall 1981 and 1983 and late-spring 1982 (Fig. 42d, e,g). Although larvae occurred at all latitudinal regions, they were most common (Table 13a) only north of the 43°N during mid-spring 1980 (Fig. 43a). Larval sand sole were also caught north of 46°N during late-spring 1982 (Fig. 43e), and the absence of statistical significance may be due to the low catches.

On/offshore distribution of egg abundances in both gears and neuston catches of larvae did not vary significantly among cruises (Table 13b), suggesting a consistent pattern during most seasons. Egg and larval abundances of sand sole were highest on the continental shelf in all seasons (Figs. 42, 43), although during late-spring 1981 and 1982 the catches were too low for adequate statistical comparisons.

Egg and larval abundances varied significantly among the eight geographic regions during many cruises (Table 13c). Egg concentrations were usually highest in regions I and VII during spring and summer cruises, suggesting two main spawning grounds: the main one on the continental shelf off the Washington coast (46-48°N) (Fig. 42a-c, e,f) and a secondary one near the northern California coast (40-42°N) (Fig. 42a,b). Larvae usually occurred between these two areas, however. During mid-spring 1980, eggs were most abundant at bongo stations near the Washington coast (region VII, 46-48°N) and at neuston stations near northern California coast (region I, 40-42°N) (Fig. 42a), while larval catches were significantly highest in the onshore Oregon and Washington (regions III, V, VII; 43-48°N) (Fig. 43a). During late-spring 1981, spawning was restricted to onshore Washington (region VII; Fig. 42c), but larvae were most abundant in the onshore area off the Oregon coast (regions III, V; Fig. 43c), suggesting southward advection. During the fall of the same year eggs were concentrated onshore off northern Oregon (region V; Fig. 42d). During mid-spring 1983 the pattern did not seem different from those in previous springs; spawning occurred at 46-47°N and in the onshore northern California region (Fig.

42f), while larvae were most abundant onshore off northern Oregon (region V; Fig. 43f).

DISCUSSION

Spawning Seasons

Based on my work and the literature, the pleuronectiforms in the study area have three major spawning seasons -- fall, winter and spring.

Fall spawners (*Parophrys vetulus*, *Citharichthys sordidus*, *C. stigmaeus*)

The eggs and recently hatched larvae of these species occur mainly during the fall. Richardson and Percy (1977), Laroche and Richardson (1979), and Matarese et al. (1986) reported extended spawning of English sole from early fall through spring. I also observed this trend for the protracted spawning, although most of the spawning ended prior to the spring surveys (Tables 2a,b; 6a,b). Low catches of stage I larvae during late-spring (1981, 1982) indicated that spawning had stopped and settlement had started by July-August, as suggested by Richardson and Percy (1977). Sampling discontinuity may account for catches of *P. vetulus* eggs during fall surveys only (Tables 2a,b). Maximum abundances of larval English sole in fall coincide with good availability of appendicularians (*Oikopleura* spp.), the most important prey for this larval fish (Gadomski and Boehlert, 1984).

Most eggs were collected during fall (1981, 1983), when surface temperatures ranged between 12.5 and 13.5°C and the lowest temperatures at 75-m depth were 8-9.5°C (Fig. 40 vs. Figs. 9a,b and 12a,b). Recently hatched larvae in bongo tows occurred at a minimum temperature of 8°C (at 75 m depth) during late-spring 1982

(Fig. 41c vs. Fig. 10b). This is consistent with Kruse and Tyler's (1983) and Mundy's (1984) observations that a temperature threshold of 7.8°C is required to trigger the spawning activity of English sole. Mild weather conditions, decreased onshore transport and reduced cloudiness, which may provide optimum conditions for growth and survival of larval English sole, may lead to a strong year-class in some years, but not in others (Laroche and Richardson, 1979).

Low egg and larval numbers of *P. vetulus* in this study suggested either low-intensity spawning, a high mortality of early stages, or high escapement rates of eggs and small larvae through 505- μ mesh and avoidance by more developed larvae. The absence of later stages (IV, V) of larvae in open waters after summer (Fig. 27a,b) agreed with previous observations that metamorphosing English sole are advected by onshore Ekman transport during the downwelling season to enter bays and estuaries as nursery grounds (Percy and Myers, 1974; Krygier and Percy, 1985).

The seasonal patterns of two sanddabs differed from other reports. In this study, *C. sordidus* showed a prolonged spawning from late summer through late spring with a major peak during fall and secondary peaks during early and mid-spring 1981 and 1983 (Tables 2a,b; 6a,b). Matarese *et al.* (1986) reported that this flatfish spawns during summer in California and during late winter-spring in Puget Sound, Washington, while Richardson and Percy (1977) collected high numbers of small *Citharichthys* (*sordidus*?) larvae 37-46 km off Newport, Oregon in October 1971. It appears then, that the onset of the Pacific sanddab spawning season occurs progressively later as latitude increases, and perhaps later in Puget Sound than open

coastal waters. Because Pacific sanddab undergoes metamorphosis at 20->39 mm SL (Matarese et al., 1986) and larvae >40 mm SL were not collected after late-spring (Fig. 21), settling to the bottom is probably complete by July-August. This agrees with observations of maximum peaks at depths >50 m among large larvae (mean = 37.8 mm SL; range 17-40 mm SL) during July (Boehlert et al., 1985).

C. stigmaeus also has an extended, low-intensity spawning season from early fall to late spring with a peak during fall (1981, 1983) (Tables 2a,b; 6a,b). Because speckled sanddab eggs were indistinguishable from those of Pacific sanddab and no larval speckled sanddab were collected during summer 1980, the onset of the major spawning season could not be clearly determined. It seems, however, that the fall spawning of speckled sanddab began later than that of Pacific sanddab, as suggested by the absence of recently hatched *C. stigmaeus* during summer 1980 and the smaller proportion of later developmental stages of larvae than *C. sordidus* during fall. However, no recently hatched *C. sordidus* were collected during July, 1982, while few larval speckled sanddab occurred in spring and summer collections, although no body sizes were given (Boehlert et al., 1985). Assuming that larval speckled sanddab transforms at 24-35.5 mm SL (Matarese et al., 1986), the absence of larvae >35 mm SL after late-spring (Fig. 22) indicates that the settling season ended by June-July.

Winter spawners (*Microstomus pacificus*)

Although winter is considered the spawning season of *Microstomus pacificus* by Hagerman (1952) and Matarese *et al.* (1986), in this study peak abundances of eggs and early larvae (<13 mm SL) were collected from April through May (Tables 2a,b; Fig. 26). Pearcy *et al.* (1977) also found premetamorphosing larvae (4-11 mm SL) from March through July. Unfortunately, in this study no survey was conducted during the winter months within the 1980-1983 period (Table 1), hence winter spawning could not be directly verified. The low numbers of larval Dover sole (Tables 6a,b; Pearcy *et al.*, 1977) could indicate high larval mortality or migration/advection out of the sampled area. Since Dover sole was the third most abundant species among the west coast groundfish landings in the 1970's decade and in 1983 (Pearcy *et al.*, 1977; Weinberg *et al.*, 1984), survival of larvae must be adequate for recruitment in some years.

No Dover sole eggs or larvae were caught in November (1981, 1983), probably because only few females begin to spawn that month (Hagerman, 1952). The pelagic phase of Dover sole may be very prolonged. Incubation of eggs take up to 27 days at 10°C (Matarese *et al.*, 1986), and premetamorphic larvae <13 mm SL may be as old as six months (Markle, D. 1989. pers. comm.). Therefore, the larvae caught in this study in the spring can be a product of winter spawning. However, catches of eggs through May (late-spring 1981, 1982) and August (summer 1980) indicated that spawning occurred as late as April and July.

Finally, determination of the settling period of Dover sole was not possible

with the data available in this study because of three factors: (a) the low larval numbers of this species usually caught (Tables 6a,b; Pearcy *et al.*, 1977), (b) the extended pelagic life associated with the slow larval development (Hagerman, 1952; Richardson and Pearcy, 1977; Markle, 1989. Unpubl. manuscr.), and (c) the lack of association between eye migration and the settling out from the pelagic habitat to the bottom (Markle, 1989. Unpubl. manuscr.).

Spring spawners (*Isopsetta isolepis*, *Psettichthys melanostictus*, *Glyptocephalus zachirus*, *Lyopsetta exilis*)

The winter/mid-spring spawning of butter sole observed in this study had also been reported by Laroche and Richardson (1979) and Matarese *et al.* (1986), and the absence of later stages (i.e., >16 mm SL; Table 11) after late spring (Fig. 24) is in good agreement with the reported restricted settling period between May and August (Hogue and Carey, 1982). The occurrence of few eggs during late-fall 1983 (Tables 2a,b) can be explained by the anomalous conditions of that year (discussed later). Or these eggs could belong to other pleuronectids (e.g., English or sand soles, or starry flounder), from which they are very difficult to distinguish (Matarese *et al.*, 1986).

The highest numbers of stage I (< 8 mm SL; Table 11) larval sand sole were found during mid-spring (Fig. 28), but eggs were found during all seasons surveyed, suggesting prolonged spawning activity (Tables 2a,b). Richardson and Pearcy (1977) and Mundy (1984) also observed this pattern of protracted spawning from late summer through late spring with a main peak from late winter through spring

(Mundy, 1984).

Although this study provided direct evidence of only spring spawning of rex sole, Hosie (1975, 1977) concluded that rex sole spawns from January through June, with a March-April peak. Eggs were most abundant in late-spring 1982 (Tables 2a,b) and small larvae (<10 mm SL) were caught from late April through August (i.e., mid-spring through late summer; Fig. 23). Richardson and Pearcy (1977) caught small (≤ 9 mm SL) larval rex sole only from April through June 1971, supporting the conclusion that *G. zachirus* is a spring spawner. Even though the pelagic life of larval rex sole is reportedly very extended (Pearcy et al., 1977; Richardson and Pearcy, 1977), little is known about the incubation time of the eggs. Considering that the egg diameter (1.80-2.05 mm; Matarese et al., 1986) is smaller than that of Dover sole eggs (≈ 2.05 -2.57 mm; Hagerman, 1952), the incubation time of rex sole eggs should be shorter than a month⁷. Thus, eggs collected through May (late-spring) were probably spawned after the first of April. Also, the occurrence of small (6 mm SL) stage I larvae in late-summer (1980) suggested spawning activity as late as early July, in relatively good agreement with the reported end of the spawning season (Matarese et al., 1986). Spawning of rex sole through August had been observed off northern California in 1949-54 (Hosie, 1975, 1977).

The temporal discontinuity in sampling provided only indirect evidence of

⁷Ware (1975), cited by Hunter (1981) found a linear relationship between duration of egg incubation and egg size at a constant temperature. Therefore, the incubation of rex sole eggs should be shorter than that of Dover sole eggs.

winter spawning. The presence of larval rex sole >15 mm SL during mid-spring (Fig. 23) suggested spawning earlier in the year, but the lack of time frame for both the body growth and the development of the *G. zachirus* larvae (Markle, D. 1989. pers. comm.), as well as the extended pelagic life of premetamorphic larvae (Pearcy et al., 1977) made it impossible to determine the month when they were spawned.

Finally, slender sole appeared to spawn exclusively through the spring months and to settle before mid-fall (Tables 2a,b; 6a,b). Despite of the temporal discontinuity in sampling, this study agreed with the March-June spawning season and end of September settling period suggested by Richardson and Pearcy (1977). Being one of the most abundant flatfishes in demersal communities on the continental shelf off Oregon (Pearcy and Hancock, 1978), it was not surprising that both eggs and larvae of slender sole were abundant and frequently occurring in the bongo catches in this study (Tables 2a, 5a; 6a, 8a).

Spawning Strategies

These eight species of flatfishes showed varied spawning strategies, ranging from an intense, restricted spawning season during spring (slender sole) to a low-intensity prolonged spawning almost all year round (sand sole). Eggs and larval stages of all these species were available during mid- and late-spring, and highest peaks of most taxa occurred during that season. Sand sole, as well as the fall spawners (English sole and Pacific and speckled sanddabs), had a prolonged spawning season that included spring months. Dover and rex soles, the two species with

extended pelagic larval phase of a year or more (Pearcy *et al.*, 1977), spawn large, relatively few eggs during spring and/or winter months. Dover sole may be planktonic through at least two springs (Markle, 1989. Unpubl. manuscr.).

Spring months may be favorable for the development of early stages of these fishes in the study area because of the decreased number and intensity of storms and increased food availability. Winter storms not only mix the upper layers below the critical depth, thus preventing phytoplankton blooms (Parsons and Takahashi, 1973), but also may cause high mortality of fish larvae by disrupting food aggregations (Lasker, 1978, 1981). Also, in a mid-latitudinal region such as off Oregon, cold, high-salinity, nutrient-rich waters are brought to the upper layers during spring and summer months by coastal upwelling (Small *et al.*, 1972; Huyer, 1983) providing favorable conditions for high planktonic productivity during that period. In this region, daily primary production is related to the amount of usable radiation and upwelling intensity, especially in the summer months when nutrient availability becomes a limiting factor in mid latitudes (Small *et al.*, 1972). Consequently, zooplankton abundance (most of it accounted for by copepods) was greater in coastal waters within 18 km off Newport, Oregon during upwelling season (April-September) than during the downwelling season (October-March) (Peterson and Miller, 1976, 1977). Farther offshore (28 to >120 km from the coast), however, Pearcy (1976) did not find seasonal differences in biomass of herbivores (copepods, euphausiids, salps-doliolids).

The eight pleuronectiforms studied in this work are good examples of different

spawning and settling strategies which may help enhance probabilities of survival. The seasonality and duration of the pelagic phase of the meroplanktonic fish larvae affect their distribution (Richardson et al., 1980). Different spawning seasons, and consequently, different settling seasons, may reduce interspecific competition during planktonic and early juvenile stages. For example, recently settled *P. vetulus* and *I. isolepis* are potential competitors because of their generalist diet (Hogue and Carey, 1982). However, *P. vetulus* has a protracted 9-month settling period (November-July), while *I. isolepis* settles over a restricted season (May-August) (Hogue and Carey, 1982). Also, prolonged low-intensity spawners (e.g., English sole, sand sole) may reduce intraspecific competition and predation by distributing their pelagic stages and recently settled juveniles over a longer period of time. They can also take advantage of good conditions whenever they occur in the year (Parrish et al., 1981), and they can prevent total year-class failure in case catastrophic events occur in a given season (Mundy, 1984). A prolonged pelagic life (e.g., Dover and rex soles) may enhance survival by permitting settling when bottom conditions (either physical or biotic) are favorable (Pearcy et al., 1977; Markle, 1989. Unpubl. manuscr.), as well as allowing dispersal of species which are more sedentary as adults (i.e., rex sole; see Hosie, 1975, 1977). Slender sole, with a restricted spawning season, produces high numbers of eggs and larvae in spring, when food availability is high. Despite of the higher potential intraspecific competition, the large numbers of individuals help balance the high mortality by predation. Fall and winter spawning reduces predation pressure because abundances of planktonic carnivores (e.g., chaetognaths, medusae, amphipods, shrimps) are lower during the November-April period than during May-October (Pearcy, 1976). Large eggs, (e.g., Dover and rex soles; Matarese et al.,

1986) may reduce the number and type of potential predators among zooplankters, particularly at lower temperatures, where incubation periods are longer (Hunter, 1981).

Geographic Distribution

Onshore-offshore

Larval fishes off Oregon have been classified into two to three assemblages (coastal⁸, offshore⁹ and transitional¹⁰) (Richardson and Percy, 1977; Richardson *et al.*, 1980; Mundy, 1984; Boehlert *et al.*, 1985; Brodeur *et al.*, 1985). Speckled sanddab, butter sole, English sole and sand sole belong to the coastal assemblage (either within 28 km off Newport, Oregon or over the continental shelf along the Oregon coast). Pacific sanddab, rex sole, slender sole and Dover sole were classified as offshore types (offshore of 37 km from Newport, Oregon) by Richardson and Percy (1977) and Boehlert *et al.* (1985). However, in Richardson *et al.* (1980), rex sole and slender sole were classified as coastal-transitional types, while Dover sole was an offshore-transitional species during winter-spring along the Oregon coast.

⁸When >80% larvae were caught between 2 and 28 km (20-95 m bottom depth) off Newport, Oregon (Richardson and Percy, 1977; Boehlert *et al.*, 1985), or within 46 km off the Oregon coast by multivariate analysis (Richardson *et al.*, 1980)

⁹When >80% larvae were caught between 37 and 111 km (142-2850 m bottom depth) off Newport, Oregon (Richardson and Percy, 1977; Boehlert *et al.*, 1985), or 18-56 km off the Oregon coast by multivariate analysis (Richardson *et al.*, 1980).

¹⁰Assemblage that roughly paralleled the 200-m isobath (i.e., the edge of the continental shelf) in March and April 1972-75, based upon multivariate analysis (Richardson *et al.*, 1980).

Most of the coastal types were consistently found in nearshore areas. As described in previous works (Richardson and Pearcy, 1977; Richardson *et al.*, 1980), the planktonic stages of butter sole (Figs. 34, 35), English sole (Figs. 40, 41) and sand sole (Figs. 42, 43) occurred mostly in coastal waters during both downwelling and upwelling seasons. Retention of planktonic stages of these species in coastal areas could be achieved by one of several mechanisms, or a combination of them. Firstly, spawning during the downwelling season (fall through early spring) reduces the advective loss of eggs and larvae (Parrish *et al.*, 1981). Part of the spawning activity of these species occurs within those months (Tables 2a,b; 6a,b). Secondly, they might spawn as close to the coast as possible, as suggested by the fact that most of the butter sole eggs (Fig. 34) and sand sole eggs (Fig. 42) were collected within ca. 9 km from shore, at bottom depths ≤ 112 m and ≤ 130 , respectively, while English sole eggs also occurred farther offshore (Fig. 41). Although these shallow waters are within the zone of intense coastal upwelling (10-25 km along the Oregon and northern California coast; Huyer, 1983), offshore Ekman transport is minimal directly adjacent to a coastal boundary (Parrish *et al.*, 1981). Peterson *et al.* (1979) proposed a two-cell circulation pattern off the Oregon coast, with a surface divergence at ca. 10 km from shore that originates two vertical cells circulating in opposite directions. The seaward advection by upwelled waters would be minimized within 10 km from shore with the presence of a thin surface Ekman layer (≤ 5 m) in that zone.

Advection of planktonic stages by Ekman transport, as well as by geostrophic

flow, depend upon the vertical distribution of the organisms throughout the water column (Parrish et al., 1981). The control of the vertical distribution of larval stages is a third mechanism that might also enhance retention in coastal waters. Avoidance of the upper few meters of the water column (Peterson et al., 1979) or vertical migration of fish larvae between layers of the water column are two examples of this mechanism. During the upwelling season off Oregon, the thin surface layer of mean offshore flow (<20 m thick) lies on top of a mid-layer of onshore flow that tends to compensate for the offshore transport (Smith, 1981), while the bottom Ekman layer has a weak flow, offshore when the poleward undercurrent is present and onshore otherwise (Huyer, 1983). Because the mixed layer is not as thick as the offshore surface Ekman layer, exchange of plankton between the onshore- and the offshore-directed layers can occur by sinking or swimming (Barber and Smith, 1981). This is supported by the fact that, although unusually high proportions of larval English sole were also caught in neuston tows, most of the larval butter sole and sand sole were collected in bongo tows in this study (Tables 6a,b). *I. isolepis* larvae were also more abundant in bongo tows than in neuston tows in March-April 1972-1975 along the Oregon coast (Laroche and Richardson, 1979) and maximum peaks of abundance were observed at 10-20 m depth in spring, while abundances of *P. vetulus* larvae were highest within 5-20 m depth during the same season (Boehlert et al., 1985). Although larval sand sole occurred throughout the water column at daytime, they were most abundant within the 5-20 m depth range during spring and 20-30 m during summer (Boehlert et al., 1985), suggesting that *P. melanostictus* larvae were closer to the sea surface at the beginning of the upwelling season (April) but deeper when upwelling intensity is maximum (July).

Interestingly, a relation between larval size and vertical distribution observed by Laroche and Richardson (1979) was also found in this study. In both works, most small *P. vetulus* larvae (<10 mm SL) occurred in bongo tows (Fig. 27a; see Fig. 3 in Laroche and Richardson, 1979), while neuston catches were dominated by larval specimens >12 mm SL (Fig. 27b; see Fig. 5 in Laroche and Richardson, 1979) during fall and mid-spring months during and after downwelling season when offshore advection was weak. This suggests an ontogenetic vertical distribution or net avoidance by larvae >10 mm SL in the water column.

A fourth mechanism to prevent offshore advection is to spawn out of the "region of maximum upwelling" (Parrish *et al.*, 1981) which extends from Point Conception to Cape Blanco (35-43°N) and includes the southernmost latitudinal region (Region I) of this study (Fig. 1; Table 12a). In this area, the upwelling season is longer and the upwelling intensity is much higher than in the other regions (Figs. 2-5). Most butter sole eggs (Fig. 34) and many sand sole eggs (Fig. 42) occurred north of 44°N while English sole eggs were caught north of 43°N (Fig. 40).

Other means of larval retention in coastal areas included deep-water spawning and the use of eddies to return the larvae to inshore waters in the region of maximum upwelling (Parrish *et al.*, 1981). However, the data obtained in this work were inadequate to test these hypotheses.

Some differences were found in the onshore-offshore classification of larval

fish between my study and those of others, possibly because this study sampled an area larger than that of Richardson and Pearcy's (1977), Richardson et al.'s (1980) and Boehlert et al. (1985). Although Richardson and Pearcy (1977) classsified larval Pacific sanddab an offshore type and considered speckled sanddab a member of the coastal assemblage, I conclude that both sanddabs probably spawn in open waters on the continental shelf along Washington, Oregon and northern California. Unfortunately, because *Citharichthys* spp. eggs were not distinguishable to the species level, specific spawning sites of Pacific and speckled sanddab could not be determined. Eggs mainly occurred inshore, near the coast (Fig. 29), although offshore Ekman transport during the upwelling season may advect the eggs far away from shore during summer (Fig. 29b). However, a localized spawning site between 45 and 46°N from 73 to 600 m depth was suggested by the high numbers collected at three bongo stations accounting for 63.2% of the 231 larval Pacific sanddab caught in mid-fall 1981 (Fig. 30). Most Pacific and speckled sanddab larvae were either close to or on the continental shelf at the end of the downwelling season (mid-spring) (Figs. 30a,e; 31a,e), but were far offshore towards the end of the upwelling season (Figs. 30c,f; 31d,f), suggesting that their onshore-offshore distribution changes seasonally as a result of directional changes in Ekman transport. While young Pacific sanddab inhabit open waters, speckled sanddab migrate into estuarine areas. The habitat of early young *C. sordidus* ^{Pacific} consists of deeper waters with finer sediments, but later they aggregate on sandy bottoms in more shallow waters (Pearcy, 1978). Yaquina Bay, Oregon has been reported as an important nursery ground with highest abundances of young speckled sanddab (30-80 mm) in the bay in May and June (Pearcy and Myers, 1974). This suggests that pelagic larvae of this species, like English sole,

eventually return to coastal areas.

Eggs of rex sole were most concentrated in coastal-transitional areas (Fig. 32), as were their larvae during mid-spring (1980) (Fig. 33a). This agrees with the observations during March-April by Richardson et al. (1980). However, larvae were farther offshore during late-spring (1981, 1982) than in mid-spring 1980 (Figs. 33c,e), again suggesting seaward advection by Ekman transport after several weeks of consistent upwelling (Figs. 3-4). At this time these larval rex sole would be in the offshore assemblage, as described by Richardson and Percy (1977). During winter, they would be advected into coastal waters by strong pulses of onshore transport caused by winter storms (Parrish et al., 1981). The geographic dispersion during the planktonic stages might be very important for this species. Since tagging experiments suggested a limited displacement of adult rex sole (Hosie, 1975, 1977), an extended pelagic phase that is influenced by currents may provide dispersion of rex sole to other areas.

Egg distributions of slender sole (Fig. 36) agreed with the coastal-transitional classification given by Richardson et al. (1980) (Fig. 36). Offshore Ekman transport does not seem to have great effect on the geographic distribution of this pleuronectid within the study area, except in spring of the 1983 El Niño year (discussed later). Like early stages of butter sole, *L. exilis* eggs and larvae are dispersed within a restricted band along the coast, in this case within 70 km from shore. The absence of larval slender sole in neuston collections despite the high numbers caught in bongo tows indicates that they occur beneath the surface, agreeing with Boehlert et al.'s

(1985) observations. They reported that larval slender sole occurred only below 10 m depth during daytime in spring and summer collections off Yaquina Head, Oregon but in shallower layers at night (5-30 m). Furthermore, all stage IV larvae occurred within 42 km from shore, suggesting that they settle in coastal waters. I believe that *L. exilis* utilizes a mechanism of vertical migration similar to that of *I. isolepis* to avoid advective loss from the nursery grounds on the continental shelf along Washington, Oregon and northern California.

Although occasionally eggs of slender sole were caught at >250 km from the coast in mid-spring 1980 and late-spring 1982 (Figs. 36a,d), larvae were mostly within 140 km from shore (except in mid-spring 1983), suggesting that waters beyond that distance were not proper nursery grounds for this species. This borderline is surprisingly similar to the one observed by Percy (1976), who found zooplankton volumes within 120 km from the Oregon coast to be greater than those farther offshore. Percy (1976) suggested that the upwelling along the Oregon coast has an influence on the productivity up to 120 km from shore, and Huyer (1983) stated that in the California Current region, "effects of coastal upwelling can extend more than a hundred kilometers out to sea". A wide distribution from the coast may reduce the pressure of both intra- and interspecific competition in an intense spawner such as *L. exilis*.

Although Dover sole reportedly spawns on the continental slope at depths >400 m (Percy et al., 1977), eggs of this species occurred in coastal waters during mid-spring 1980, 1983 (Figs. 38a,e). These eggs, probably spawned during winter, might

have been advected eastward of the spawning sites by the onshore Ekman transport in the last months of the downwelling season. By late-spring (1981, 1982), persistent upwelling during the weeks preceding the surveys (Figs. 3-4) probably kept the eggs (spawned after the first of April) beyond the continental shelf (Figs. 31c,d). Larval Dover sole were mostly offshore but close to the outer edge of the continental break, coinciding with the offshore and offshore-transitional classifications assigned by Richardson and Percy (1977) and Laroche et al. (1982), respectively. Parrish et al. (1981) hypothesized that larval *M. pacificus* are advected onshore during downwelling season by winter storms and offshore during upwelling season. I could not test their hypothesis because of the low larval numbers caught and because on-offshore distribution of late stages may not necessarily reflect the intensity of Ekman transport in a given season of a particular year because of the extended pelagic life of Dover sole.

Aside of the coastal/offshore classification of ichthyoplankton, advection of early stages away from the spawning grounds is expected. Parrish et al. (1981) emphasized the importance of Ekman transport in the advective loss of ichthyoplankton from nursery grounds. They suggested that the occurrence of later stages (or larger larvae) farther offshore than earlier stages during or after the upwelling season would indicate Ekman transport. Because physical conditions (e.g., water density; direction of slope of isopycnals) change almost immediately with an upwelling event (Huyer, 1983), effects of offshore Ekman transport should be apparent within a short period of time. Although limitations due to sampling gear and patchiness, as well as the mechanisms of retention within coastal areas, usually

obscure these patterns, some observations in this study support Parrish *et al.*'s (1981) emphasis on Ekman transport. For example, during late-spring and mid-fall of 1981 and late-fall 1983 (during and after upwelling season), later stages of larval Pacific sanddab were farther offshore than both eggs and recently hatched larvae (Figs. 44a,c,d). Also, later stages (III, IV) of larval butter sole were far offshore (116 km from the coast) while recently hatched specimens (stage I) occurred within 9 km from shore (Fig. 44b) during late-spring 1982.

The onshore-offshore and vertical distributions of a species may also be related to salinity, temperature and density patterns caused by the Columbia Plume. The plume may represent an offshore limit to the effects of upwelling (Huyer, 1983). The plume is not only less saline than the upwelled waters, but in spring and summer it also can be warmer because of a rapid heating of this thin low-density layer (Huyer and Smith, 1978; Huyer, 1983). The effects of the Columbia Plume on early stages of fishes may vary with the species. For example, Richardson (1981) concluded that the plume provided a stable and productive environment within 100 km from the river's mouth that is favorable for survival of early stages of the northern anchovy, and that spawning areas of this species would be associated with these waters. Larvae of coastal species were only collected in bongo tows and not in neuston catches in areas influenced by the Columbia Plume (Figs. 35, 41, 43 vs. Figs. 6a-12a). A combination of factors may explain this distribution. Displacement of larvae by low density plume waters or vertical distribution of larval stages in response to Ekman transport, as well as alongshore currents, may have a role of variable importance in the horizontal distribution of these species.

Latitudinal trends

Some hydrographic conditions change with latitude. For example, as latitude increases, temperature normally decreases (Figs. 6-12) and the upwelling season is shorter and less intense (Figs. 2-5). Also, the Columbia Plume extends to the south beyond Cape Blanco ($42^{\circ}30'$ lat N) (Fig. 7a), and sometimes as far as Cape Mendocino (40°N) during the summer (Huyer, 1983). However, because the habitat changes more dramatically with distance from shore than along the coast (Parrish *et al.*, 1981 and Figs. 6-12) and the study area (40 - 48°N) covers the central region of the geographic range of the eight species analyzed in this work (see Miller and Lea, 1972), strong latitudinal trends are not expected.

Not surprisingly, eggs of most species usually occurred evenly across the four latitudinal regions during most of the surveys (Table 13a), suggesting spawning along most of the study area¹¹ (Figs. 29-43). Slender sole is a good example; eggs and larvae of this species were very common at all latitudes of the study area (Fig. 36, 37).

Coastal species showed an interesting latitudinal trend, however. Eggs of coastal species such as butter sole, English sole and sand sole were most abundant north of 43°N (Figs. 34, 40, 42), north of the region of maximum upwelling, where

¹¹Sometimes, however, lack of statistically significant differences were due rather to low catches than to even distribution. In those cases, a qualitative interpretation was given to the data.

offshore advection is most continuous and strongest between Cape Blanco and Point Conception (Parrish et al., 1981). Sand sole, however, seemed to have two general spawning regions during spring: a northern area on the continental shelf off Washington (46-48°N) and a southern spawning region in coastal waters off northern California (40-42°N) (Fig. 42). Because larval sand sole were common between these two sites (Fig. 43), the existence of separate stocks was unlikely. Finally, unusually high abundances of metamorphosing larval butter sole¹² (stages III and IV; 16.8-22.2 mm SL; mean = 19.7 ± 1.5 mm SL) occurred at three nearshore neuston stations of mid-spring 1980 (Table 6b) at 47°20' lat N (off the mouth of the Quinault River, Washington) and between 41°40' and 42°0' lat N (northern California), closer to shore but far from any major river (Fig. 35a). Interpretation of this observation in terms of ontogenetic vertical distribution was discussed above.

Although Parrish et al. (1981) suggested alongshore advection of larval stages for species with a long pelagic life (e.g., Dover and rex soles), this trend was most evident in other species with shorter pelagic lives. For example, in 1980 recently hatched slender sole were most abundant north of 43°N during mid-spring (Fig. 37a), i.e., towards the end of the downwelling season (Fig. 5) but by late summer, after several weeks of a southward mean alongshore flow (Huyer et al., 1979; Strub et al., 1987) later stages of larval slender sole occurred only south of 44°N (Fig. 37b). Because the northern stations were usually occupied before the southern stations

¹² These 18 *I. isolepis* specimens were reclassified as *P. vetulus* by NWAFC staff at Seattle, but because I did not find evidence (based on dorsal ray counts) for that re-identification, those 18 larvae are considered butter sole in the present work.

(except during late-fall 1983), within-cruise observations of alongshore advection are not expected to be conclusive. Later larval stages occurring farther south than earlier stages during and after the upwelling season were sometimes observed¹³ (e.g., Pacific sanddab and rex sole during late-spring 1981 (Fig. 44a); Pacific and speckled sanddabs during mid-fall 1981 (Fig. 44c); slender sole during late-spring 1982 (Fig. 44b).

High concentrations of larval stages of several flatfishes were often found on the continental shelf off northern Oregon (Region V). Although sanddab eggs and larvae were widely distributed along the coast, recently hatched Pacific and speckled sanddab were concentrated off the northern Oregon coast during mid-fall 1981 (Figs. 30d and 31c). Eggs and larvae of slender sole and English sole were also usually most abundant in this area despite their wide latitudinal range (Figs. 36, 37; 40a,c, 41a). This can be due to several factors. First, this particular zone might have the right combination of a broad continental shelf (Fig. 1) (i.e., a more extended coastal habitat and consequently a broader nutrient-rich neritic zone), and an intermediate (in terms of intensity and duration) upwelling activity relative to the other regions (Figs. 2-5). Second, the presence of several estuarine areas (e.g., Yaquina Bay, etc.) which are important for some of these species as nursery grounds (Pearcy and Myers, 1974).

¹³ Again, assuming that spawning occurs at different latitudes at the same time, the occurrence of later stages downstream and earlier stages upstream of the direction of the mean flow gives evidence of advection (Parrish *et al.*, 1981).

The 1982-1983 El Niño

The 1982-1983 El Niño Norte, or El Niño North, resulted in anomalous hydrographic conditions caused off the west coast of the United States (Schoener, 1985; Wooster and Fluharty, 1985). This 1983 El Niño was different from previous El Niño's because of the long duration of the event, its timing and the intensity and extension of its signals (Percy and Schoener, 1987). Four main signals of this event were: (a) anomalously high sea levels; (b) high coastal sea surface temperature; (c) increased poleward flow; and (d) reduced upwelling (Huyer and Smith, 1985; abstr.). Detailed descriptions of the changes in oceanographic conditions in the northeastern Pacific are given elsewhere (Huyer and Smith, 1985; Wooster and Fluharty, 1985; Schoener, 1985; Brodeur *et al.*, 1985; Percy *et al.*, 1985; Enfield, 1987; Percy and Schoener, 1987).

Dramatic changes in biota from California to British Columbia during 1983 have been related to the effects of the 1982-1983 El Niño Norte. These changes included: (a) reduced primary productivity; (b) 70% reduction in zooplankton abundances relative to those in non-El Niño years; (c) changes in relative abundances of larval fishes; (d) northern range extensions of zooplankton and nekton organisms; (e) increased occurrence of offshore species in inshore waters; (f) changes in landings of commercial species; (g) diet shifts in nekton organisms; (h) reduced condition factors; (i) poor growth and survival of important taxa, *et cetera*. (Schoener, 1985; Percy *et al.*, 1985; Miller *et al.*, 1985; Brodeur *et al.*, 1985; Percy and Schoener, 1987; see Alvial, 1987).

Changes were observed in the distribution and abundances of larval fishes off Oregon during the 1982-1983 El Niño (Brodeur *et al.*, 1985; Alvial, 1987; see Table 2 in Pearcy and Schoener, 1987. p. 14420). In my study, however, most of the ichthyoplankton collected during the mid-spring 1983 survey showed no major differences in numbers and species composition compared to mid-spring 1980, except for decreased abundances of larval smelt (*Osmeridae*) and increased catches of larval anchovies (*Engraulis mordax*) (Clark and Kendall, 1985; Kendall and Clark, 1982a. See also Schoener, 1985). Other changes in distributions and abundances were observed for some species.

Sand sole egg and larvae showed no differences within the study area in abundances or geographic distribution during mid-spring between 1980 and 1983 (Tables 2a,b; 6a,b and Figs. 42a,f; 43a,f). The prolonged spawning season from late summer through late spring (discussed above) suggests that this species must have a high tolerance to different physical conditions, and the weak upwelling in 1983 was rather favorable for larval retention in coastal waters.

The tenfold increase in egg and larval numbers of sanddabs (Tables 2a,b; 6a,b) and the greater concentration of eggs farther south (Fig. 29a,f) during mid-spring 1983 relative to 1980 were related to both the increased temperatures during the 1982-1983 El Niño Norte (Fig. 11) and advection from regions south of the study area by the strengthened poleward flow described by Huyer and Smith (1985). Because *Citharichthys* spp. spawns mainly during fall, when temperatures are higher due to

downwelling (or lack of upwelling), the warmer waters that prevailed in 1983 might have stimulated spawning activity in this species. Also, the presence of larval Pacific and speckled sanddab on the continental shelf off Oregon during mid-spring 1983 (Figs. 30e, 31e) is consistent with a reduced Ekman transport (Huyer and Smith, 1985). Because most of the anomalous physical conditions associated with the 1982-1983 El Niño Norte returned to "average" values by September of 1983, the considerably lower catches of eggs and recently hatched sanddabs during late-fall 1983 might reflect unfavorable conditions for the ripening of the spawner stock during summer.

Although total abundances of rex sole eggs during mid-spring were not different between 1980 and 1983 (Tables 2a,b), greater concentrations of eggs occurred in offshore waters off the Washington coast (Fig. 32e). This suggested northward advection. The fivefold-increase in larval abundances, which were evenly distributed throughout the study area both latitudinally and longitudinally (Fig. 33f), is consistent with the reported higher numbers of larval rex sole within 18 km off Newport, Oregon from April through September 1983 (Brodeur *et al.*, 1985). It does not suggest onshore advection of larvae, however, because it is precisely during mid-spring 1983 that larval rex sole occurred farthest offshore (Fig. 33f), but it may indicate advection of larvae into the study area. The higher larval catches are accounted for by the high numbers of relatively recently hatched larvae (<10 mm SL), as well as the presence of larger specimens (26-48 mm SL) (Fig. 23) suggesting prolonged pelagic life. Large numbers of stage I larvae suggest either delayed hatching or delayed body growth rate. Because the first signals of the 1982-1983 El

Niño Norte were detected in October 1982, occurrence of giant rex sole larvae (not observed in mid-spring 1980) indicated unfavorable conditions for settling during this period. It is noteworthy that while during mid-spring 1980 most rex sole eggs were caught in neuston tows, in 1983 they occurred mostly in bongo catches (Tables 2a,b). Either spawning vertical patterns changed or eggs were not as buoyant in the less dense water due to higher temperatures in 1983 (Fig. 11) as they were in 1980.

Egg and larval distributions of Dover sole responded very similarly to those of rex sole. Both eggs and larvae were more concentrated off Washington in mid-spring 1983 than in 1980 (Figs. 38e, 39e). Although no giant Dover sole larvae were collected, stage II and III specimens (which did not occur in catches of mid-spring 1980) were common in 1983, suggesting earlier hatching within the study area or advection of individuals from southern regions that were spawned earlier in the year.

The abundances of butter sole eggs during the 1983 El Niño Norte was drastically reduced (Tables 2a,b) while larval numbers remain unchanged (Table 6a). This suggested advection of larvae into the study area. Weakened upwelling and advection of larvae from southern regions may explain the high larval numbers off northern California and southern Oregon (i.e., near the region of maximum upwelling) during mid-spring 1983 (Fig. 35d). This is radically different from the distribution of larval butter sole during mid-spring 1980, when large numbers were captured off Washington (Fig. 35a). The reduced larval numbers of butter sole in coastal waters off Newport, Oregon in spring-summer 1983 reported by Brodeur *et*

al. (1985) is consistent with the lower egg abundances in the region and the change of geographic distribution of the larvae.

Slender sole showed an interesting response during the 1983 El Niño Norte. While egg and larval total abundances during mid-spring were not significantly different between 1980 and 1983, geographic patterns changed. First, slender sole egg abundances, which were highest off the northern California (regions I, II) and Oregon coasts (regions III-VI) during mid-spring 1980 (Fig. 36a), were lowest south of 44°N in 1983 (Fig. 36e), suggesting northward advection by the increased poleward flow during this period (Huyer and Smith, 1985). Larval slender sole, otherwise a coastal-transitional species (Figs. 37a-d), occurred far offshore during mid-spring 1983 (Fig. 37e). Ekman transport is unlikely, because of the weakened upwelling that characterized that period (Huyer and Smith, 1985). Northward advection coupled with lower temperatures offshore than onshore might explain this unusual pattern. Also, a greater proportion of stage III larvae in 1983 than in 1980 (Fig. 25) suggested either spawning earlier in the year or a faster growth and development rate during El Niño Norte, which would be expected because of the higher water temperatures.

Finally, changes of the fall-spawning English sole in 1983 were more subtle than for the other species. Mundy (1984) and Laroche and Richardson (1979) observed extreme interannual variation in the spawning season during non-El Niño years; therefore the differences in abundances and distribution of early stages of English sole between 1983 and previous years might not necessarily be related to the anomalous conditions during the 1982-1983 El Niño Norte. Larval *P. vetulus*

had similar numbers in mid-spring 1980 and 1983 (Table 6a,b), although the offshore occurrence off Washington in 1983 (Fig. 41d) may indicate northward advection of larvae that otherwise would occur off central Oregon (Fig. 41a). The dramatic reduction of egg numbers in late-fall 1983 compared to mid-fall 1981 ($p < 0.05$) suggested either low fecundity, emigration of spawners out of the study area, or delayed spawning.

SUMMARY AND CONCLUSIONS

The flatfish fauna off northern California, Oregon and Washington displays very diverse spawning seasons and regional geographic distributions. The eight species considered in this study included protracted spawners with main peaks in fall (e.g., *Parophrys vetulus*, *Citharichthys sordidus* and *C. stigmaeus*) or in spring (e.g., *Psettichthys melanostictus*), spring spawners (e.g., *Isopsetta isolepis*, *Glyptocephalus zachirus* and *Lyopsetta exilis*), and a winter spawner (*Microstomus pacificus*).

Onshore-offshore trends were more evident than latitudinal patterns, probably because in the California Current System, habitat changes more dramatically with distance from shore than alongshore. Coastal types (more abundant on the continental shelf) included *I. isolepis*, *P. vetulus* and *P. melanostictus*. Several mechanisms of larval retention in nearshore areas were suggested by the data available: spawning during downwelling season to prevent offshore Ekman transport; spawning as close to shore as possible because Ekman transport is minimal within 10 km from shore; a vertical distribution that avoids top offshore Ekman layer or vertical migration between layers to use flow in different directions to enhance retention within a given area; avoidance of zones of intense upwelling (e.g., the waters near the region of maximum upwelling in northern California). *G. zachirus* and *L. exilis* were classified as coastal-transitional (i.e., between the shore and the outer side of the continental shelf break) types that were differentially affected by offshore Ekman transport, while *M. pacificus* was considered an offshore-transitional species (offshore of the inner side of the continental shelf break). The effects of upwelling intensity (with the

consequent offshore Ekman transport) and the seasonal development of the Columbia Plume on the on/offshore and vertical distribution of early stages of these eight pleuronectiforms were emphasized. The classification of larval fishes off Washington, Oregon and northern California into coastal and offshore types depends heavily upon the direction of the Ekman transport, which varies both seasonally and interannually.

The continental shelf off the northern Oregon coast appears to be an important spawning and nursery ground for several flatfishes, such as both *Citharichthys* spp., *L. exilis* and *P. vetulus*. This may be due to a combination of three major factors: (a) a broad continental shelf, (b) intermediate upwelling intensity, which yields high productivity and not excessive offshore advection, and (c) the presence of important nursery grounds for juveniles of some of these species.

Anomalous egg and larval distributions in most of the taxa analyzed in this study coincided with the occurrence of the 1982-1983 El Niño Norte, compared to mid-spring 1980. Although no major changes in egg and larval distributions of *P. melanostictus* were observed, abundances and/or geographic distributions of the other species differed from those in previous years. Most of these changes were consistent with advection from regions south of the study area by increased poleward flow, weakened upwelling intensity and higher temperatures.

The cooperative U.S.-U.S.S.R. project from which the data of this work have been extracted is the first ichthyoplankton large-scale survey north of California (Kendall and Clark, 1982a), covering all seasons from 1980 to 1985 (Dunn, 1986).

Valuable information obtained with this research will give more insights about the spawning grounds and seasons of many fishes of this region, as well as the relation between variation in both abundance and distribution of early stages and variation in some physical conditions. A data base of this kind is important for the development of adequate resource management plans. Also, when results of this project will be compared to those of CalCOFI (off California and Baja California), a better understanding of the global ichthyoplankton patterns of West Coast of the United States, a major portion of the Northeast Pacific, will be achieved.

REFERENCES

1. Ahlstrom, E.H., K. Amaoka, D.A. Hensley, H.G. Moser and B.Y. Sumida. 1984. Pleuronectiformes: Development. In: American Society of Ichthyologists and Herpetologists (eds.). Ontogeny and systematics of fishes Symposium, Aug. 15-18, 1983, LaJolla, California. Allen Press, Inc. pp. 640-670.
2. Alvial, A.L. 1987. ENSO impacts on pelagic ecosystems in the Eastern Pacific, with emphasis on fishery resources. M.S. Special Project. Marine Resource Management Program, College of Oceanography, Oregon State University, Corvallis, Oregon. 84 pp.
3. Amaoka, K. 1981. Phylogeny and larval morphology of pleuronectiform fishes (Psettodidae, Citharidae, Paralichthyidae and Bothidae). Translated from Japanese by A. Shiga. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC Processed report 81-12. Seattle. 21 pp.
4. Barber, R.T. and R.L. Smith. 1981. Coastal upwelling ecosystems. In: Longhurst, A.R. (ed.). Analysis of marine ecosystems. Academic Press. pp. 31-68.
5. Bates, R.D. 1984. Ichthyoplankton off Washington, Oregon and Northern California; October-November 1981. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 84-12. Seattle. 41 pp.
6. Boehlert, G.W.; D.M. Gadomski and B.C. Mundy. 1980. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83(4): 611-621.
7. 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 and Shelf Science 21: 365-378.
8. Byrne, J.V. 1962. Geomorphology of the continental terrace off the central coast of Oregon. The Ore Bin 24(5): 65-74.
9. _____. 1963a. Geomorphology of the Oregon continental terrace south of Coos Bay. The Ore Bin 25(9): 149-157.
10. _____. 1963b. Geomorphology of the continental terrace off the northern coast of Oregon. The Ore Bin 25(12): 201-209.

11. Chiu, Tai-sheng. 1987. Phylogeny and zoogeography of glyptocephalines (Pisces: Pleuronectidae). Ph.D. Thesis. School of Fisheries and Wildlife, Oregon State Univ., Corvallis, OR. 277 pp.
12. Clark, J.B. 1984. Ichthyoplankton off Washington, Oregon and Northern California; May-June 1981. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 84-11. Seattle. 45 pp.
13. _____. 1986a. Ichthyoplankton off Washington, Oregon and Northern California; May-June 1982. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 87-01. Seattle. 44 pp.
14. _____. 1986b. Ichthyoplankton off Washington, Oregon and Northern California; November-December 1983. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 86-14. Seattle. 43 pp.
15. _____ and A. Kendall. 1985. Ichthyoplankton off Washington, Oregon and Northern California; April-May 1983. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 85-10. Seattle. 48 pp.
16. Devore, J.L. and R.L. Peck. 1986. Statistics; the exploration and analysis of data. West Publishing Co. 699 pp.
17. Dunn, J.R. 1986. A catalog of Northwest and Alaska Fisheries Center Ichthyoplankton cruises 1965-1985. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 86-08. Seattle. 78 pp.
18. Enfield, D.B. 1987. Progress in understanding El Niño. College of Oceanography, Oregon State University, Corvallis, Oregon. Manuscript. 14 pp.
19. Gabriel, W.L. and W.G. Pearcy. 1981. Feeding selectivity of Dover sole, *Microstomus pacificus*, off Oregon. Fish. Bull. 79(4): 749-763.
20. Gadomski, D.M. and G.W. Boehlert. 1984. Feeding ecology of pelagic larvae of English sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* off the Oregon coast. Mar. Ecol. Prog. Ser. 20: 1-12.
21. Hagerman, F.B. 1952. The biology of the Dover sole. State of California, Department of Fish and Game Bureau of Marine Fisheries. Fish bulletin No. 85. 49 pp.

22. Hewitt, G.R. 1980. Seasonal changes in English sole distribution: an analysis of the inshore trawl fishery off Oregon. M.S. Thesis. College of Oceanography, Oregon State University, Corvallis, Oregon. 59 pp.23.
- Hickey, B.M. 1979. The California Current System-hypotheses and facts. In: Angel, M.V. and J. O'Brien (eds.) Progress in Oceanography 8(4): 191-279.
24. Hickman, C.P. Jr. 1959. The larval development of the Sand sole (*Psettichthys melanostictus*). Fisheries Research Papers, Washington Department of Fisheries 2(2): 38-47.
25. Hoar, W.S.; V.S. Black and E.C. Black. 1951. Hormones in fish. Pub. Ontario Fish. Res. Lab. 71. Univ. Toronto Biol. Ser. 59: 1-111.
26. Hogue, E.W. and A.G. Carey, Jr. 1982. Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast. Fish. Bull. 80(3): 555-567.
27. Hosie, M.J. 1975. Biology of the rex sole, *Glyptocephalus zachirus* Lockington, in waters off Oregon. M.S. Thesis. Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon. 43 pp.
28. _____. 1977. Biology of the rex sole, *Glyptocephalus zachirus*, in waters off Oregon. Fish. Bull. 75(1): 51-60.
29. Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. In: Lasker, R. (ed.) Marine fish larval morphology, ecology and relation to fisheries. Wash. Sea Grant, Univ. Wash. Press. pp. 33-77.
30. Huyer, A. 1983. Coastal upwelling in the California Current System. Prog. Oceanogr. 12: 259-284.
31. _____ and R.L. Smith. 1978. Physical characteristics of Pacific northwestern coastal waters. In: Krauss, R. (ed.) The marine plant biomass of the Pacific Northwest Coast. Oregon State University Press. pp. 37-55.
32. _____. 1985. The signature of El Niño off Oregon, 1982-1983. Journal of Geophysical Research 90(C4): 7133-7142.
33. Huyer, A.; E.J.C. Sobey and R.L. Smith. 1979. The spring transition in currents over the Oregon continental shelf. J. Geophys. Res. 84(11): 6995-7011.
34. Inui, Y. and S. Miwa. 1985. Thyroid hormone induces metamorphosis of flounder larvae. Gen. Comp. Endocrinol. 60(3): 450-454.

35. Kendall, A.W. and J.B. Clark. 1982a. Ichthyoplankton off Washington, Oregon and Northern California; April-May 1980. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 82-11. Seattle. 44 pp.
36. _____. 1982b. Ichthyoplankton off Washington, Oregon and Northern California; August 1980. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 82-12. Seattle. 43 pp.
37. Kravitz, M.J.; W.G. Pearcy and M.P. Guin. 1977. Food of five species of cooccurring flatfishes on Oregon's continental shelf. Fish. Bull. 74(4): 984-990.
38. Kruse, G.H. and A.V. Tyler. 1983. Simulation of temperature and upwelling effects on the English sole, (*Parophrys vetulus*) spawning season. Can J Fish Aquat Sci 40: 230-237.
39. Krygier, E.E. and W.G. Pearcy. 1985. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. Fish. Bull. 84(1): 119-1323.
40. Landry, M.R. and C.J. Lorenzen. 1989. Abundance, distribution, and grazing impact of zooplankton on the Washington shelf. In: Landry, M.R. and B.M. Hickey (Eds.) Coastal Oceanography of Washington and Oregon. Elsevier Science Publishers B.V. Netherlands. Chapter 5, pp. 175-210.
41. _____. J.R. Postel; W.K. Peterson and J. Newman. 1989. Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. In: Landry, M.R. and B.M. Hickey (eds.) Coastal Oceanography of Washington and Oregon. Elsevier Oceanographic Series 47: 1-40.
42. Laroche, J.L. and S.L. Richardson. 1979. Winter-spring abundance of larval English sole, *P. vetulus*, between the Columbia River and Cape Blanco, Oregon during 1972-1975 with notes on occurrences of three other pleuronectids. Estuar. Coast. Mar. Sci. 8: 455-476.
43. _____. S.L. Richardson and A.A. Rosenberg. 1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull. 80(1): 93-104.
44. Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp.p.-v. Reun. Cons. Int. Explor. Mer. 178: 375-388.

45. _____. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In: Lasker, R. (ed.) Marine fish larval morphology, ecology and relation to fisheries. Wash. Sea Grant, Univ. Wash. Press. pp. 80-87.
46. _____ and P.E. Smith. 1977. Estimation of the effects of environmental variations on the eggs and larvae of the Northern Anchovy. Calif. Coop. Ocean. Fish. Invest. Report 19:128-137.
47. Leonard, S.B. 1971. Larvae of the Fourspot flounder, *Hippoglossina oblonga* (Pisces: Bothidae) from the Chesapeake Bight, Western North Atlantic. Copeia 4: 676-681.
48. Markle, D.F. 1989. Evidence for a greatly prolonged, pelagic, early life history stage in Dover sole (*Microstomus pacificus*). Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon. Unpubl. manuscript. 25 p.
49. Mason, J.E. and A. Bakun. 1986. Upwelling Index Update, U.S. West Coast, 33N-48N Latitude. U.S. Dept. of Commerce. Southwest Fisheries Center. NOAA Technical Memorandum NMFS. NOAA-TM-NMFS-SWFC-67. 81 pp.
50. Matarese, A.C.; A.W. Kendall, Jr.; D.M. Blood and B.M. Vinter. 1986 (In press). Laboratory guide to early life history stages of Northeast Pacific fishes. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center.
51. Miller, C.B.; H.D. Batchelder; R.D. Brodeur and W.G. Pearcy. 1985. Response of the zooplankton and ichthyoplankton off Oregon to the El Niño event of 1983. In: Wooster, W.S. and D.L. Fluharty (eds.). El Niño North. University of Washington, Washington Sea Grant Program. pp. 185-187.
52. Miller, D.J. and R.N. Lea. 1972. Guide to the coastal marine fishes of California. California Fish Bulletin No. 157. University of California. 249 pp.
53. Mundy, B.C. 1984. Yearly variation in the abundance and distribution of fish larvae in the coastal zone off Yaquina Head, Oregon, from June 1969 to August 1972. M.S. Thesis. College of Oceanography, Oregon State University, Corvallis, OR. 158 pp.
54. Nelson, J.S. 1984. Fishes of the world. 2nd ed. A Wiley-Interscience publication. John Wiley & Sons, Inc. pp. 373-379.

55. Parrish, R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography* 1(2): 175-203.
56. Parsons, T.R. and M. Takahashi. 1973. *Biological oceanographic processes*. Pergamon Press. 186 pp.
57. Percy, W.G. 1976. Seasonal and inshore-offshore variations in the standing stocks of micronekton and macrozooplankton off Oregon. *Fish. Bull.* 74(1): 70-80.
58. _____. 1978. Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. *Fish. Bull.* 76(3): 629-640.
59. _____ and D. Hancock. 1978. Feeding habits of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; and Pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. *Fish. Bull.* 76(3): 641-651.
60. _____ and S.S. Myers. 1974. Larval fishes of Yaquina Bay, Oregon: a nursery ground for marine fishes? *Fish. Bull.* 72(1): 201-213.
61. _____ and A. Schoener. 1987. Changes in the marine biota coincident with the 1982-1983 El Niño in the Northeastern Subarctic Pacific ocean. *J. Geophys. Res.* 92(C13): 14417-14428.
62. _____; M.J. Hosie and S.L. Richardson. 1977. Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus*, Rex sole, *Glyptocephalus zachirus* and Petrale sole, *Eopsetta jordani*, in waters off Oregon. *Fish. Bull.* 75(1): 173-183.
63. _____; J. Fisher; R. Brodeur and S. Johnson. 1985. Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. In: Wooster, W.S. and D.L. Fluharty (eds.). *El Niño North*. Appendix B. University of Washington, Washington Sea Grant Program. pp. 188-205.
64. W.T. Peterson and C.B. Miller. 1975. Year-to-year variations in the planktology of the Oregon upwelling zone. *Fish. Bull.* 73(3): 642-653.
65. _____. 1976. Zooplankton along the continental shelf off Newport, Oregon, 1969-1972: distribution, abundance, seasonal cycle and year-to-year variations. Oregon State University Sea Grant College Program. Publication No. ORESU-T-78-002. School of Oceanography, Oregon State University. 57 pp.

66. _____. 1977. Seasonal cycle of zooplankton abundance and species composition along the Central Oregon Coast. Fish. Bull. 75(4): 717-724.
67. _____.; C.B. Miller and A. Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26A: 467-494
68. Richardson, S.L. 1981. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull. 78(4): 855-876.
69. _____ and E.B. Joseph. 1973. Larvae and young of the Western North Atlantic bothid flatfishes, *Etropus microstomus* and *Citharichthys arctifrons* in the Chesapeake Bight. Fish. Bull. 71(3): 735-767.
70. _____ and W.G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull. 75(1): 125-145.
71. _____; J.R. Dunn and N.A. Naplin. 1980. Eggs and larvae of Butter Sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington. Fish. Bull. 78(2): 401-417.
72. _____; J.L. Laroche and M.D. Richardson. 1980. Larval fish assemblages and associations in the North-east Pacific Ocean along the Oregon coast, Winter-spring 1972-1975. Est. Coast. Mar. Sci. 11: 671-699.
73. Russell, F.S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press 524 pp.
74. Sameoto, D.D. and L.O. Jaroszynski. 1969. Otter surface sampler: a new neuston net. J. Fish. Res. Board Can. 25: 2240-2244.
75. Savage, D.S. 1989. Salinity and temperature data comparisons for 1980-1987 cruises off the coasts of Washington, Oregon and California. U.S. Dept. of Commerce. Northwest and Alaska Fisheries Center. NWAFC processed report 89-16. Seattle. 169 pp.
76. Schoener, A. 1985. El Niño Norte. The Northwest Environmental Journal 1(2): 19-33.
77. Shelbourne, J.E., J.D. Riley and G.T. Thacker. 1963. Marine Fish Culture in Great Britain I. Place rearing in closed circulation at Lowestoft, 1957-1960. J. Cons. Int. Expl. Mer 28: 50-70.

78. Smith, B. 1987. CLUSB Version 3; recoding for microcomputer and manual revision. Non-paged manuscript. Oregon State University, College of Forest Science.
79. Smith, D.G. and M.P. Fahay. 1970. Description of eggs and larvae of Summer flounder, *Paralichthys dentatus*. U.S. Department of Interior, Fish and Wildlife Service. Bureau of Sport Fisheries and Wildlife. 75:1-21.
80. Smith, P.E. 1981. Fisheries on coastal pelagic schooling fish. In: Lasker, R. (ed.) Marine fish larval morphology, ecology and relation to fisheries. Wash. Sea Grant, Univ. Wash. Press. pp. 1-28.
81. _____ and S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. Food and Agriculture Organization of the United Nations. FAO Fisheries Technical Paper No. 175. 100 pp.
82. Smith, R.L. 1981. A comparison of the structure and variability of the flow field in three coastal upwelling regions: Oregon, Northwest Africa and Peru. In: Richards, F.A. (ed.). Coastal Upwelling. Amer. Geophys. Union. pp. 107-118.
83. Small, L.F.; H. Curl, Jr. and W.A. Glooschenko. 1972. Effects of solar radiation and upwelling on daily primary production off Oregon. J. Fish. Res. Bd. Can. 29: 1269-1275.
84. Snedecor, G.W. and W.G. Cochran. 1974. Statistical methods. 6th ed., 7th printing. The Iowa State University Press. pp. 325-330.
85. Strub, P.T.; J.S. Allen; A. Huyer; R.L. Smith; R.C. Beardsley. 1987. Seasonal cycles of currents, temperatures, winds and sea level over the Northeast Pacific continental shelf: 35°N to 48°N. J. Geophys. Res. 92(C2): 1507-1526.
86. Tate, M.W. and R.C. Clelland. 1959. Non-parametric and shortcut statistics. Interstate Printers and Publishers, Inc. 171 pp.
87. UNESCO. 1981. Tenth report of the Joint Panel on Oceanographic Tables and Standards. UNESCO Technical Papers in Marine Science 36: p.24.
88. Weinberg, K.L.; M.E. Wilkins and T.A. Dark. 1984. The 1983 Pacific West Coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, age and length composition. U.S. Dept. of Commerce. NOAA Technical Memorandum NMFS-F/NWC-70. 106 pp.
89. Zar, J.H. 1984. Biostatistical Analysis. 2nd ed. Chapter 12: Multiple Comparisons. Prentice-Hall, Inc. New Jersey. pp. 185-205.

APPENDICES

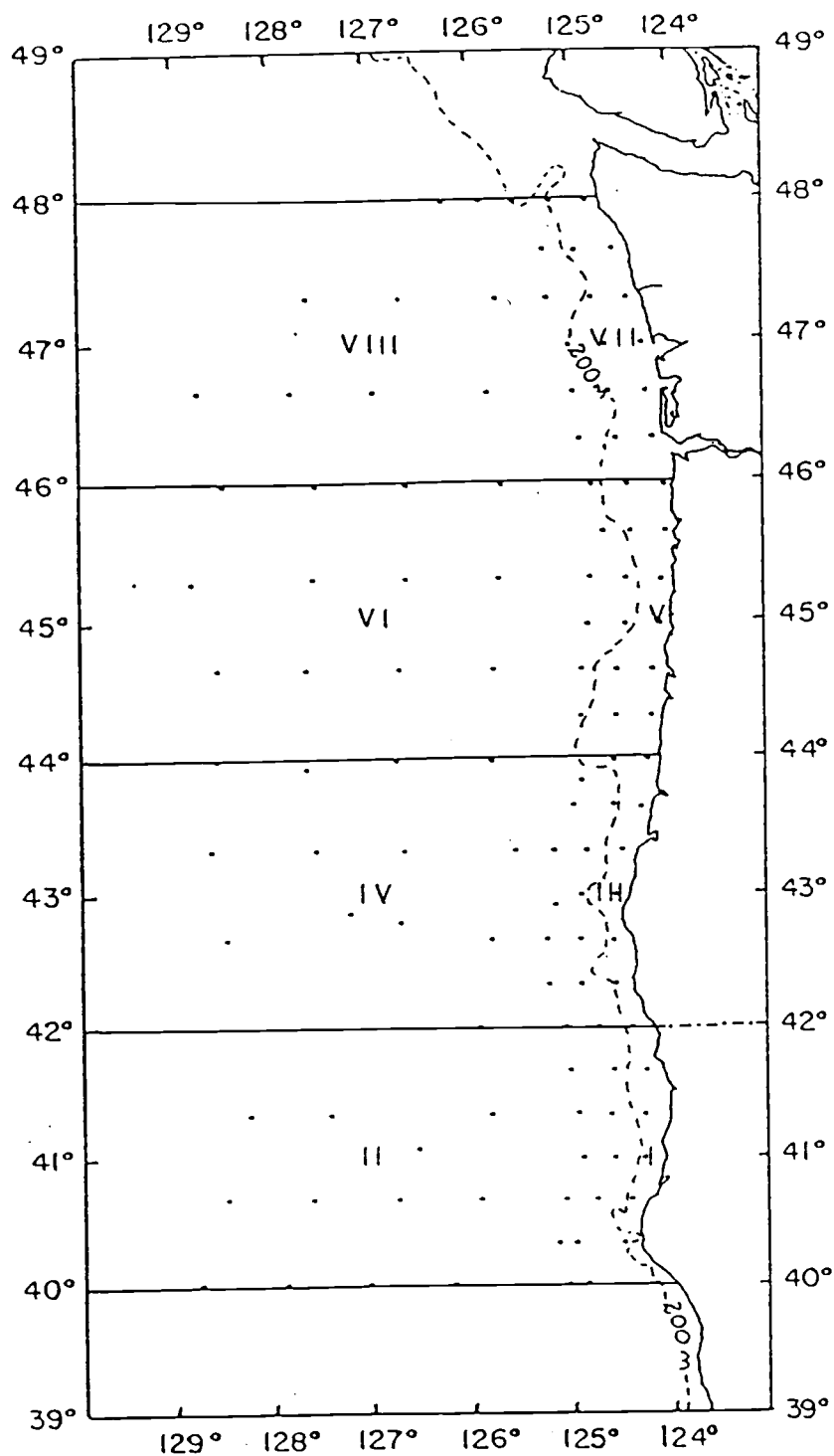


Fig. 1. General sampling locations of bongo and neuston stations off Washington, Oregon and northern California for seven cruises during the 1980-1983 period. The eight geographical regions considered in this study are also shown.

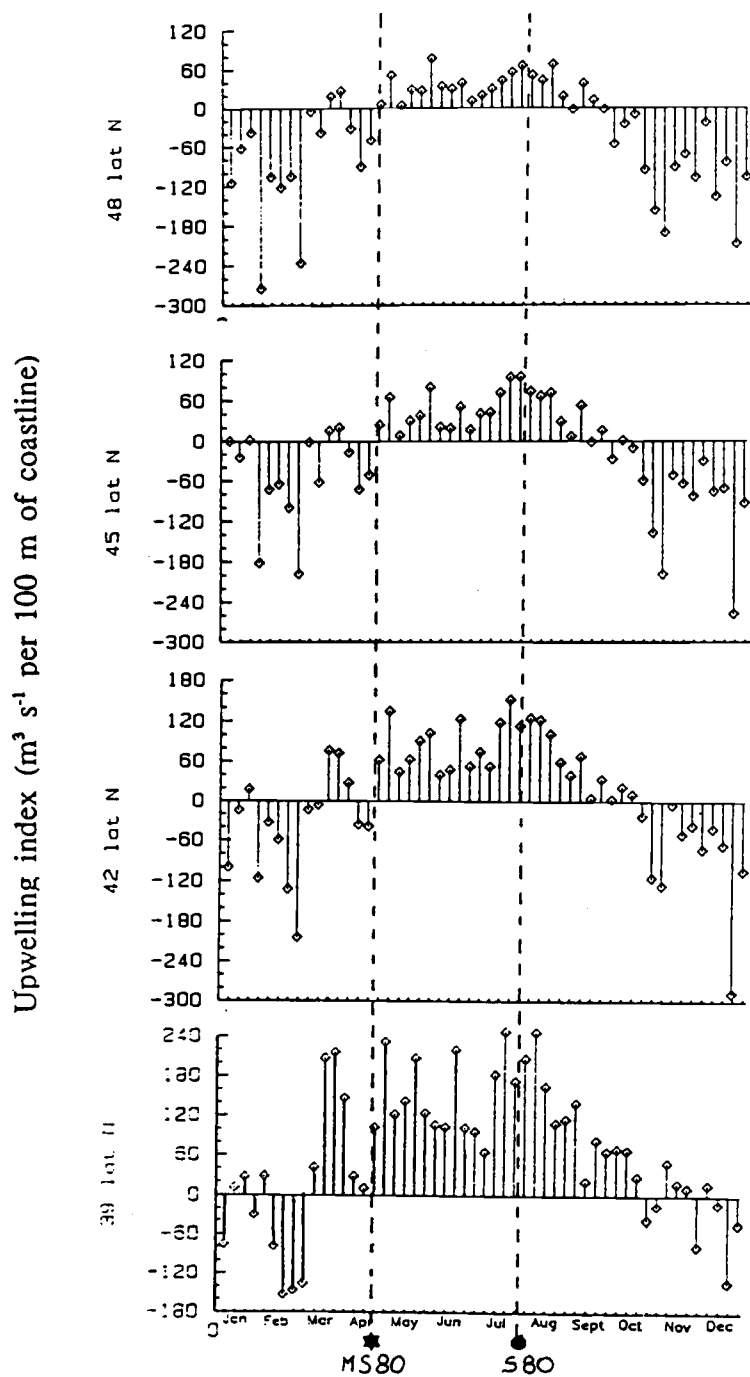
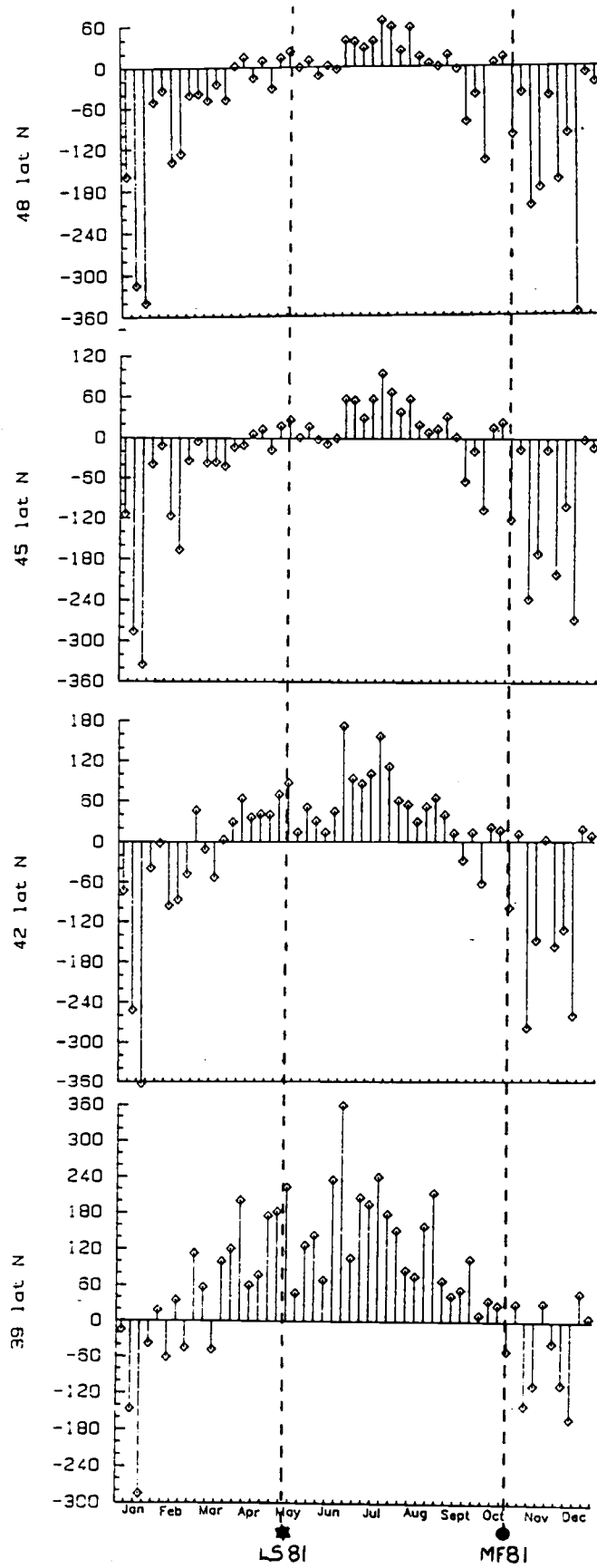


Fig. 2. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1980.

Fig. 3. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1981.

Upwelling index ($\text{m}^3 \text{s}^{-1}$ per 100 m of coastline)

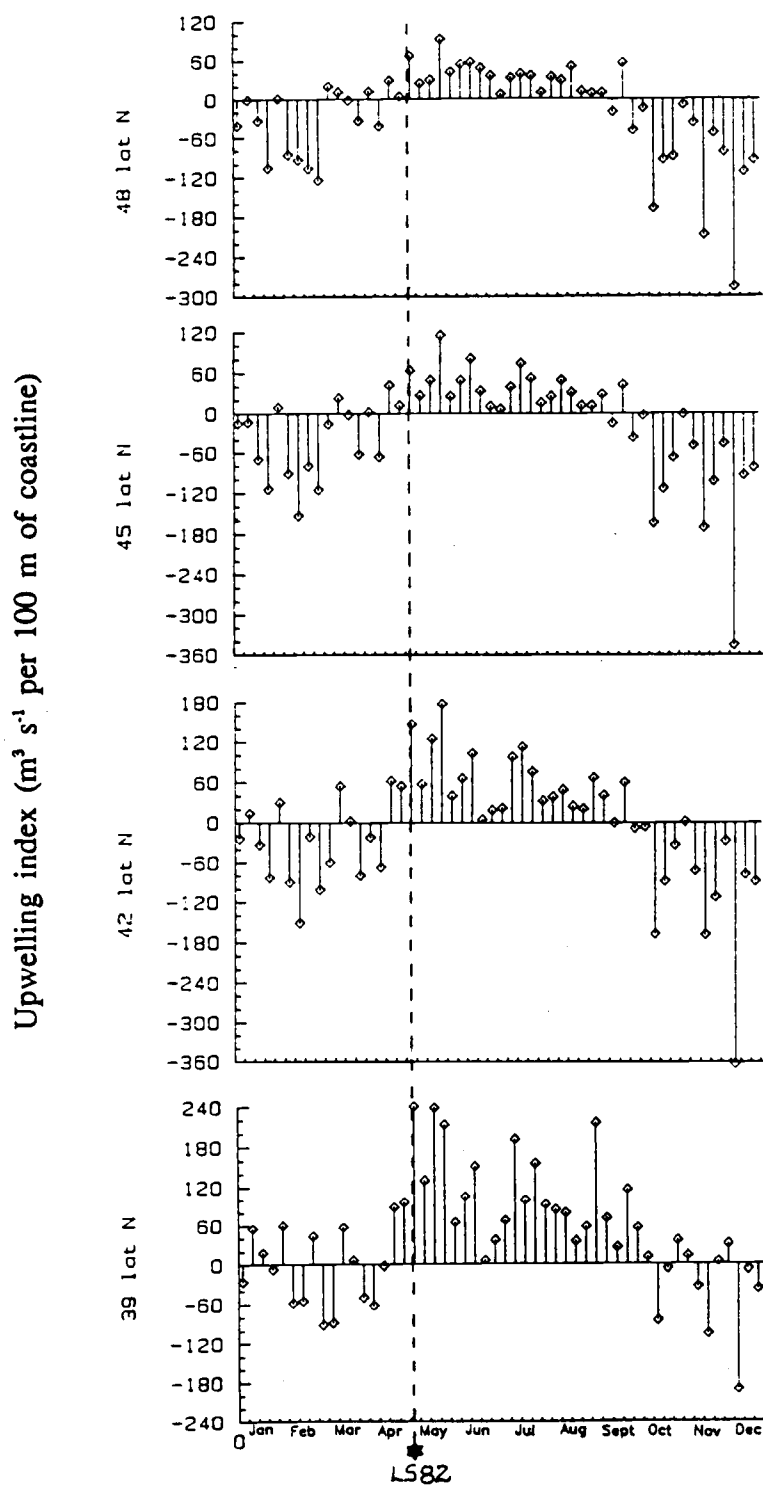


Fig. 4. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1982.

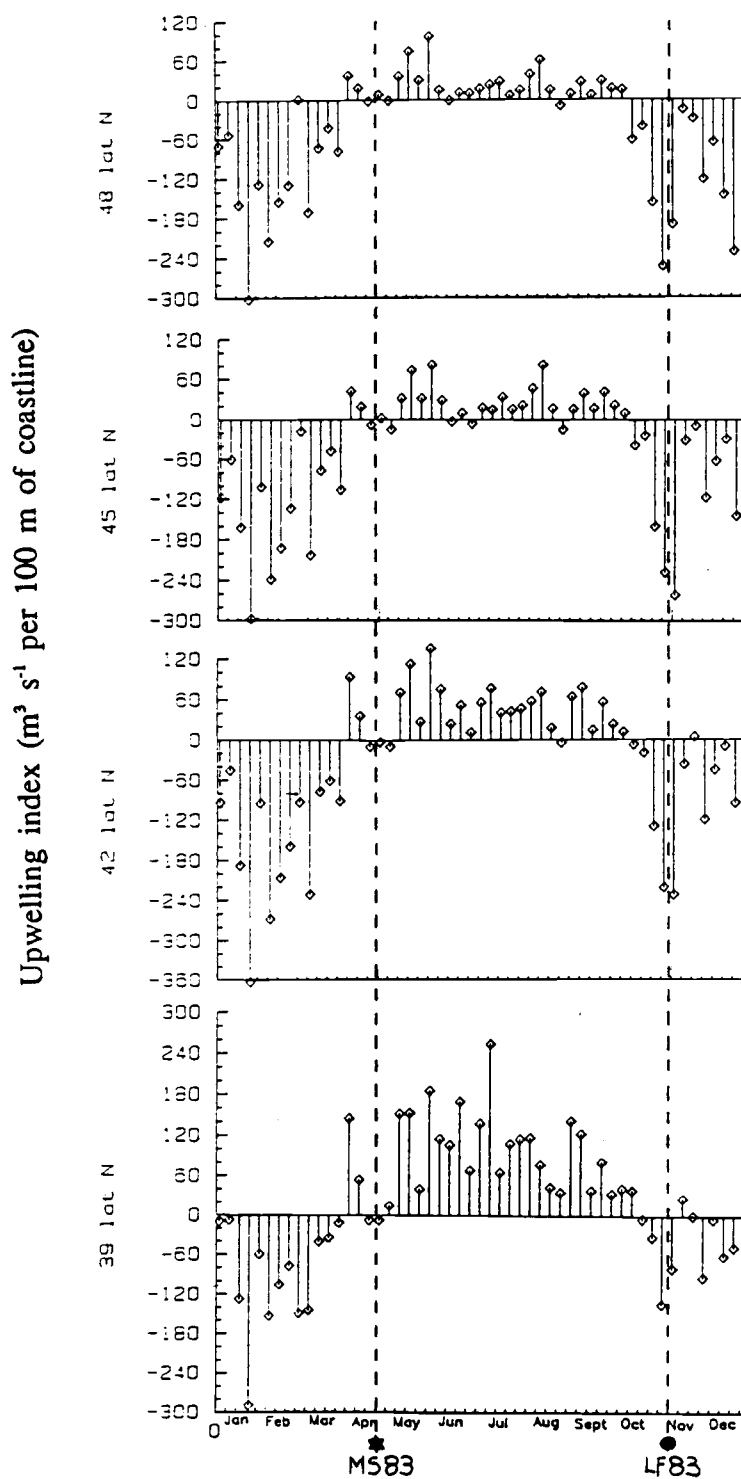


Fig. 5. Weekly Upwelling Index at 125W longitude and four different latitudes off northern California, Oregon and Washington coasts during 1983.

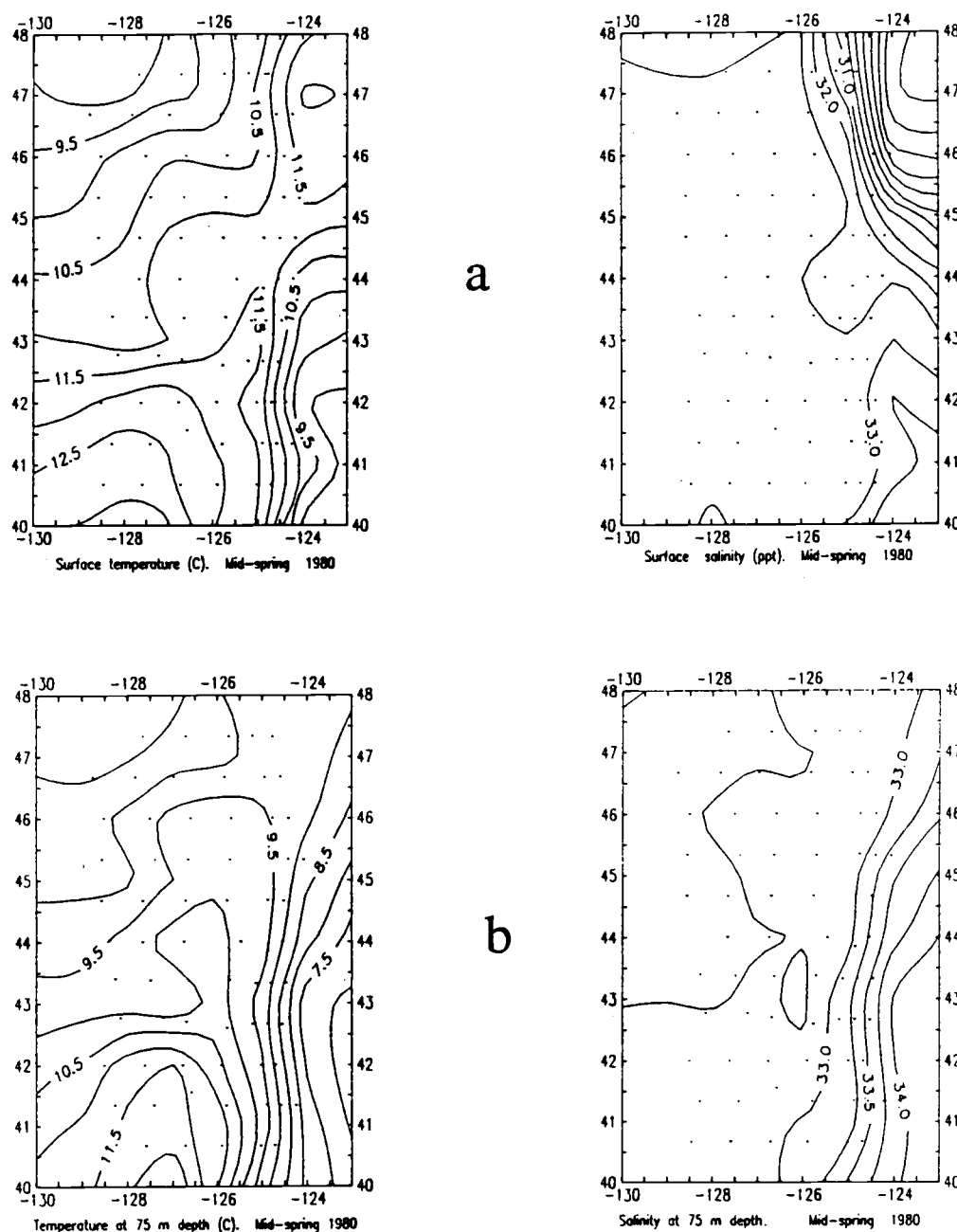


Fig. 6. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during mid-spring, 1980.

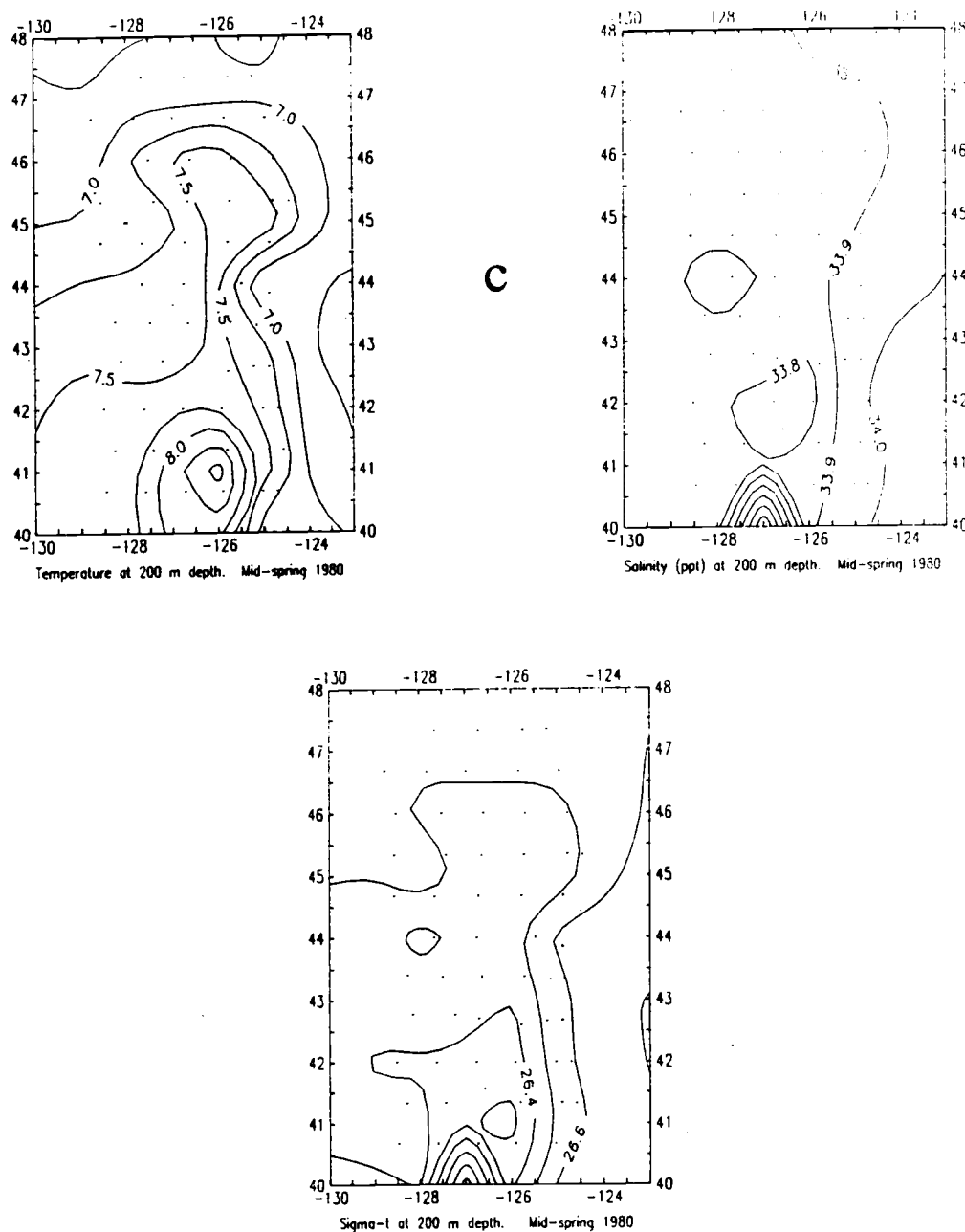


Fig. 6 (cont.)

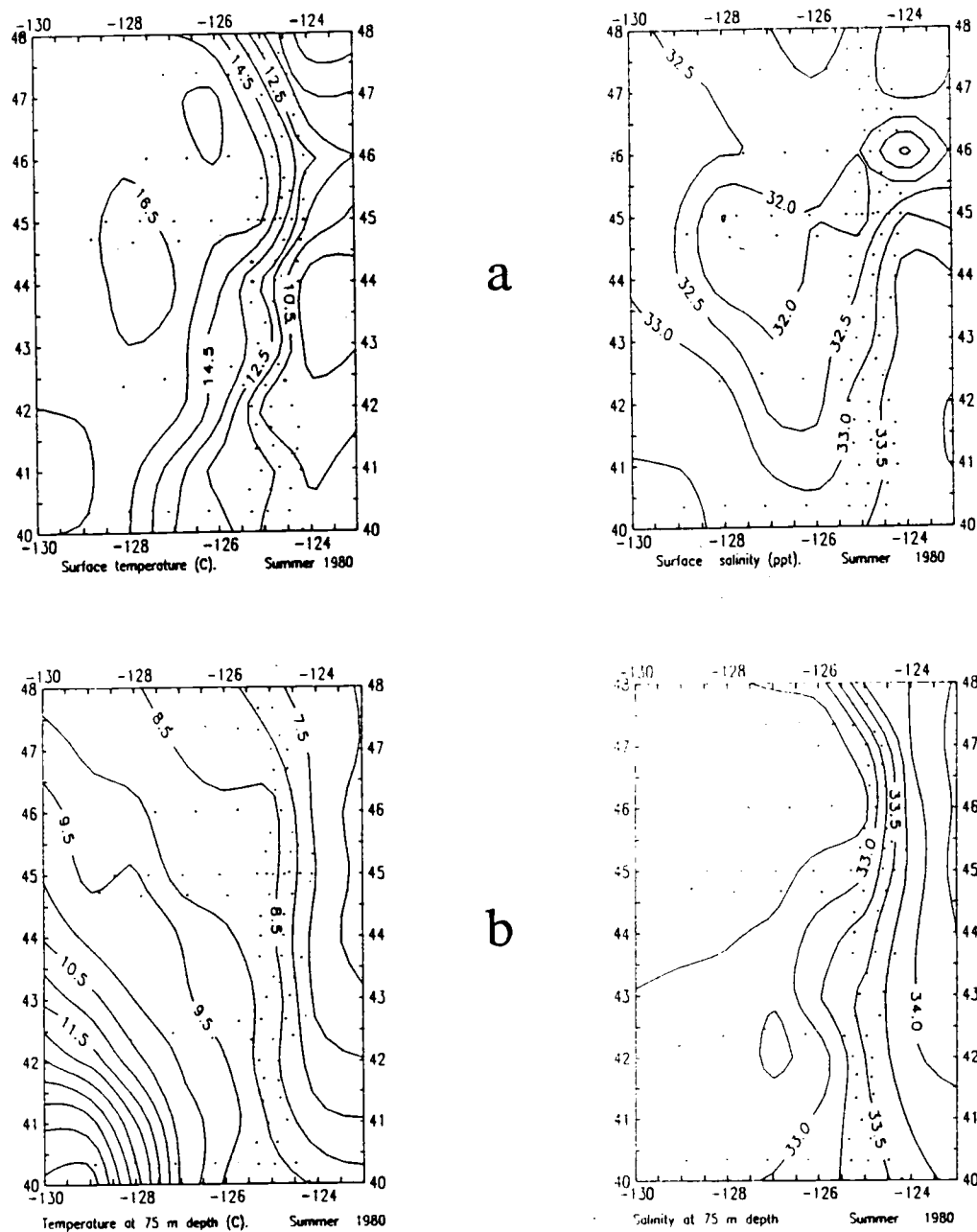


Fig. 7. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during summer, 1980.

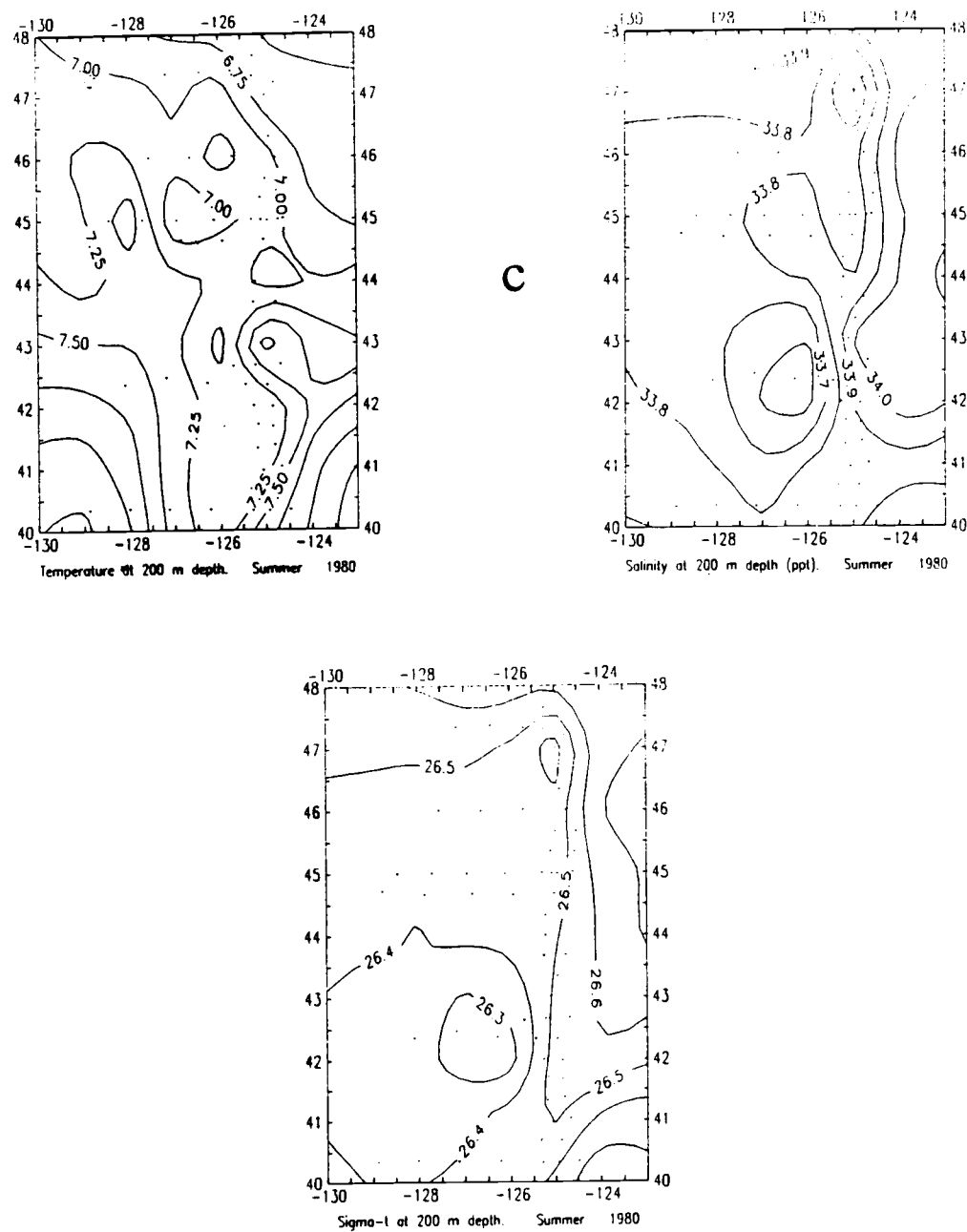


Fig. 7 (cont.)

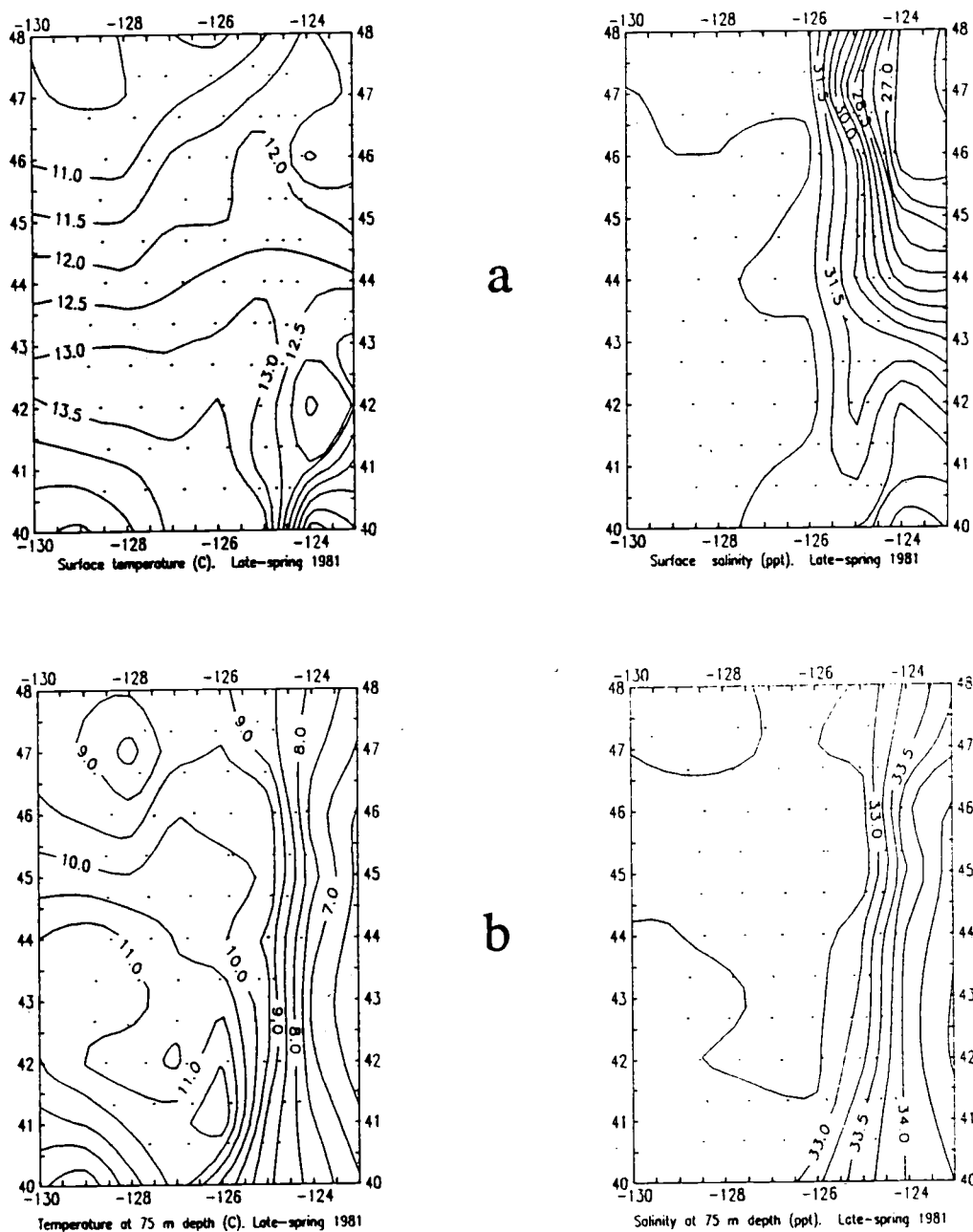
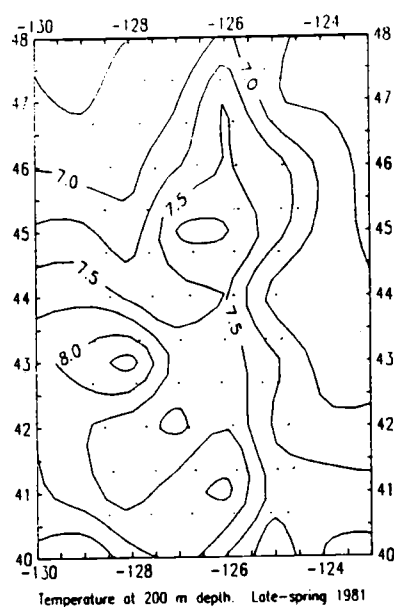


Fig. 8. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during late-spring, 1981.



C

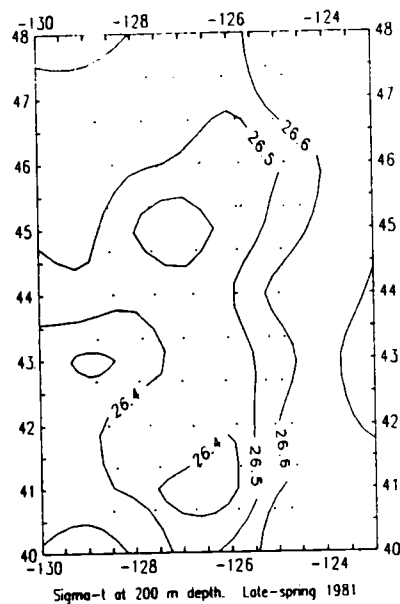
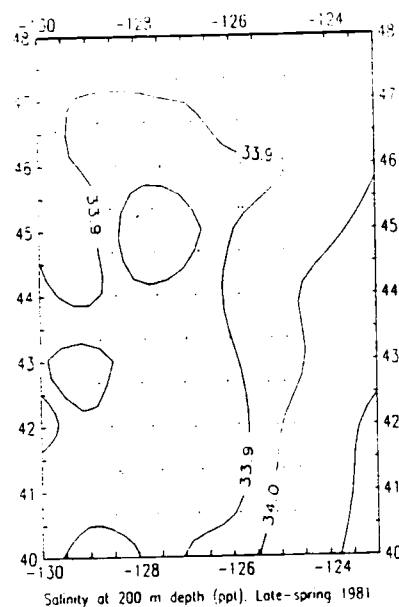


Fig. 8 (cont.)

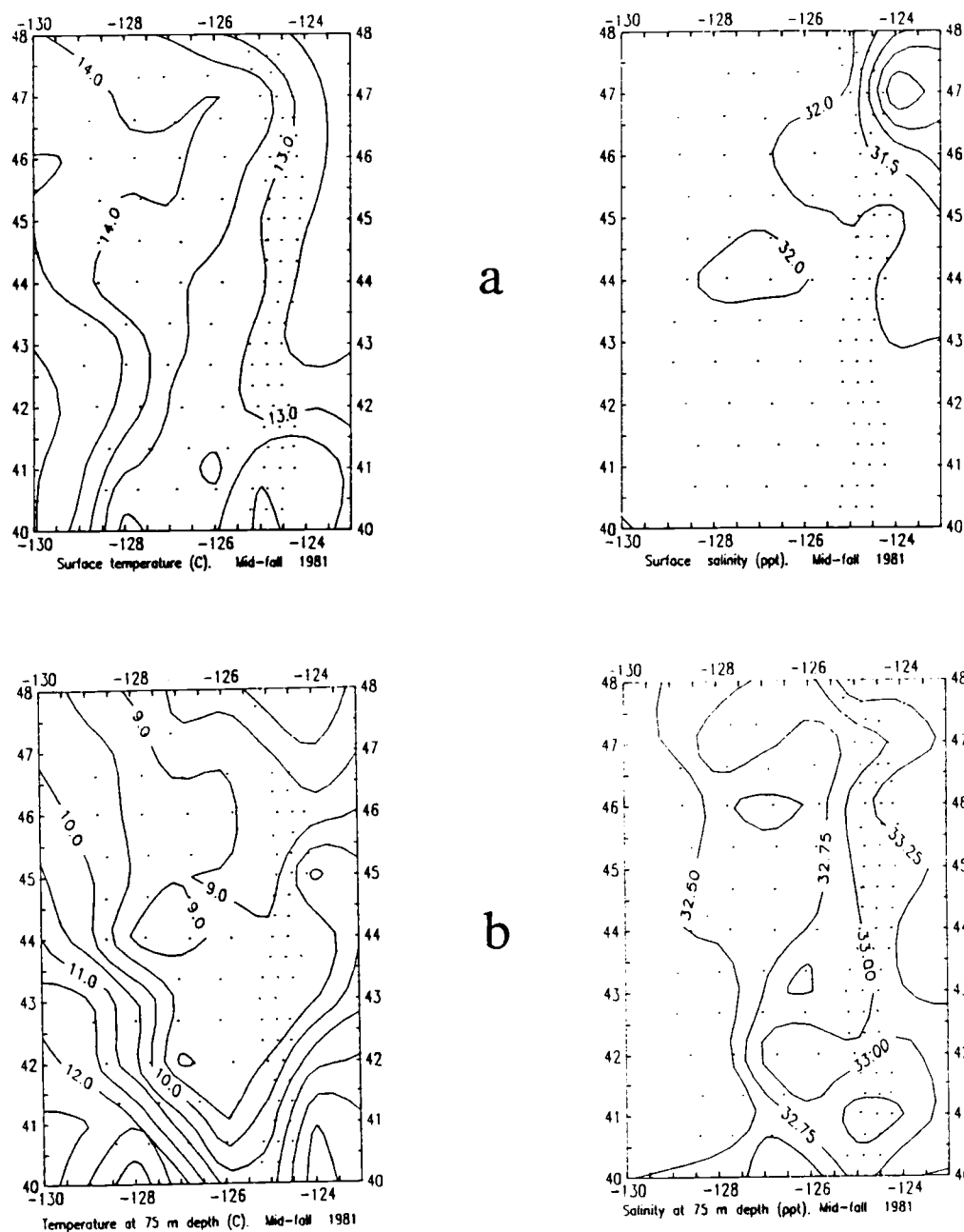


Fig. 9. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during mid-fall, 1981.

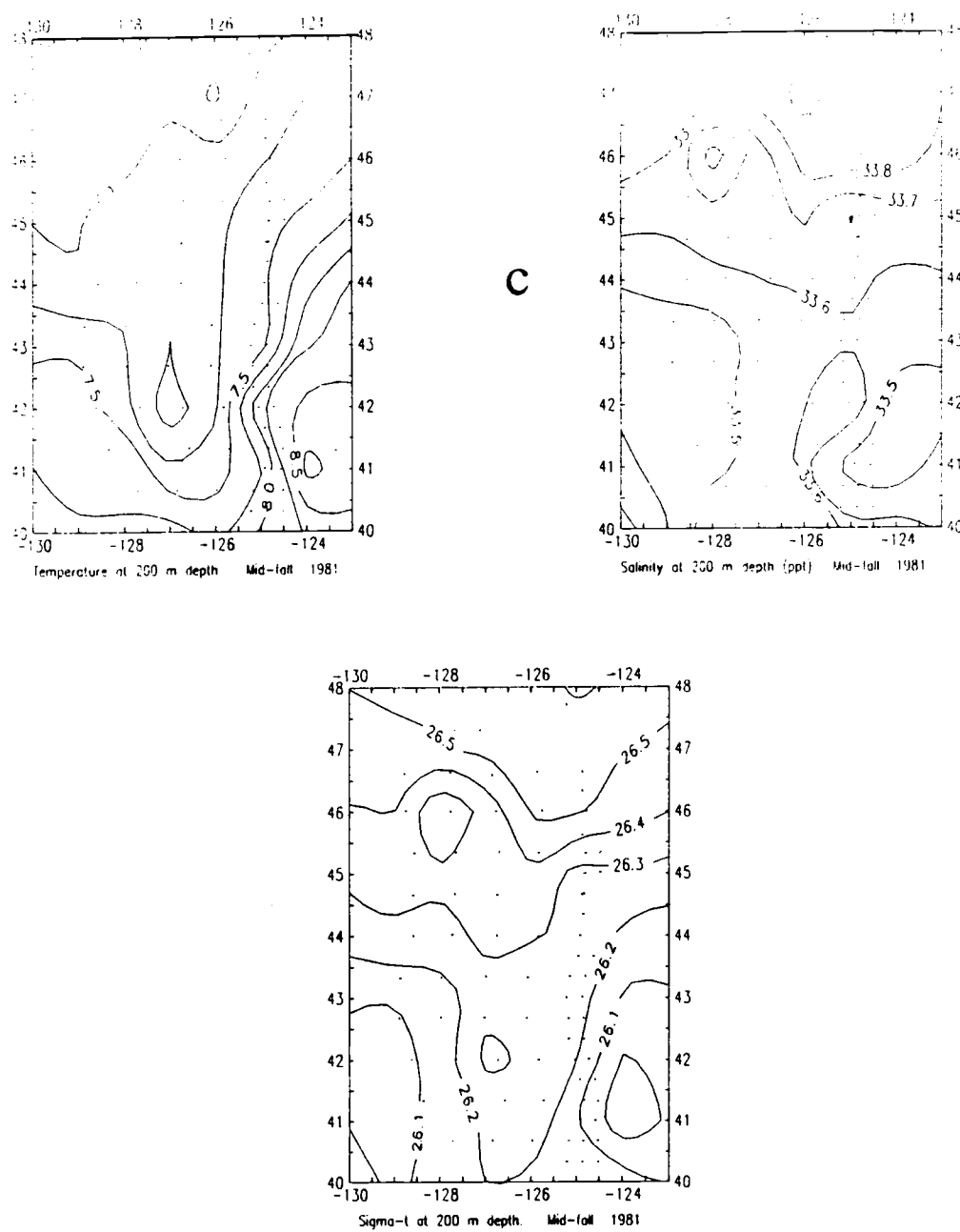


Fig. 9 (cont.)

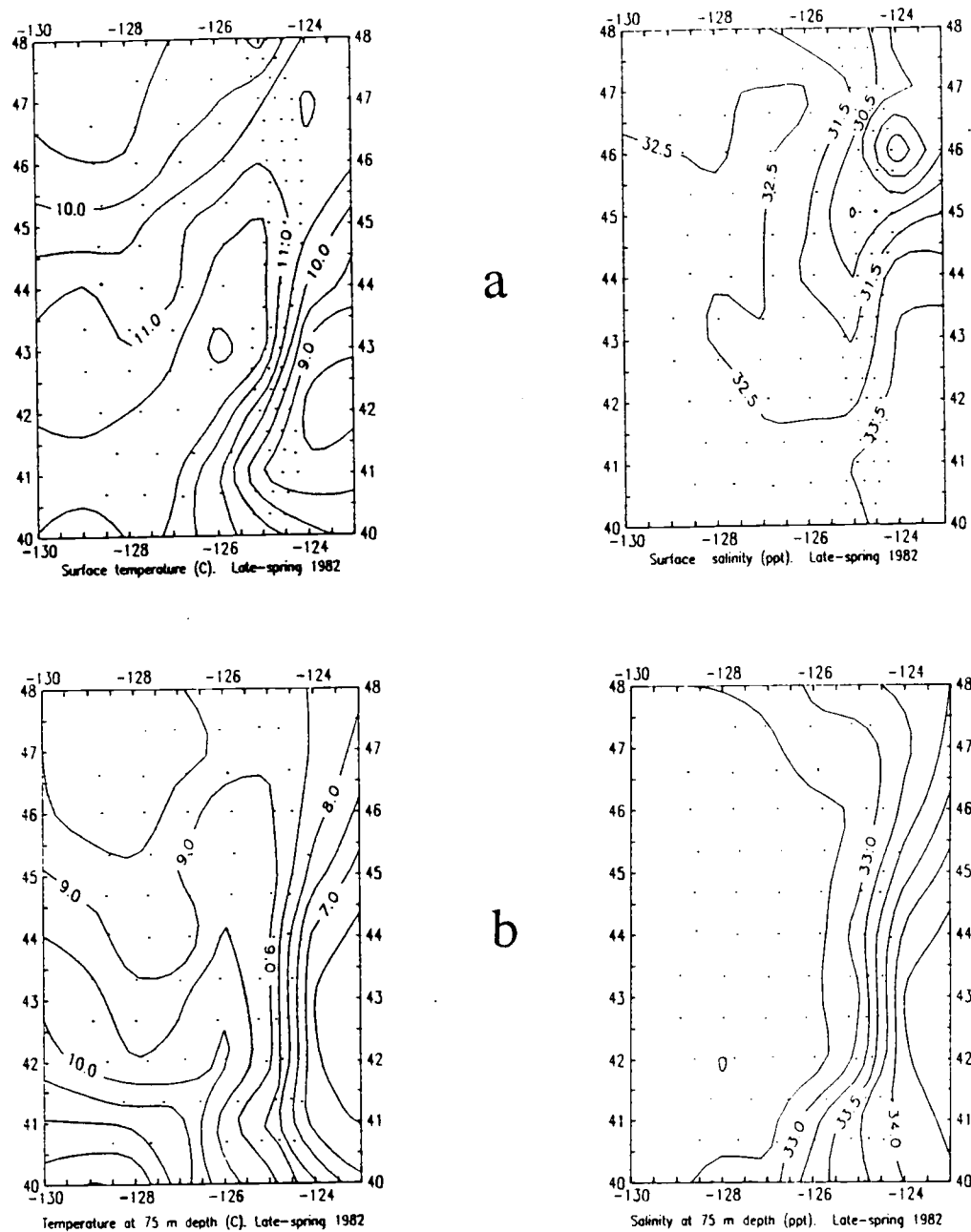


Fig. 10. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during late-spring, 1982.

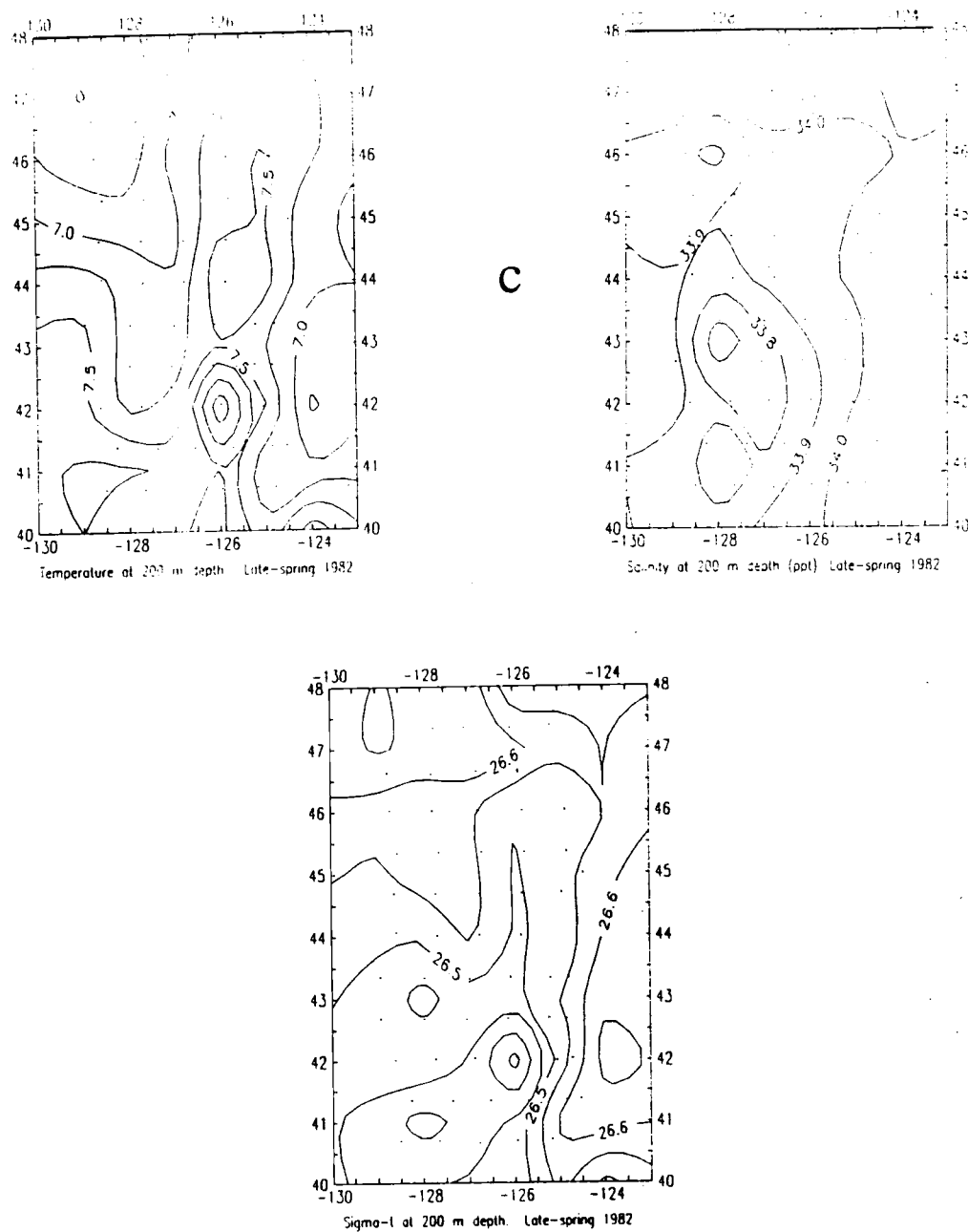


Fig. 10 (cont.)

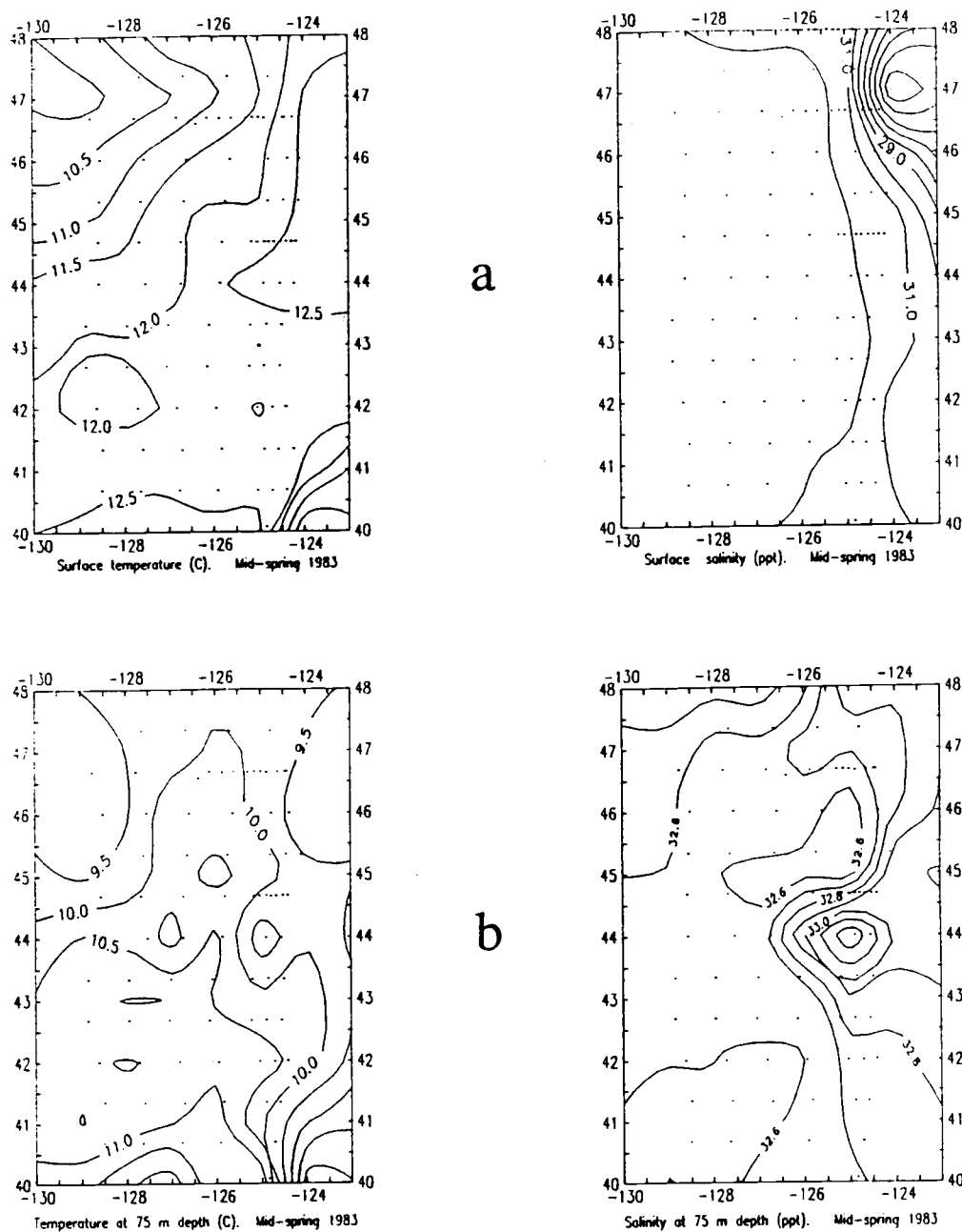


Fig. 11. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during mid-spring, 1983.

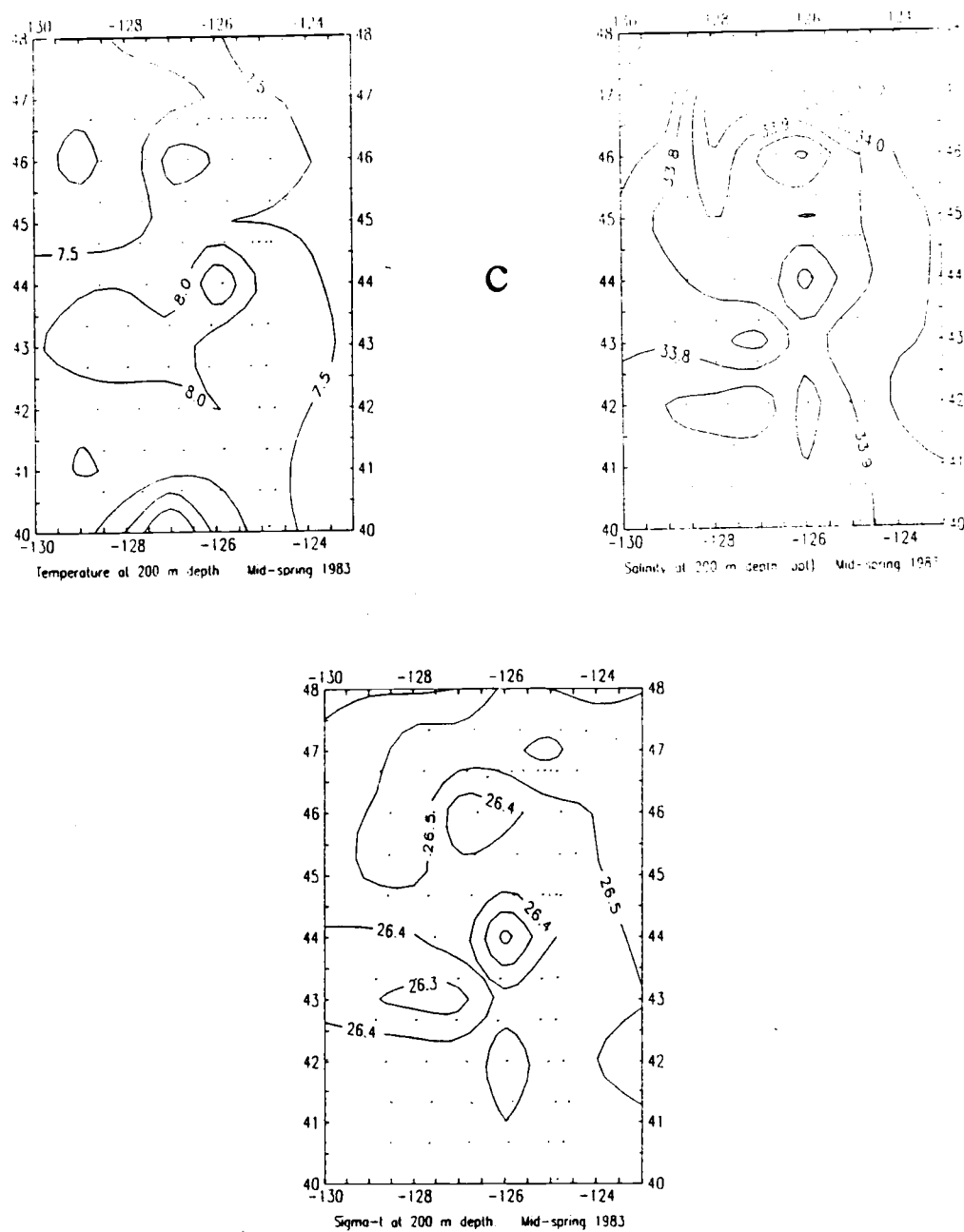


Fig. 11 (cont.)

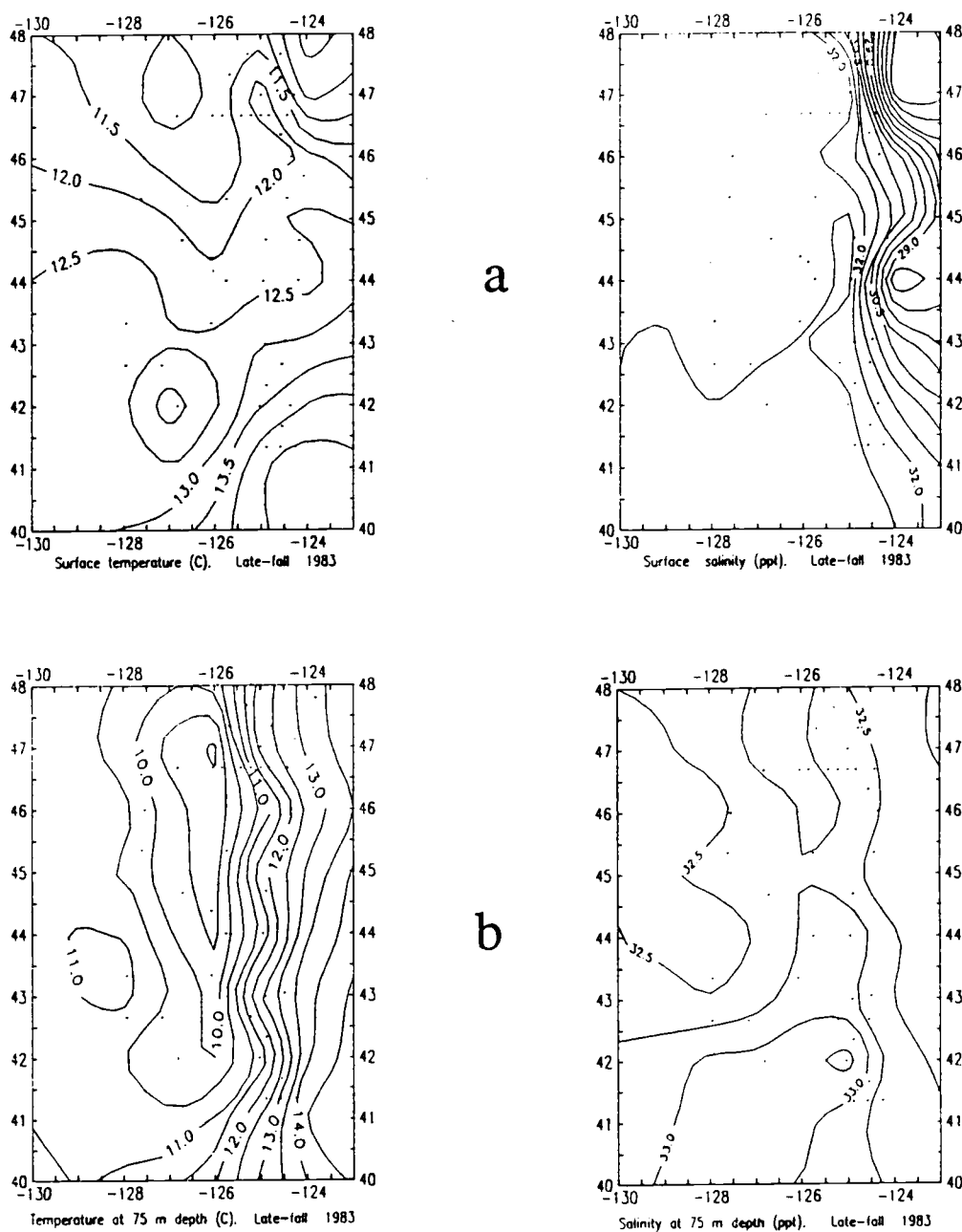


Fig. 12. Temperature and salinity contours at (a) sea surface, (b) 75 m depth and temperature, salinity and sigma-t (σ_t) at (c) 200 m depth between 40 and 48° lat N during late-fall, 1983.

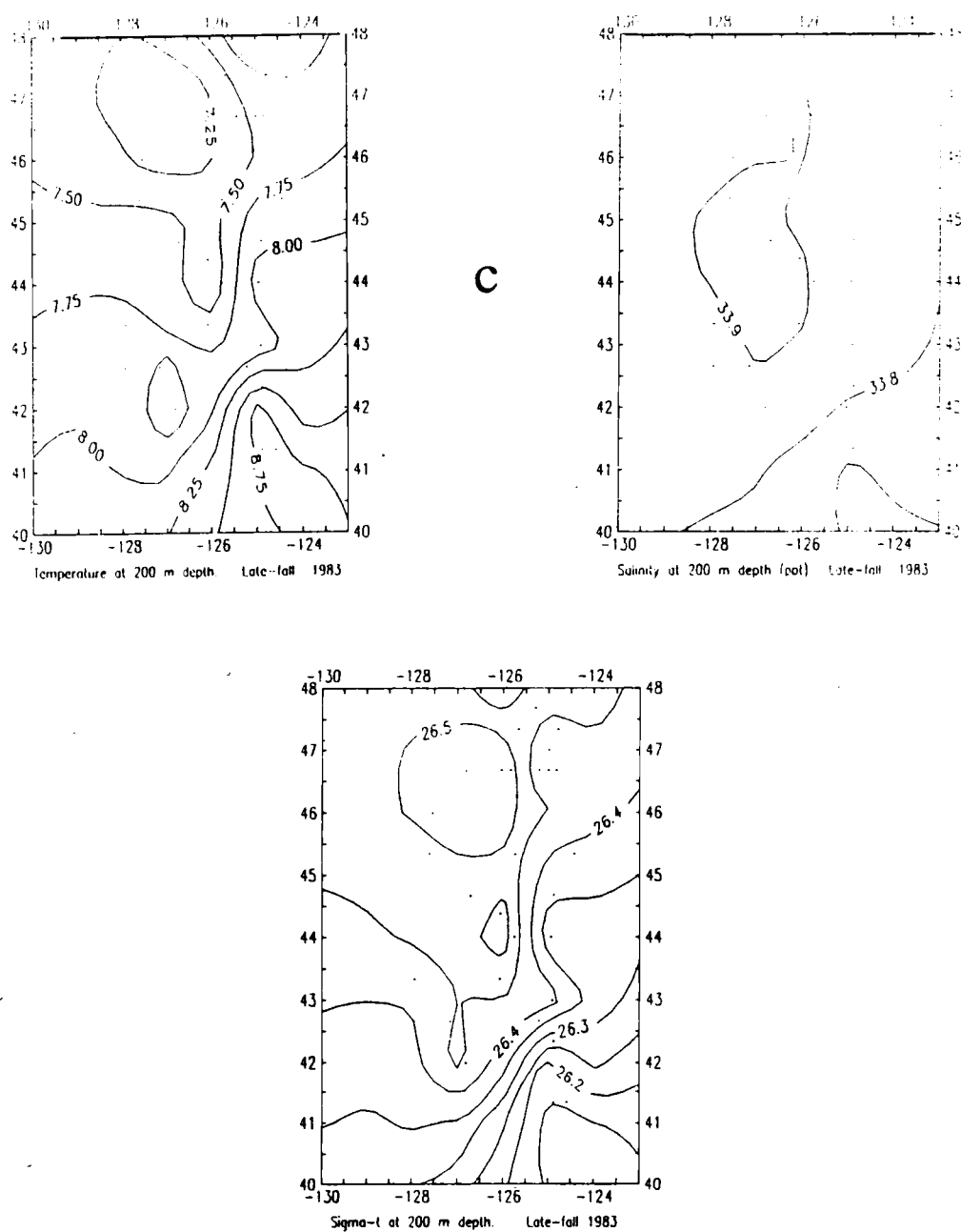


Fig. 12 (cont.)

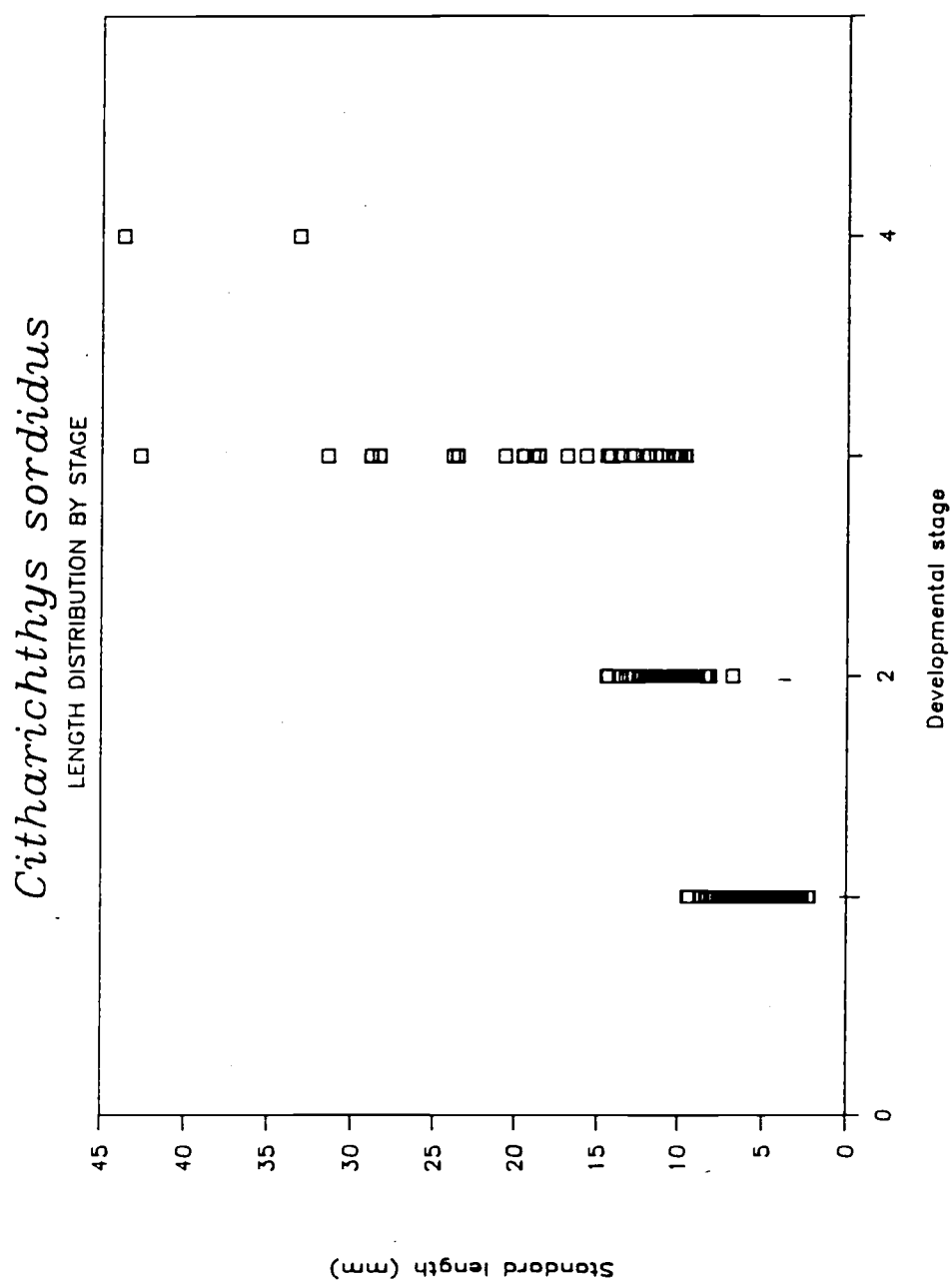


Fig. 13. Standard length (mm) distribution by developmental stage of larval Pacific sanddab (*Citharichthys sordidus*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

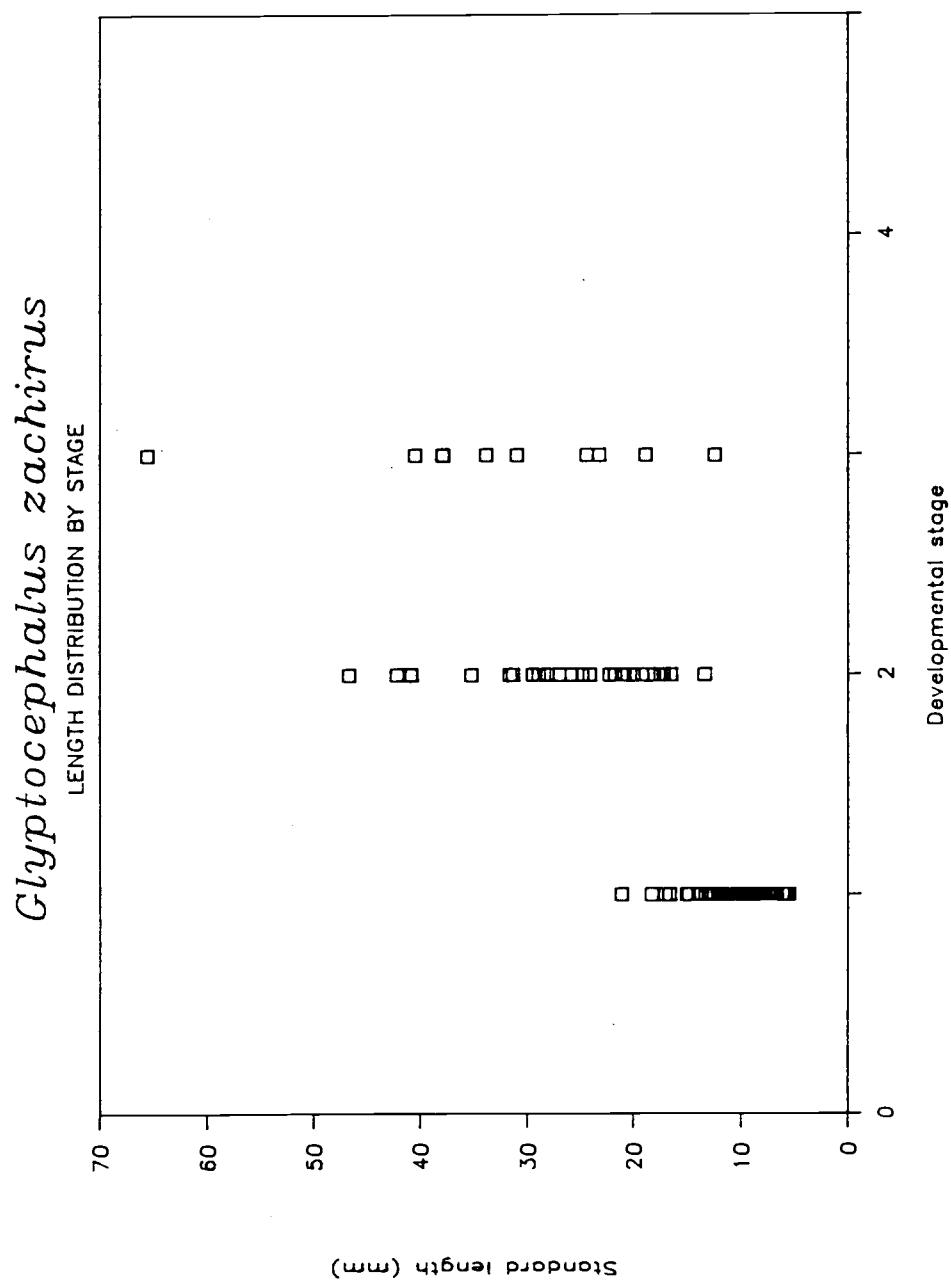


Fig. 15. Standard length (mm) distribution by developmental stage of larval rex sole (*Glyptocephalus zachirus*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

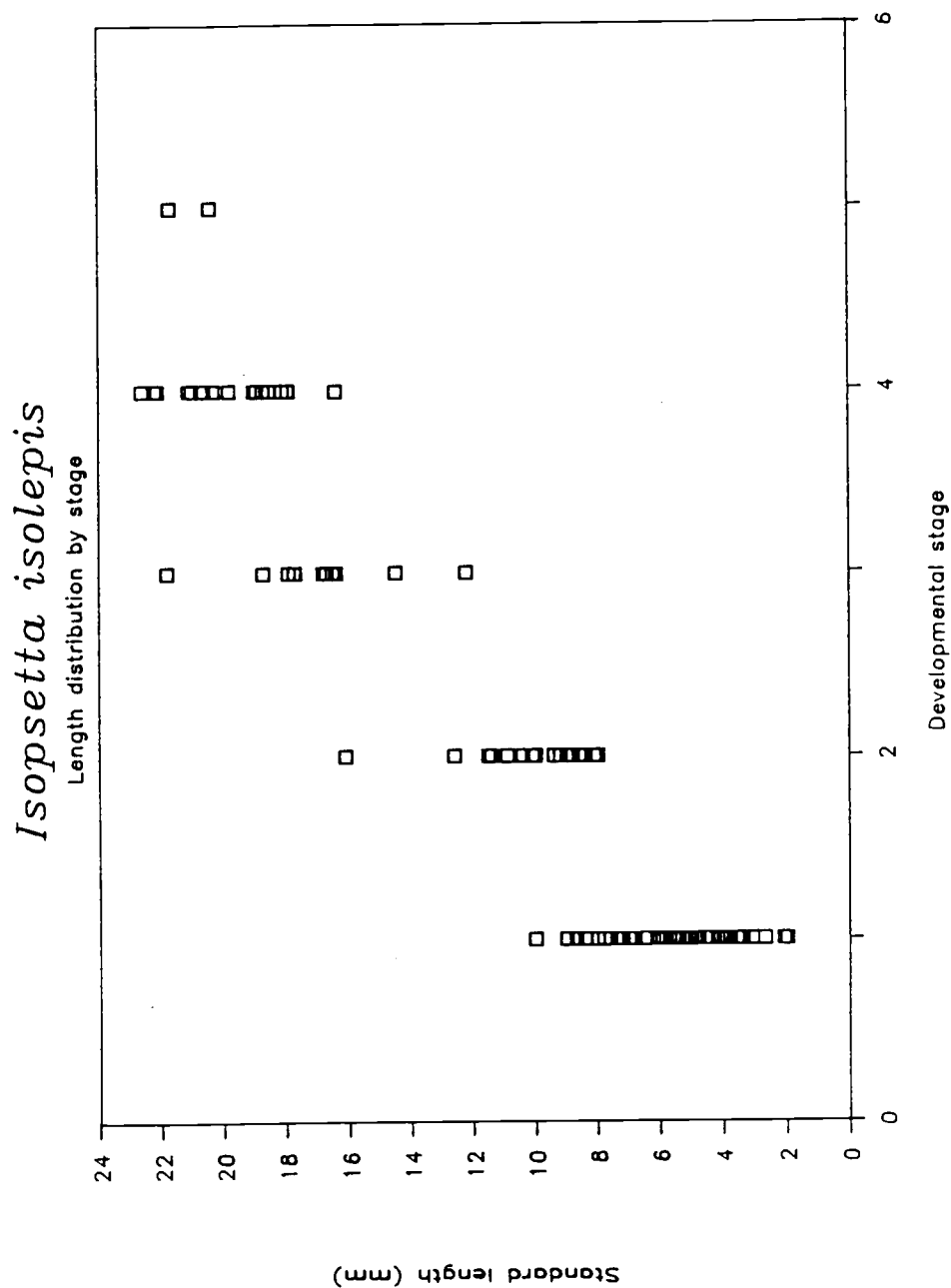


Fig. 16. Standard length (mm) distribution by developmental stage of larval butter sole (*Isopsetta isolepis*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

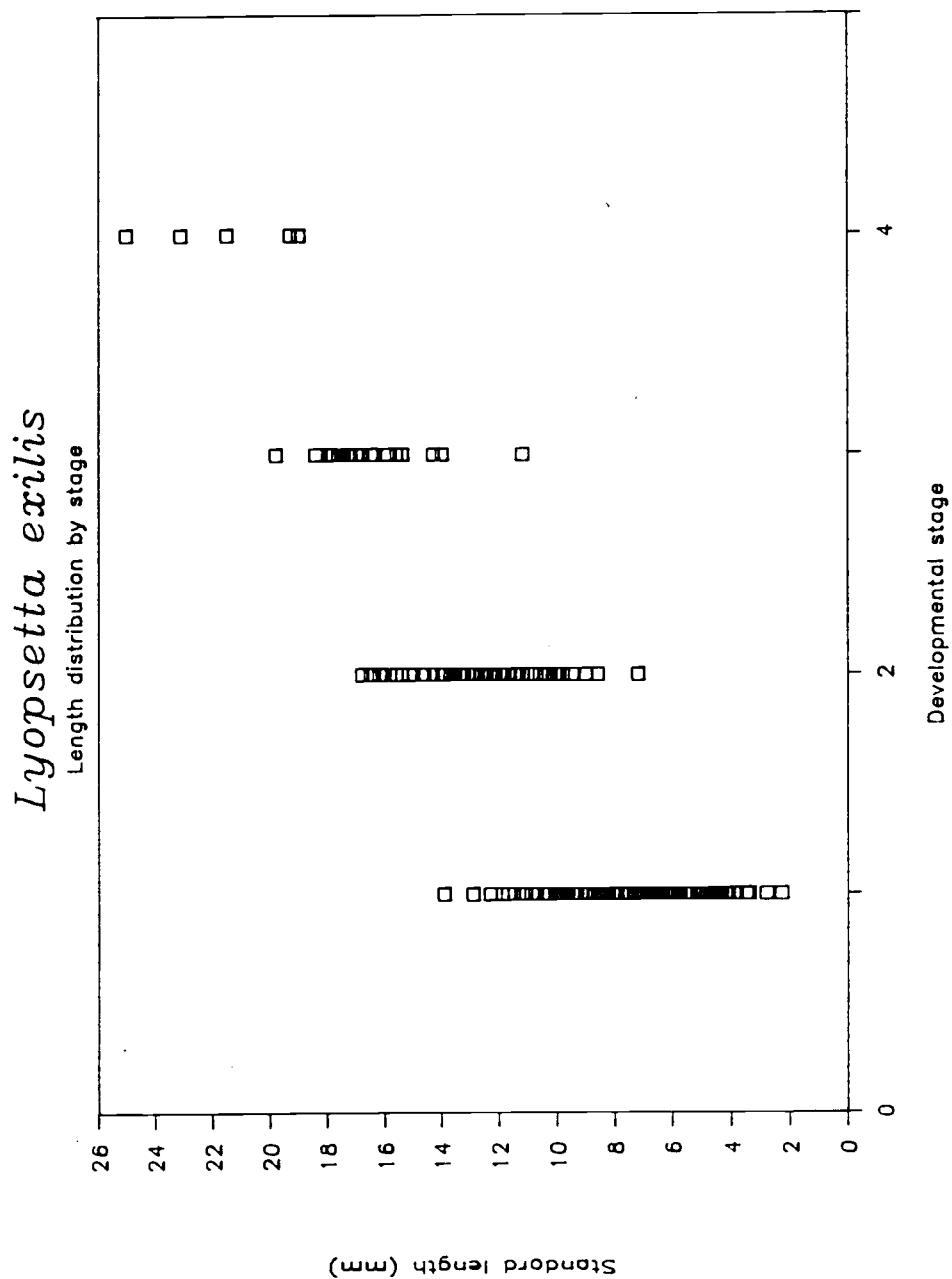


Fig. 17. Standard length (mm) distribution by developmental stage of larval slender sole (*Lyopsetta exilis*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

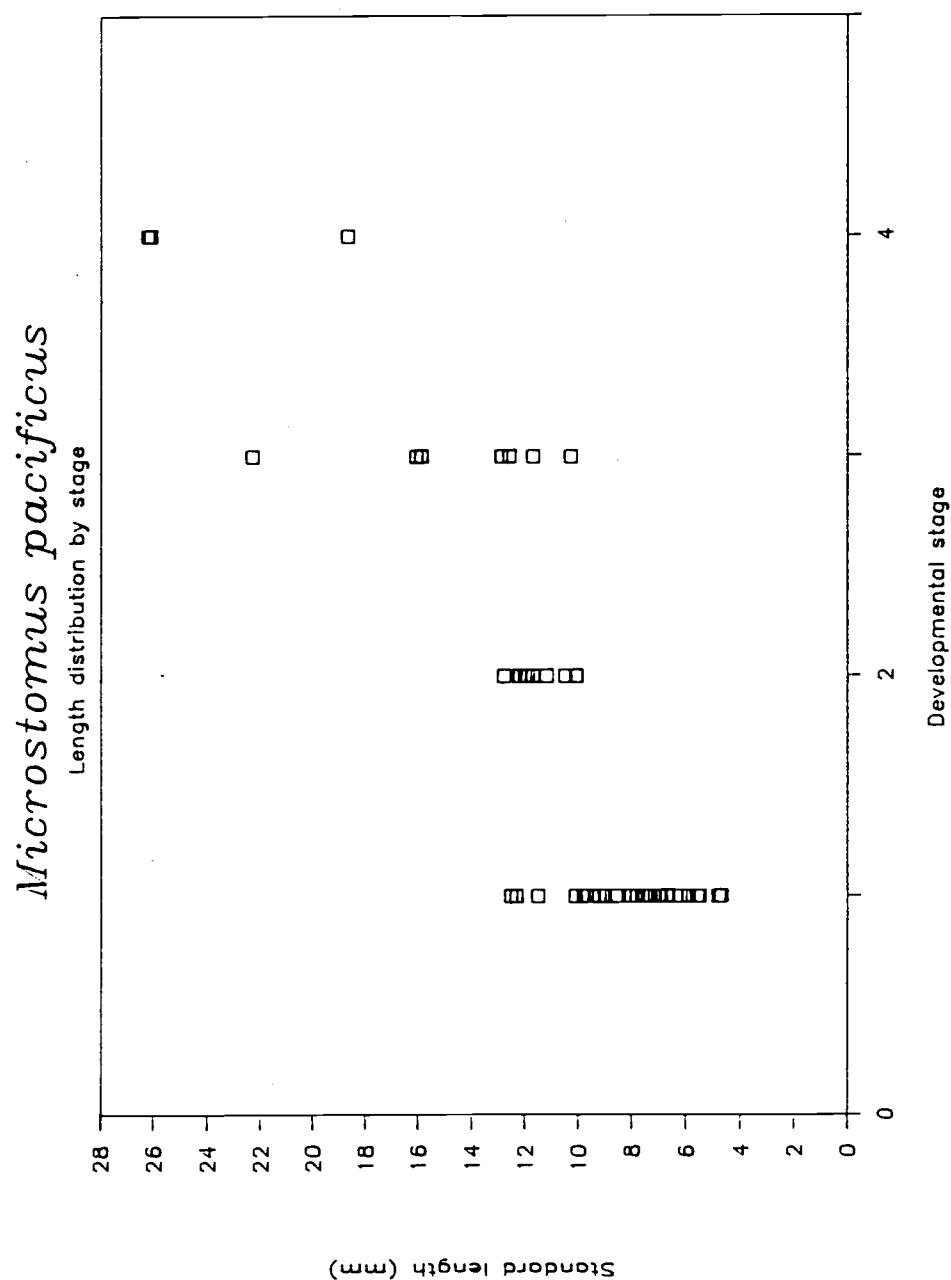


Fig. 18. Standard length (mm) distribution by developmental stage of larval Dover sole (*Microstomus pacificus*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

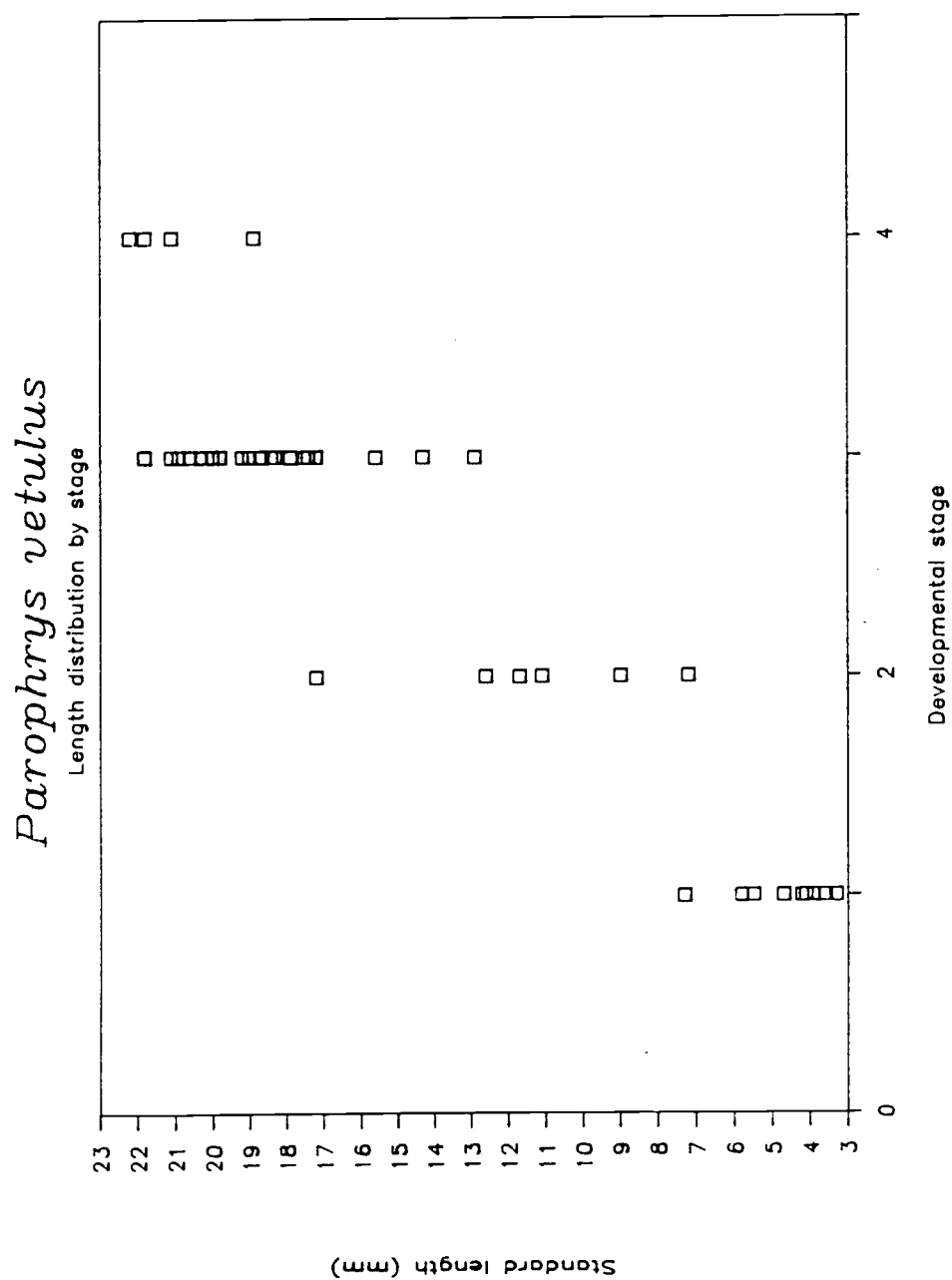


Fig. 19. Standard length (mm) distribution by developmental stage of larval English sole (*Parophrys vetulus*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

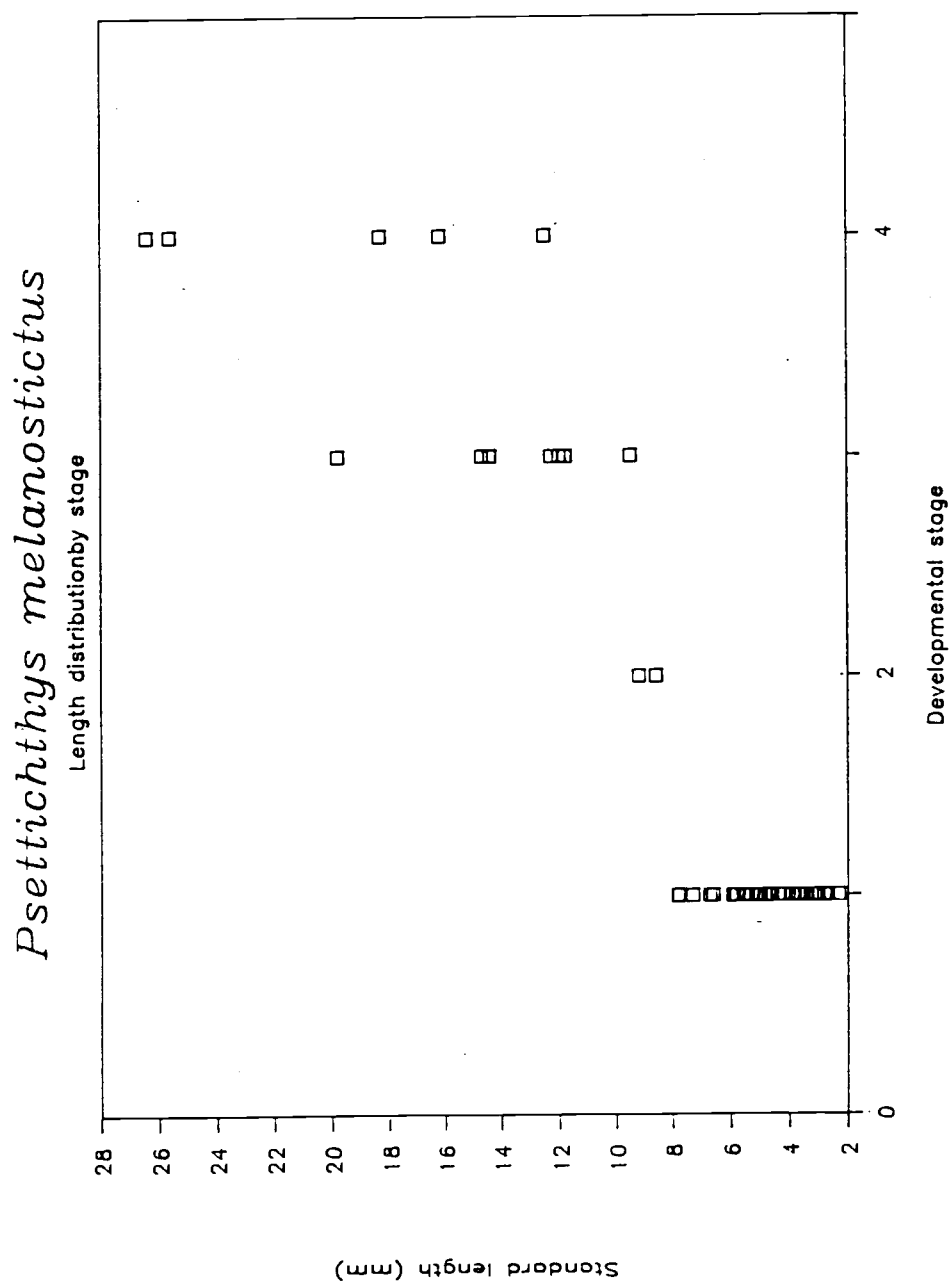


Fig. 20. Standard length (mm) distribution by developmental stage of larval sand sole (*Psettiichthys melanostictus*) caught off Washington, Oregon and northern California in the period between 1980 and 1983.

Fig. 21. Standard length frequency distribution of Pacific sanddab (*C. sordidus*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.

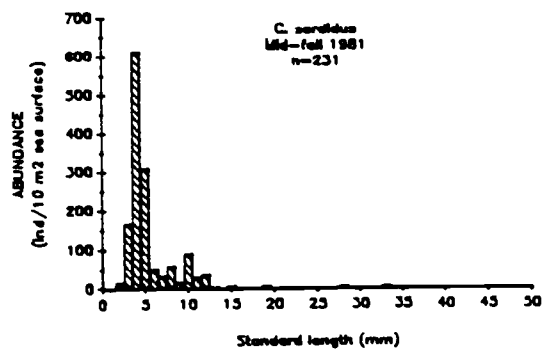
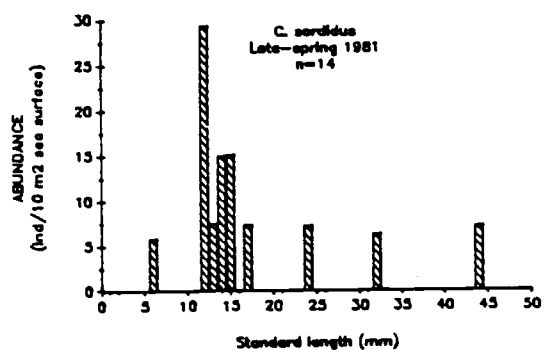
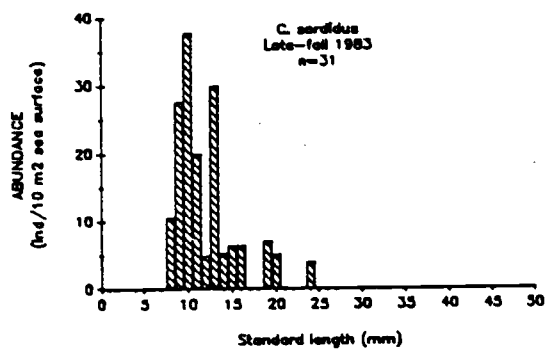
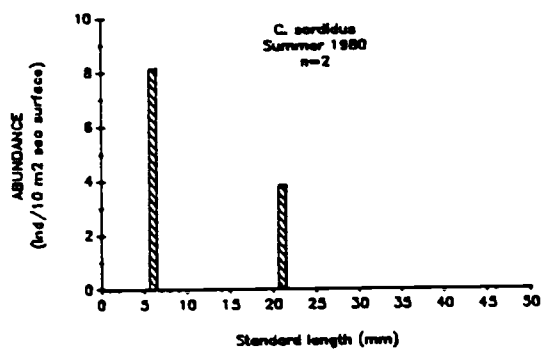
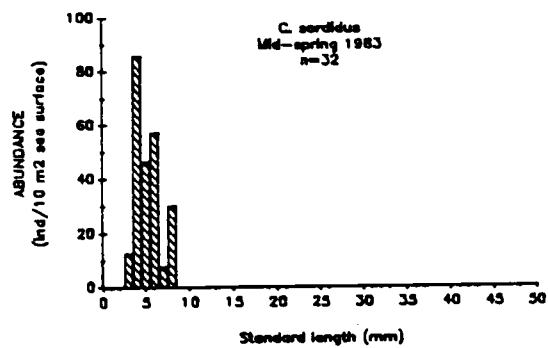
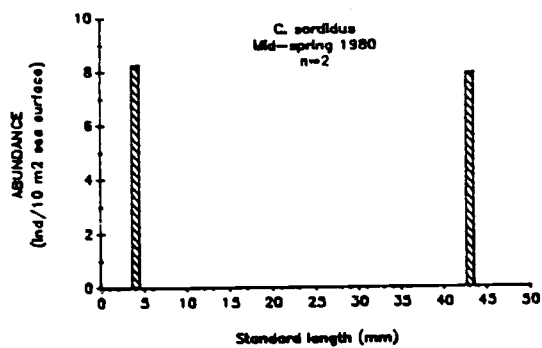


Fig. 22. Standard length frequency distribution of speckled sanddab (*C. stigmaeus*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.

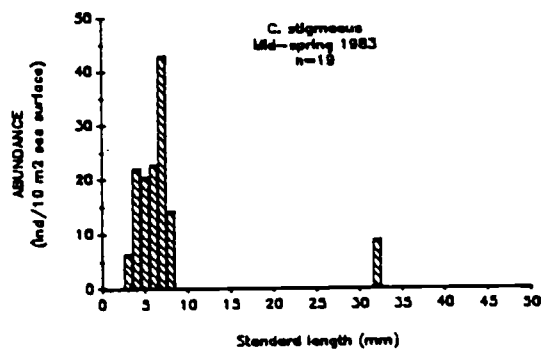
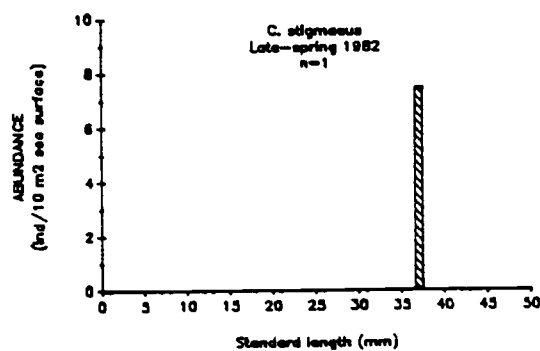
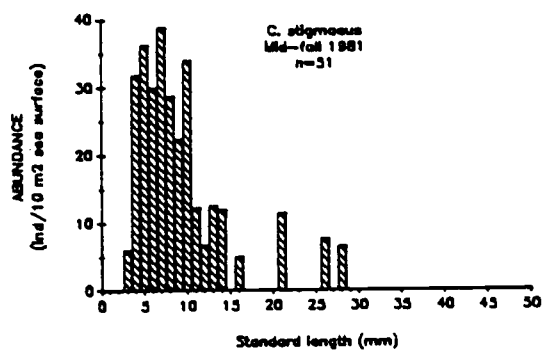
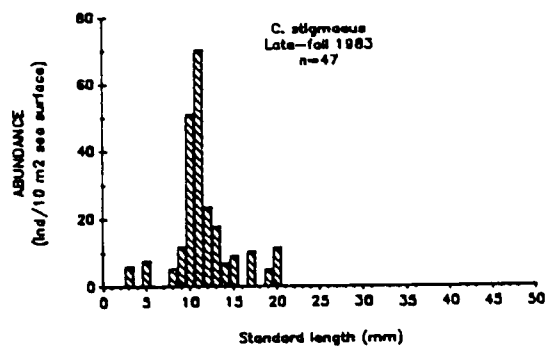
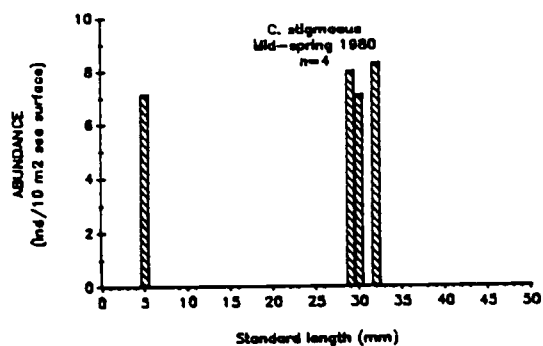


Fig. 23. Standard length frequency distribution of rex sole (*G. zachirus*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.

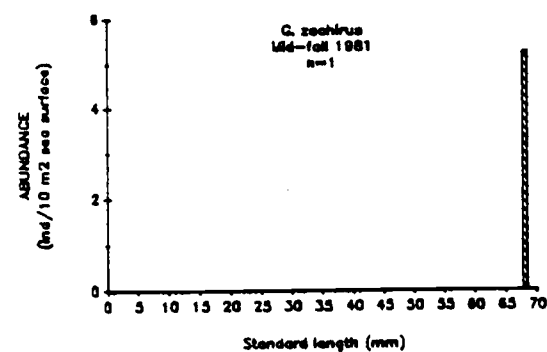
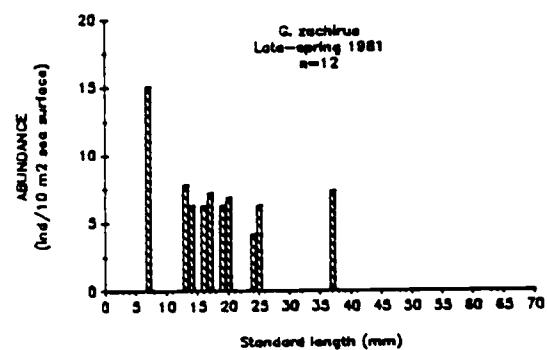
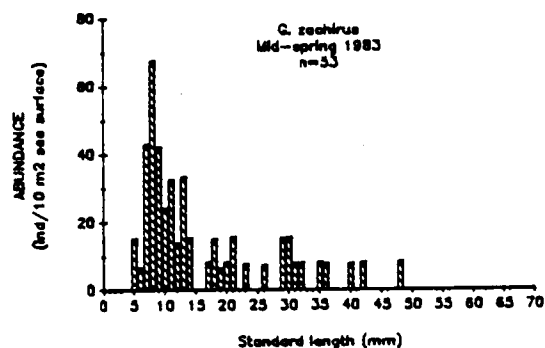
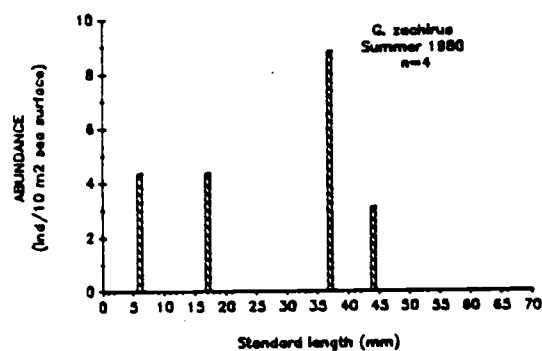
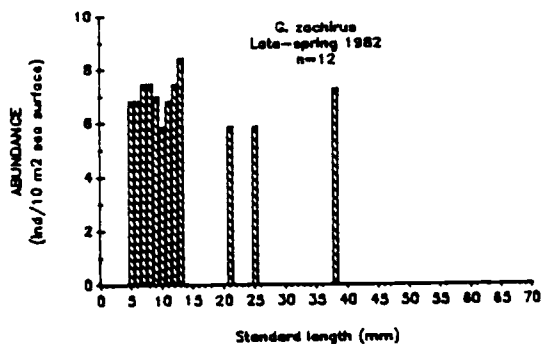
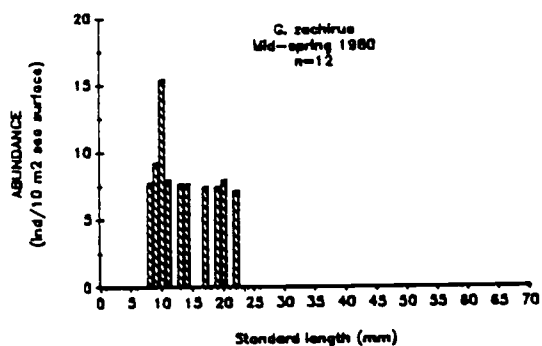


Fig. 24. Standard length frequency distribution of butter sole (*I. isolepis*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.

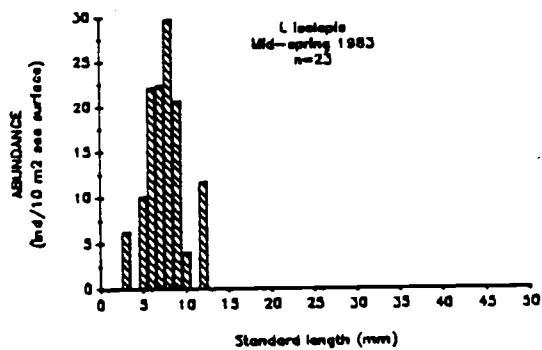
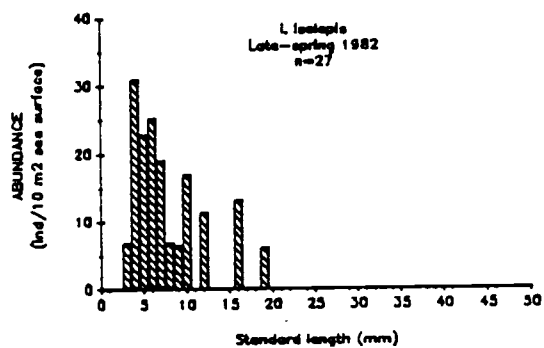
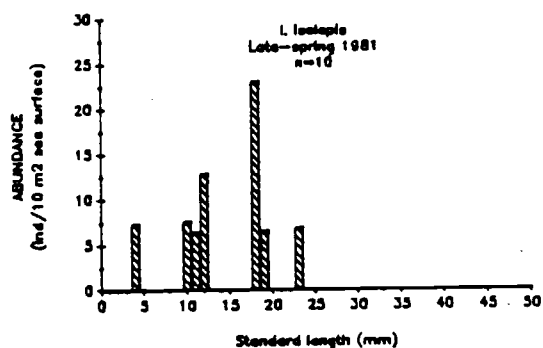
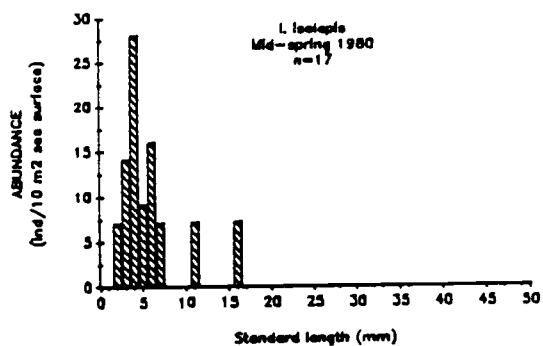


Fig. 25. Standard length frequency distribution of slender sole (*L. exilis*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.

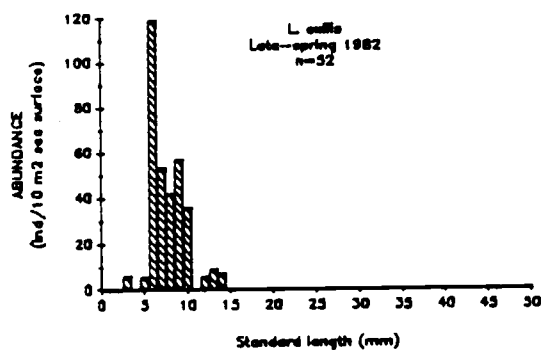
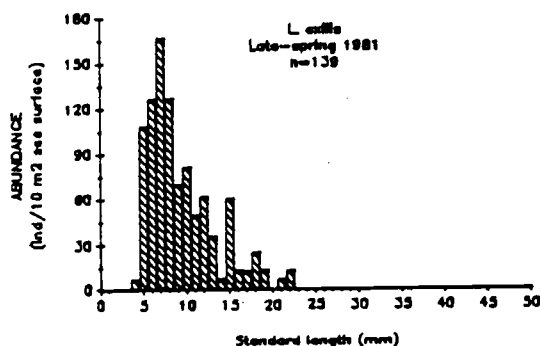
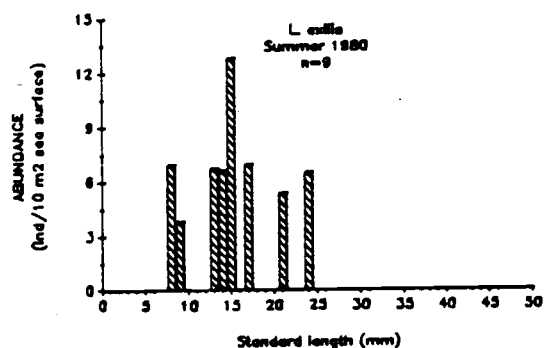
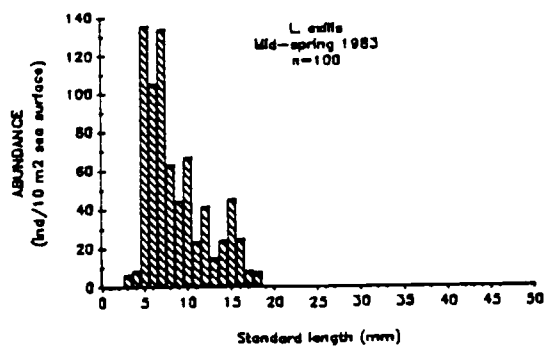
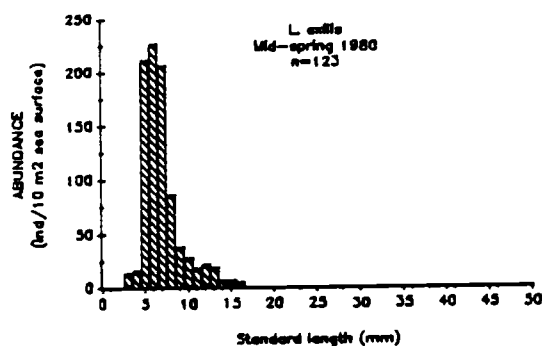


Fig. 26. Standard length frequency distribution of Dover sole (*M. pacificus*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.

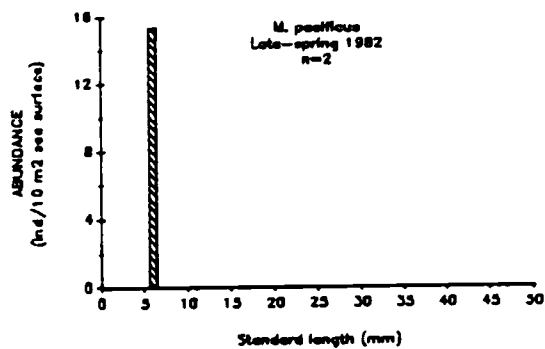
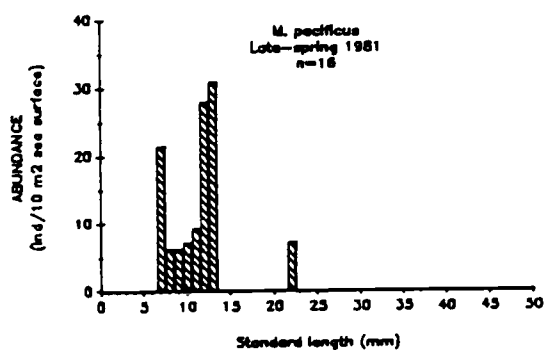
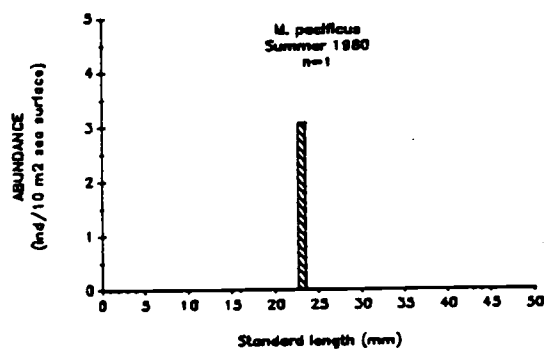
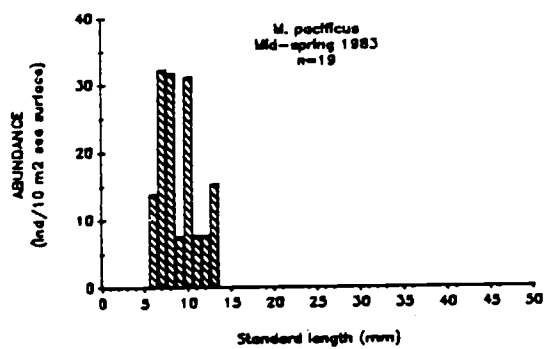
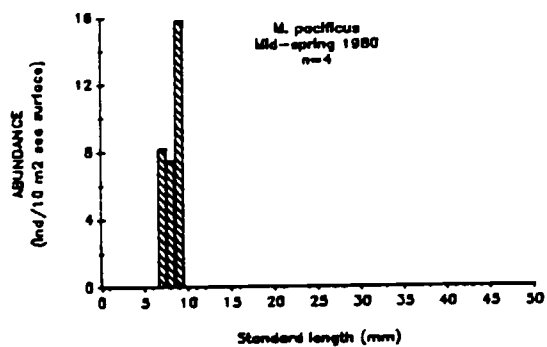
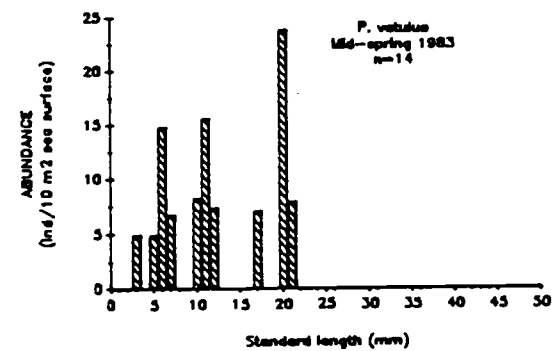
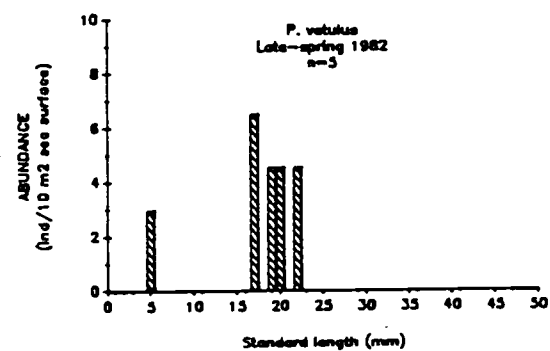
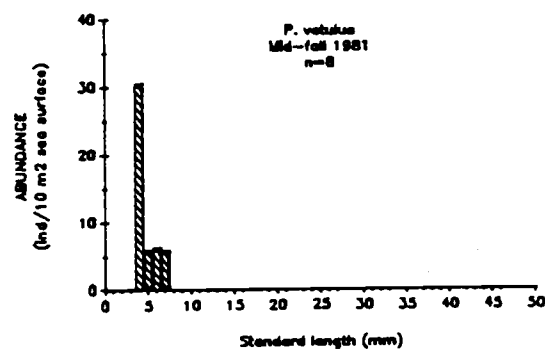
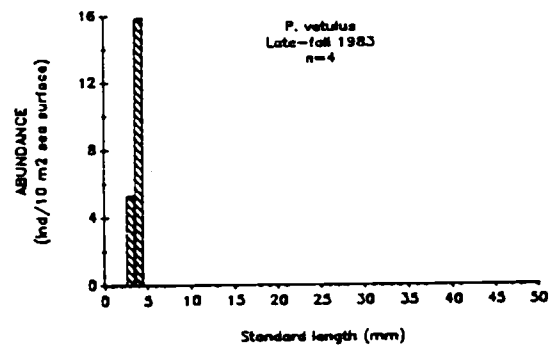
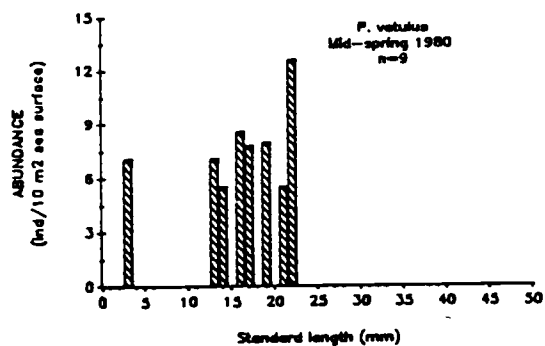
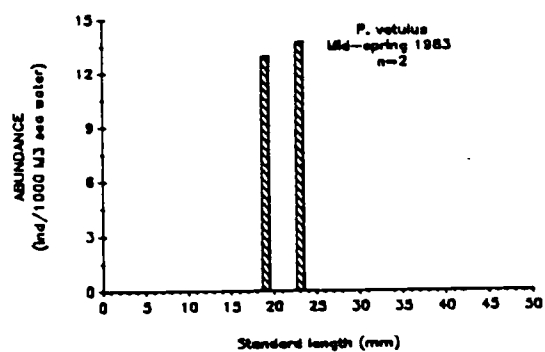
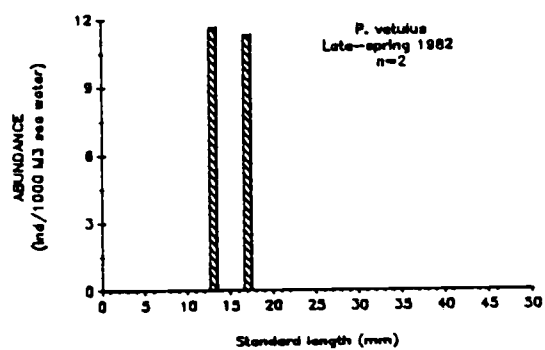
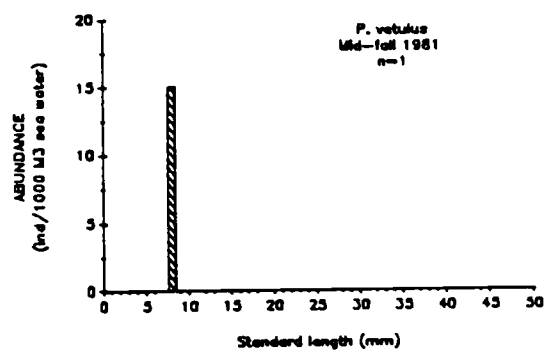
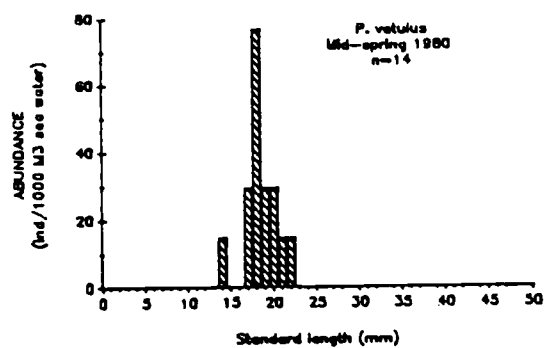


Fig. 27. Standard length frequency distribution of English sole (*P. vetulus*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983. (a) Bongo tows. (b) Neuston tows

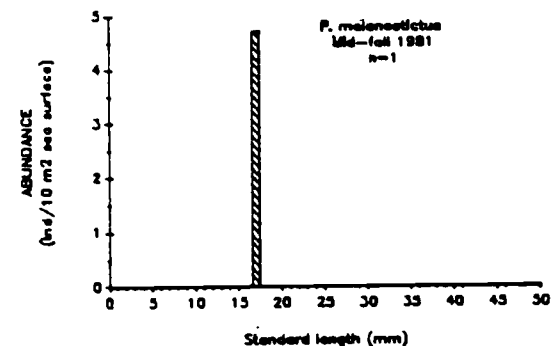
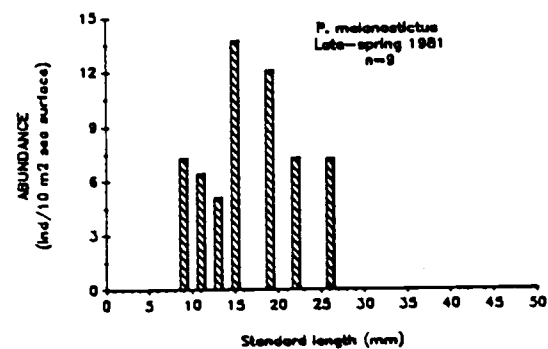
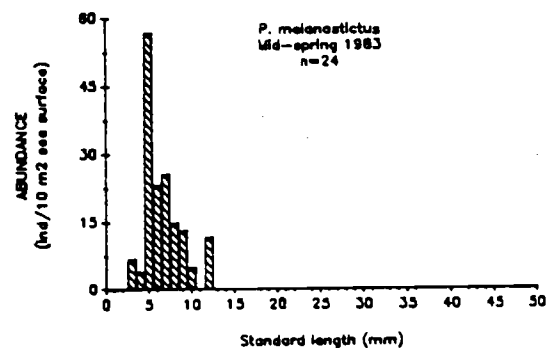
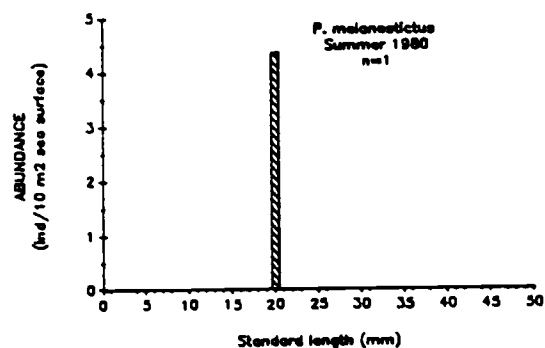
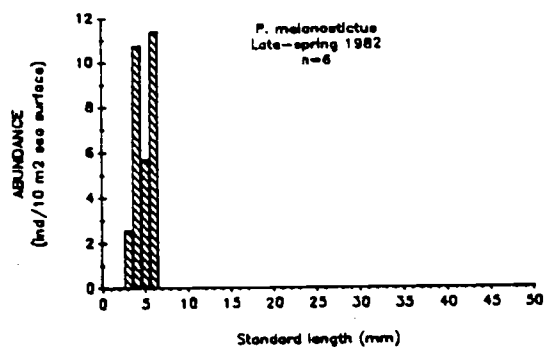
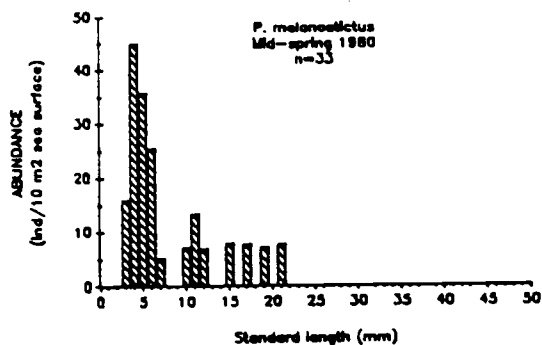


a



b

Fig. 28. Standard length frequency distribution of sand sole (*P. melanostictus*) caught in bongo tows off Washington, Oregon and northern California, between 1980 and 1983.



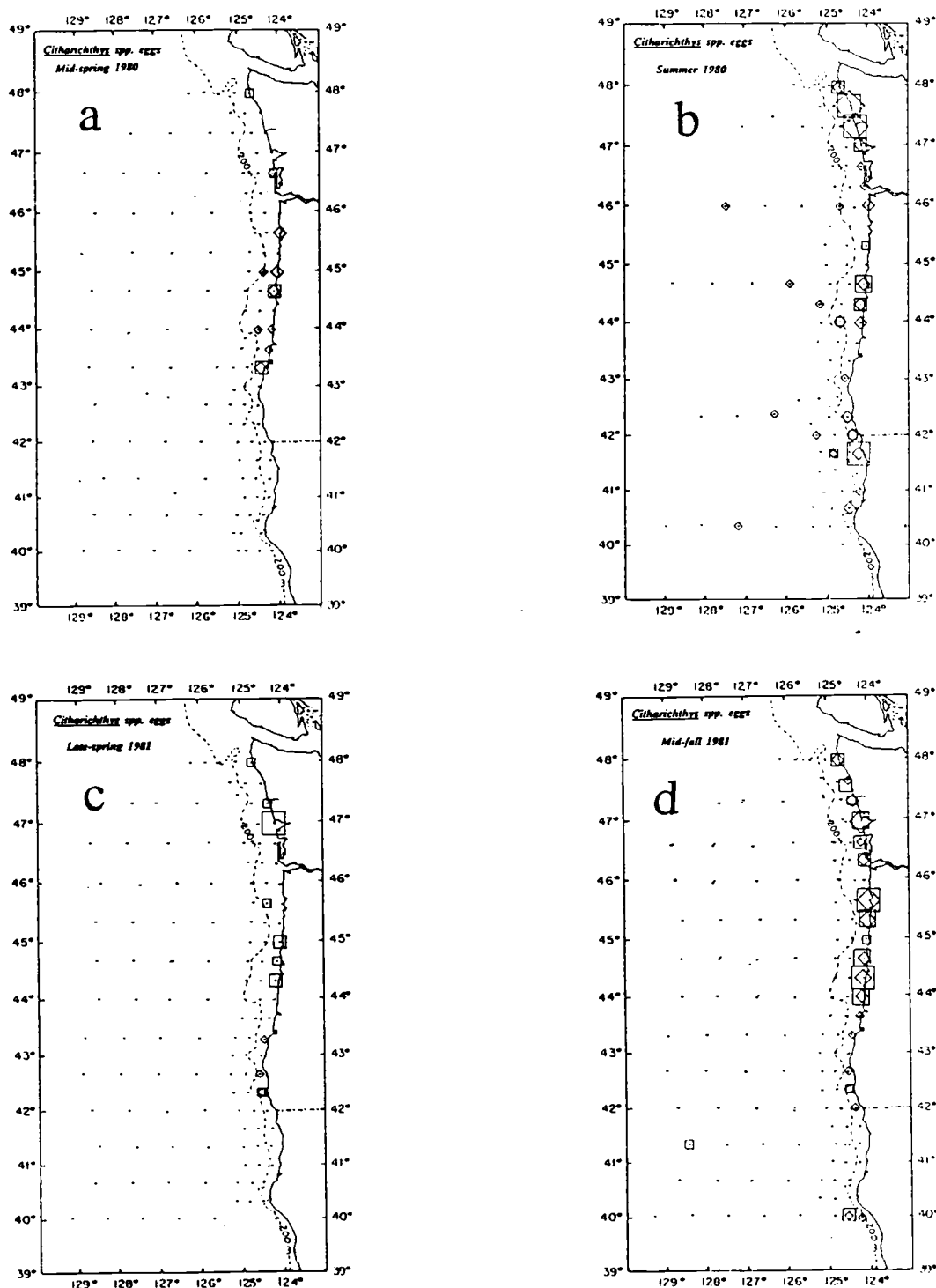


Fig. 29. Distribution of egg abundances of *Citharichthys* spp. off Washington, Oregon and northern Washington between 1980 and 1983.

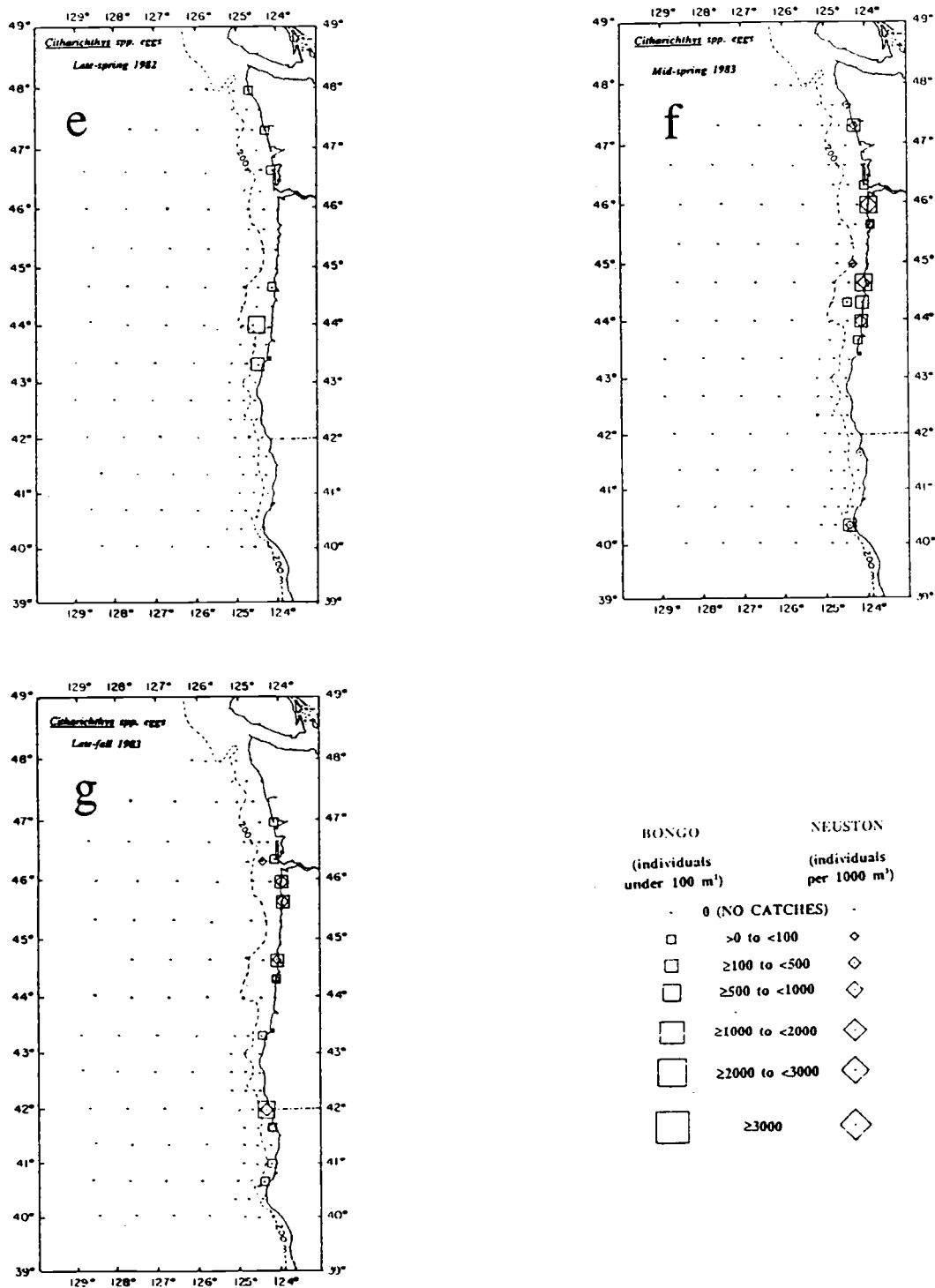


Fig. 29 (cont.)

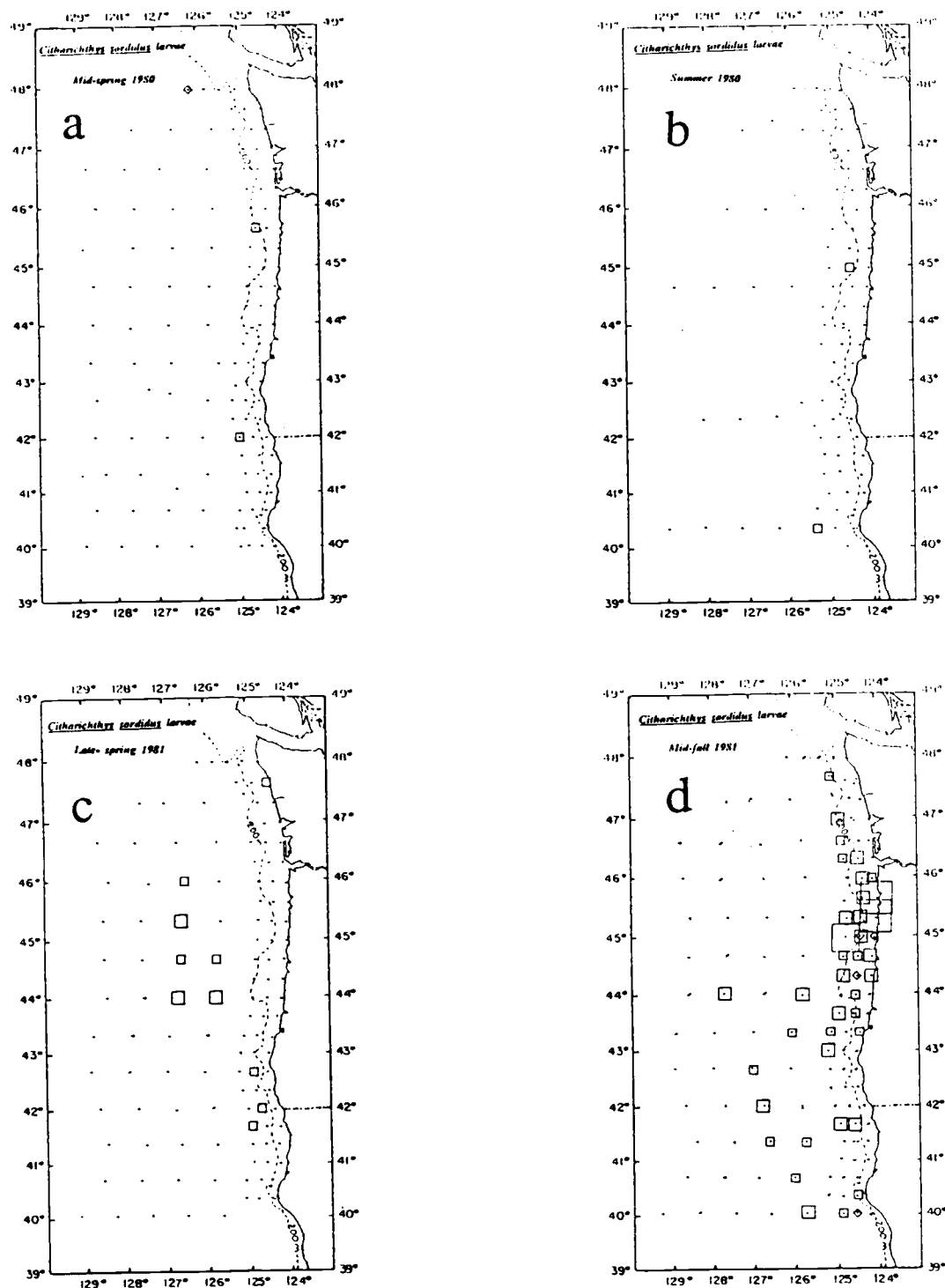
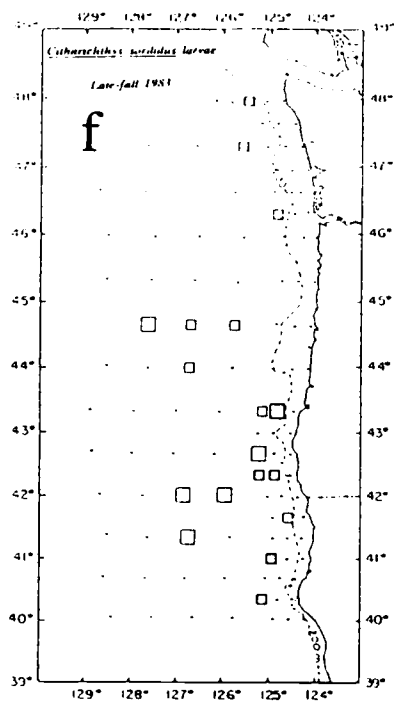
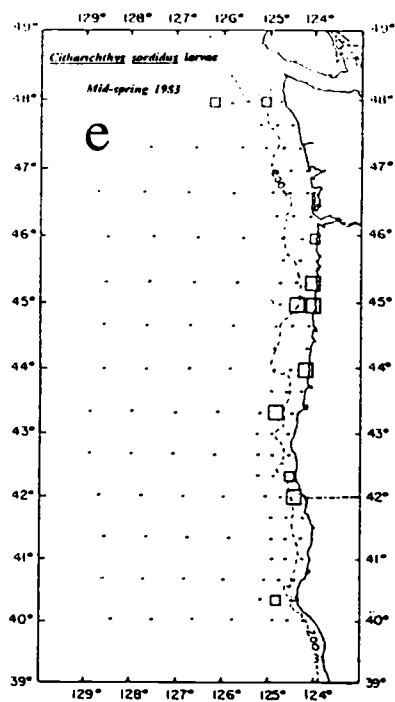


Fig. 30. Distribution of larval abundances of *C. sordidus* off Washington, Oregon and northern California, between 1980 and 1983.



BONGO	NEUSTON
(individuals under 100 m³)	(individuals per 1000 m³)
• 0 (NO CATCHES)	•
□ >0 to <100	◊
□ ≥100 to <500	◊
□ ≥500 to <1000	◊
□ ≥1000 to <2000	◊
□ ≥2000 to <3000	◊
□ ≥3000	◊

Fig. 30 (cont.)

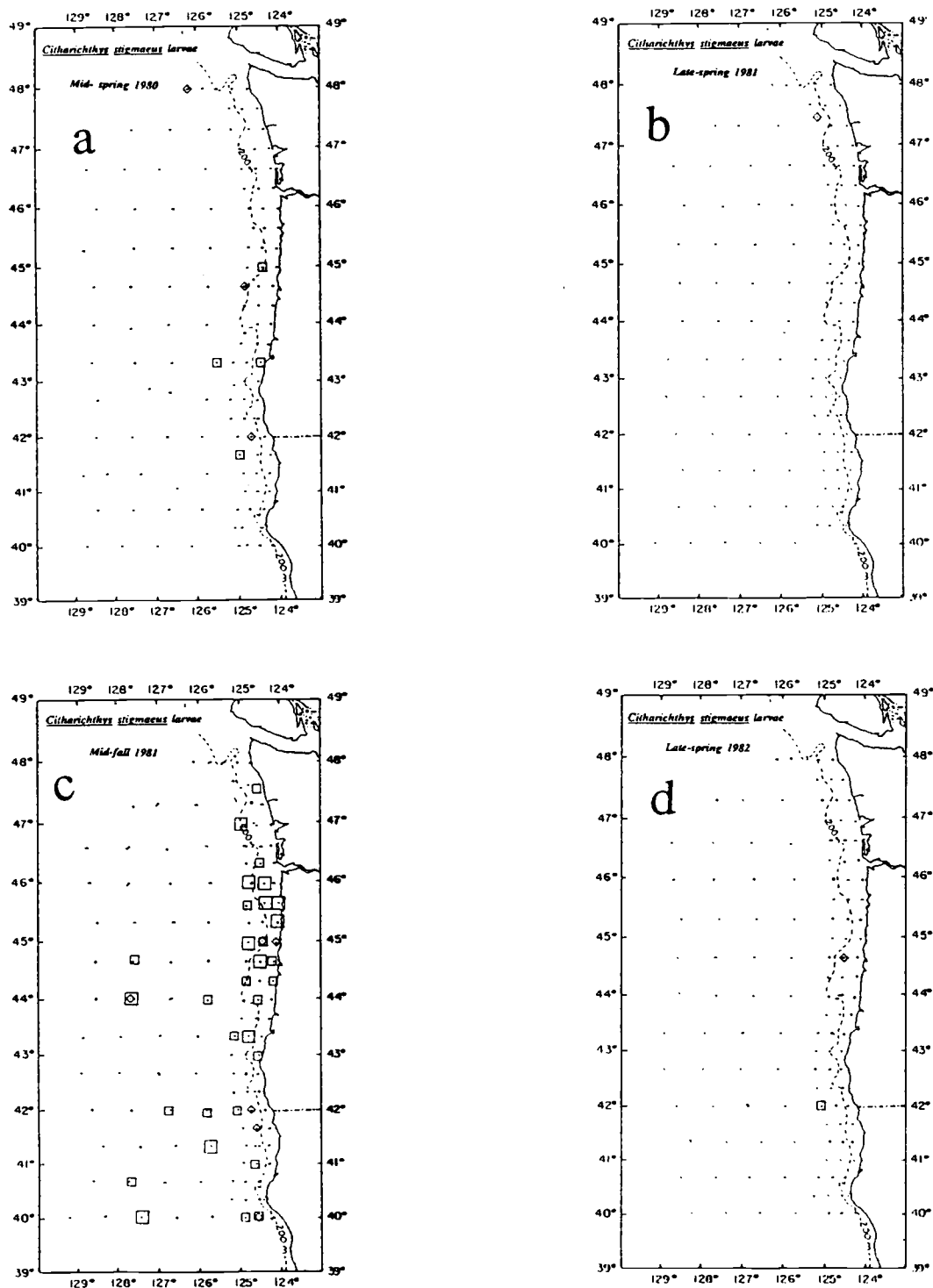
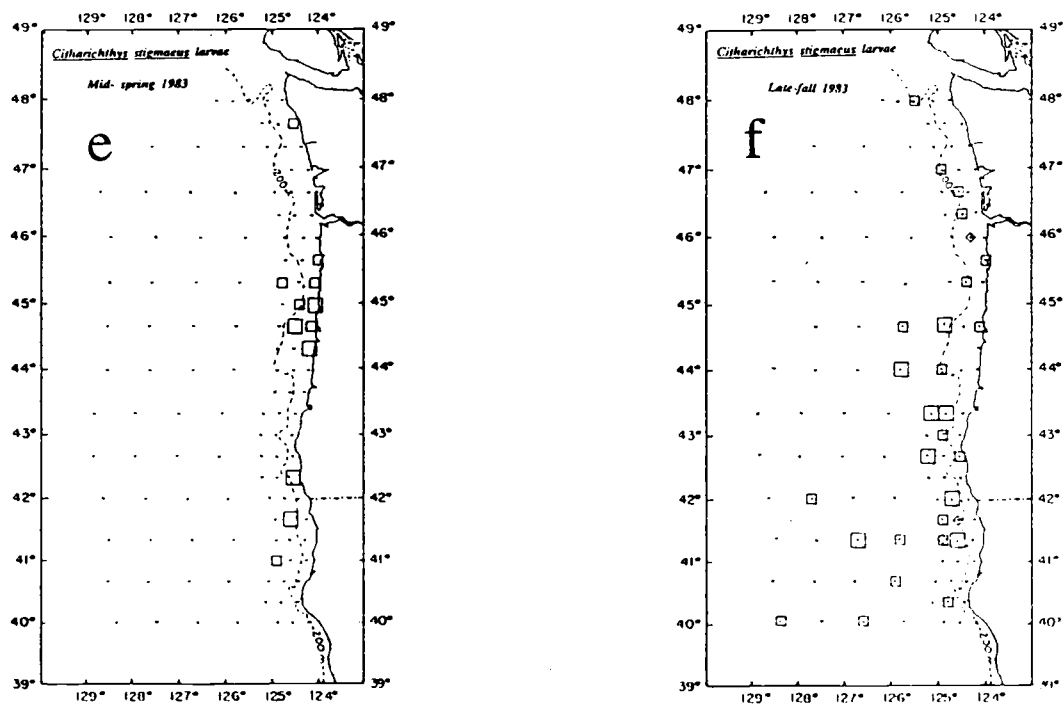


Fig. 31. Distribution of larval abundances of *C. stigmaeus* off Washington, Oregon and northern California, between 1980 and 1983.



BONGO	NEUSTON
(individuals under 100 m ³)	(individuals per 1000 m ³)
• 0 (NO CATCHES)	•
□ >0 to <100	◊
□ ≥100 to <500	◊
□ ≥500 to <1000	◊
□ ≥1000 to <2000	◊
□ ≥2000 to <3000	◊
□ ≥3000	◊

Fig. 31 (cont.)

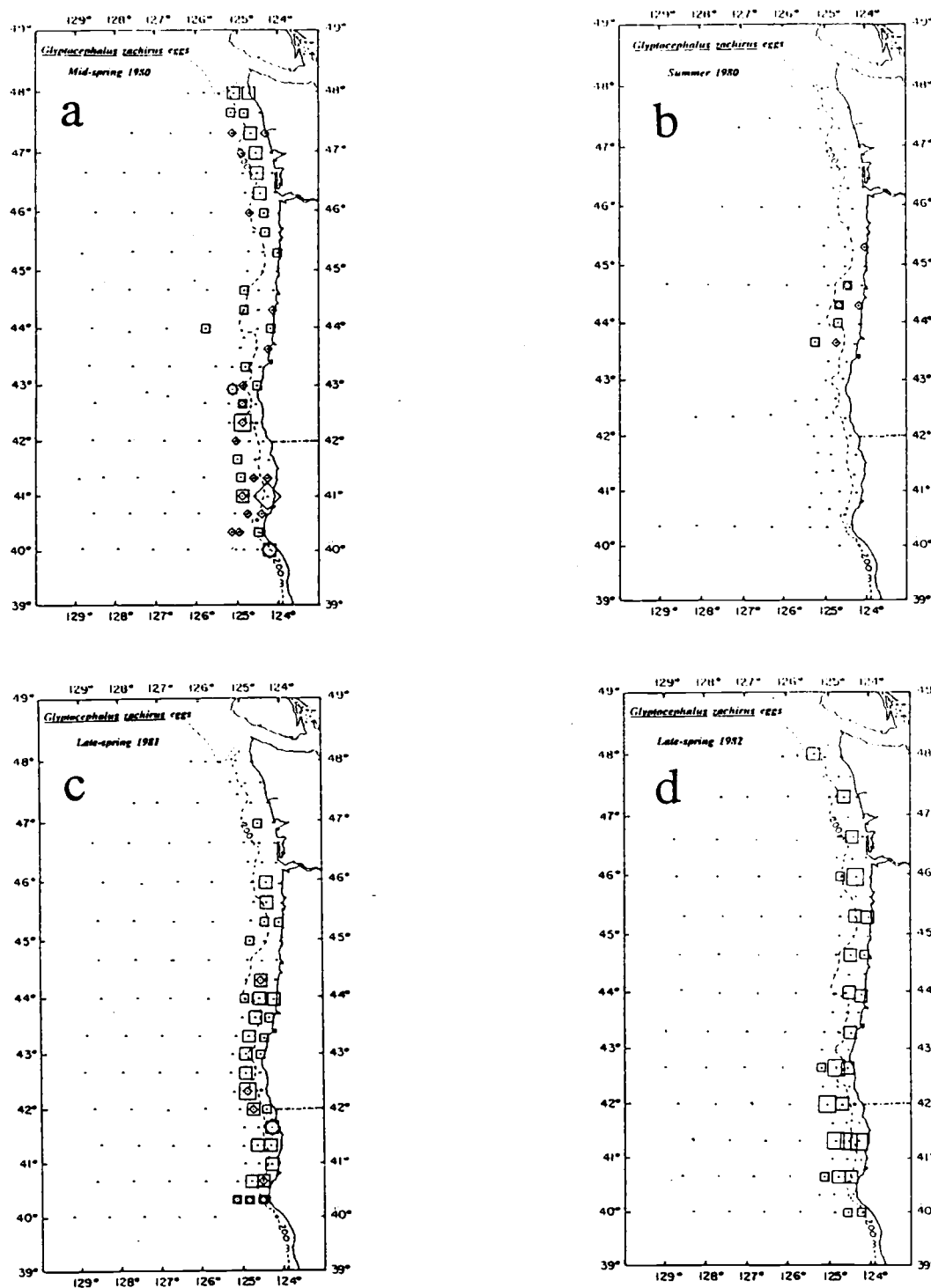


Fig. 32. Distribution of egg abundances of *G. zachirus* off Washington, Oregon and northern California, between 1980 and 1983.

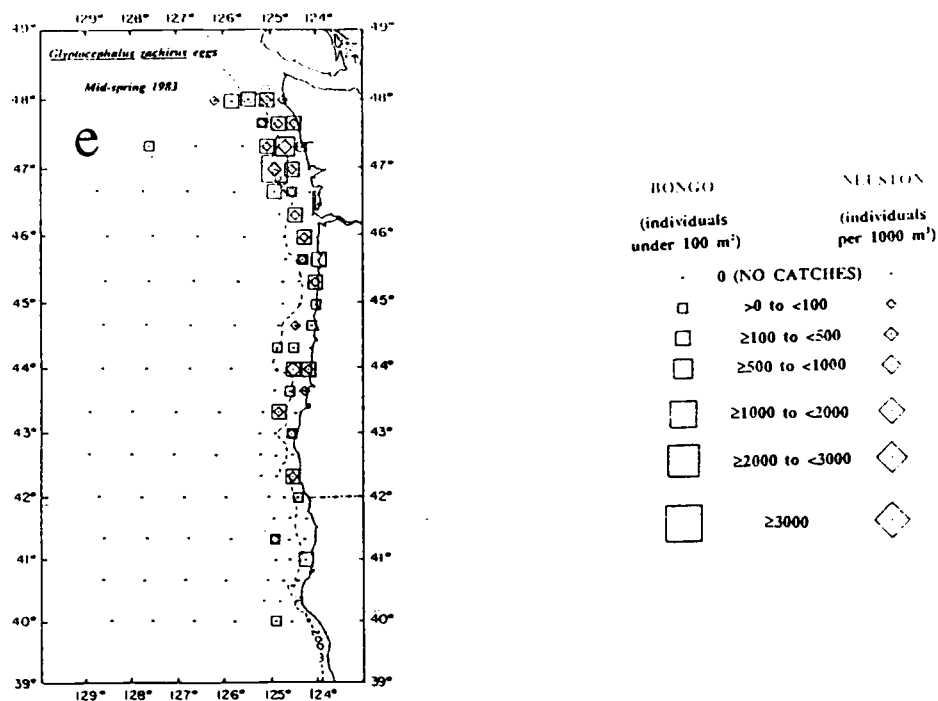


Fig. 32 (cont.)

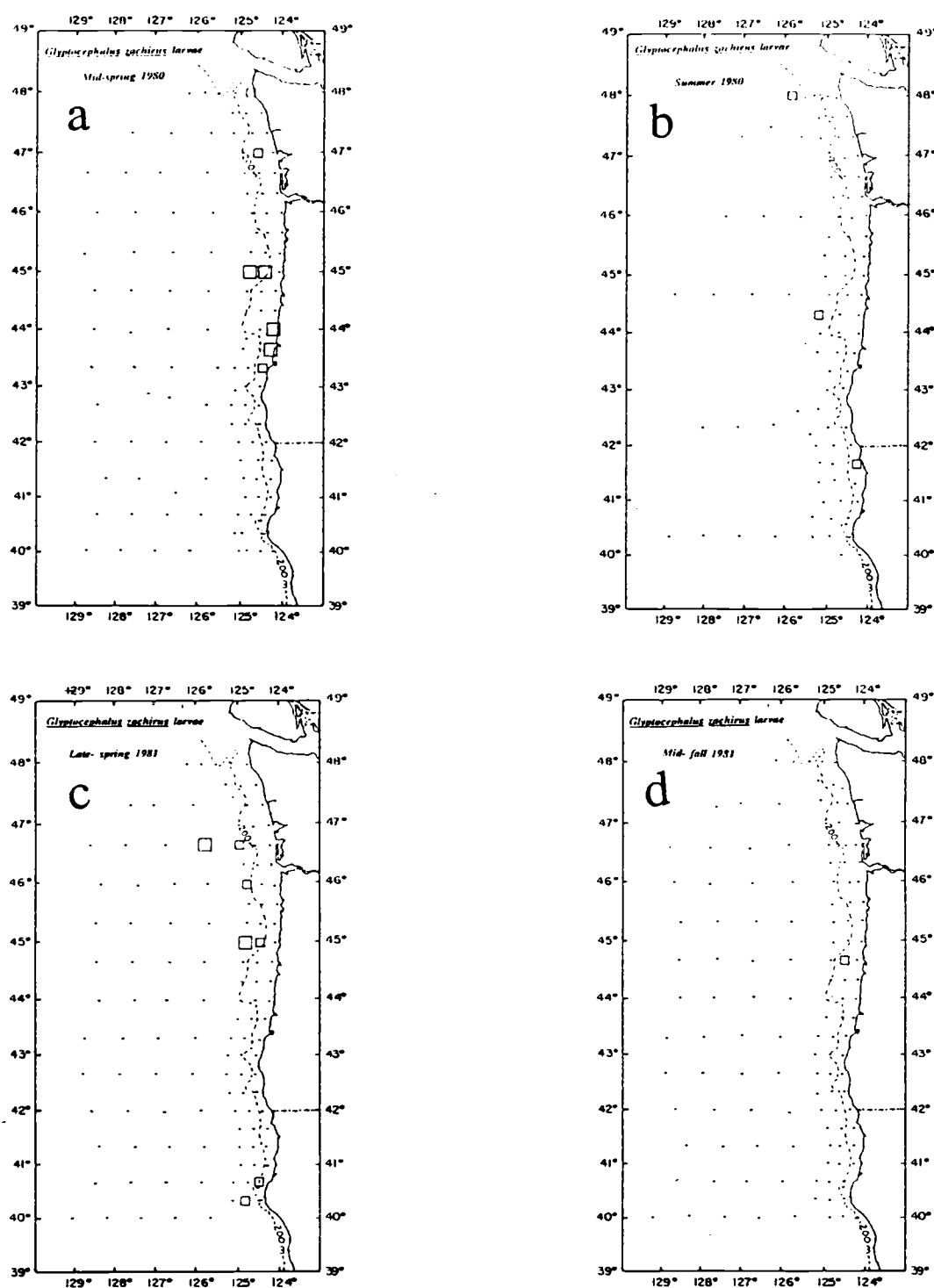


Fig. 33. Distribution of larval abundances of *G. zachirus* off Washington, Oregon and northern California, between 1980 and 1983.

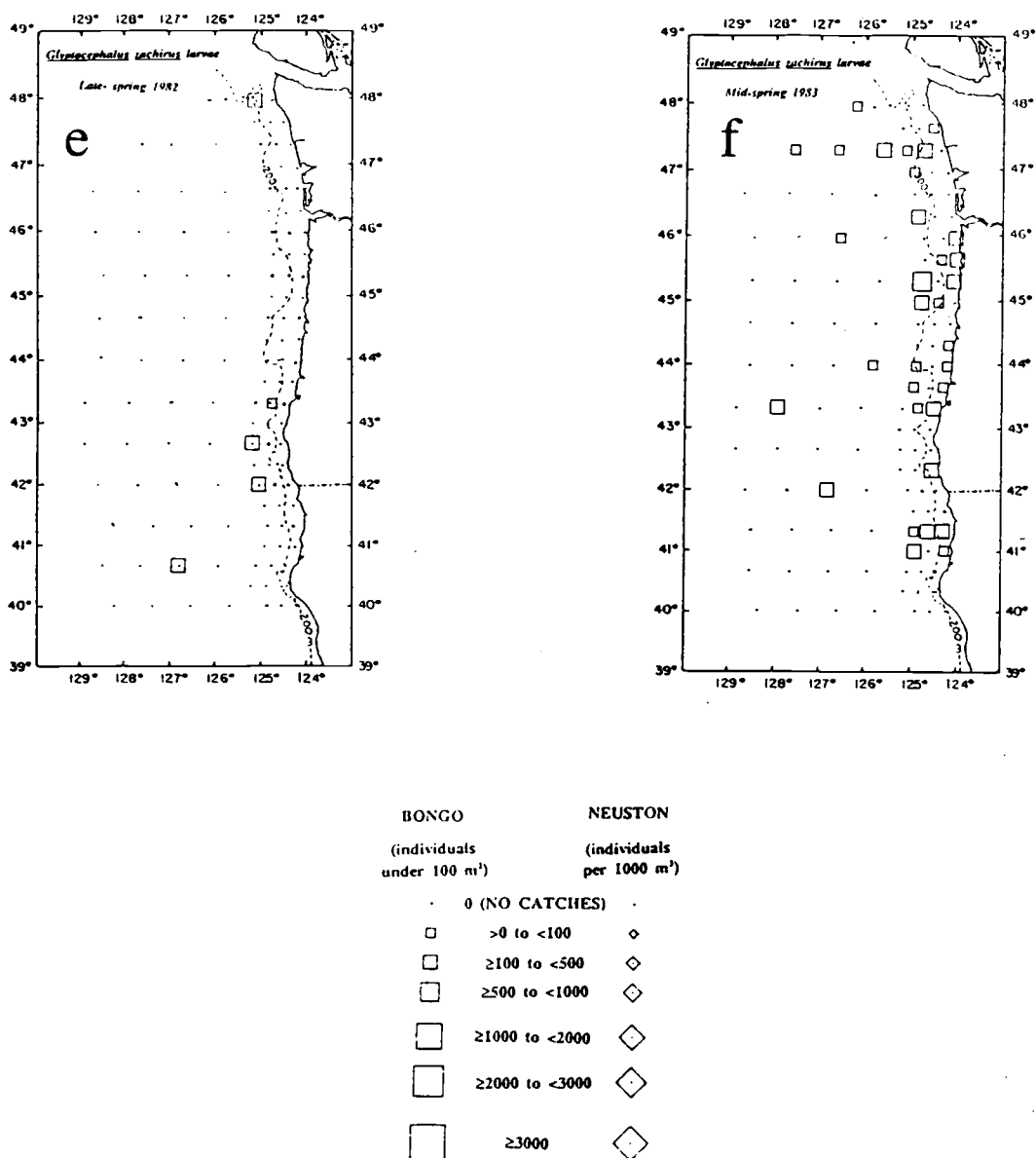


Fig. 33 (cont.)

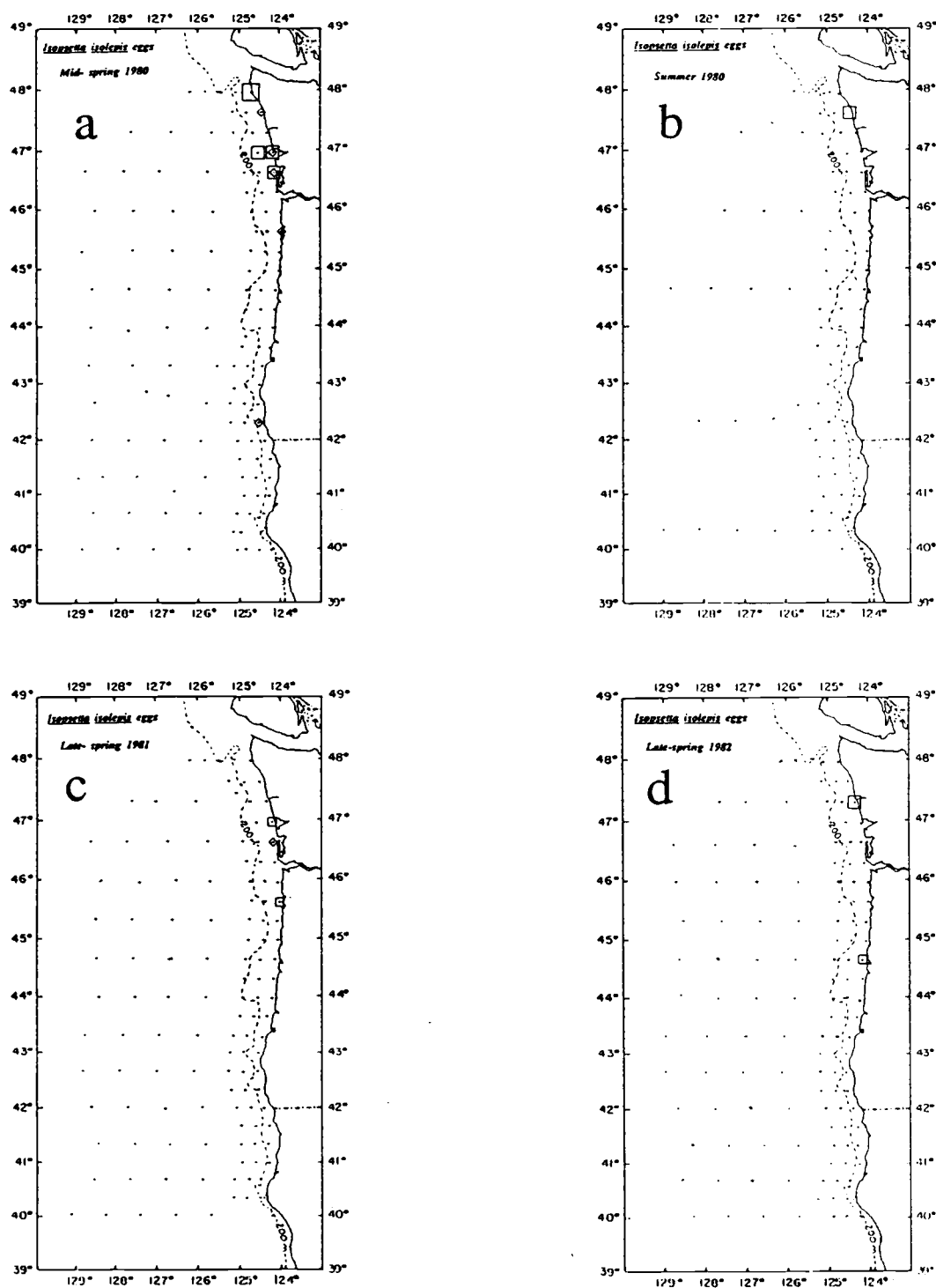
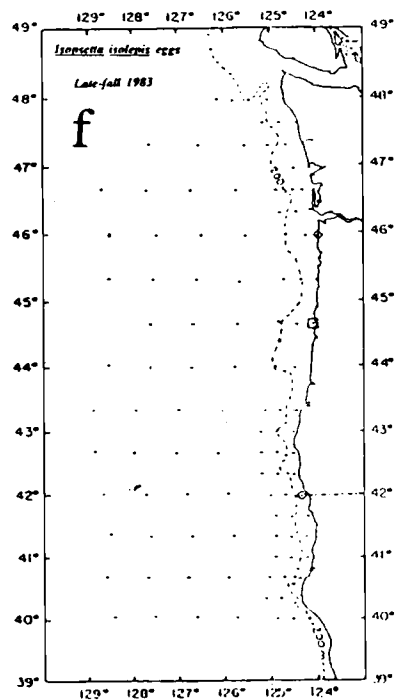
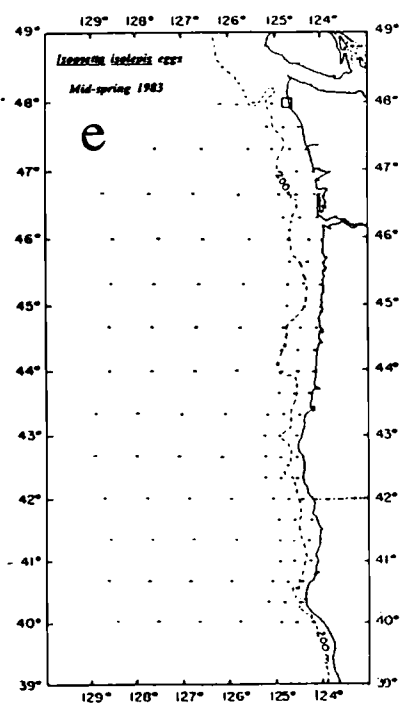


Fig. 34. Distribution of egg abundances of *I. isolepis* off Washington, Oregon and northern California, between 1980 and 1983.



BONGO (individuals under 100 m ²)	NEUSTON (individuals per 1000 m ³)
• 0 (NO CATCHES)	•
□ >0 to <100	◇
□ ≥100 to <500	◇
□ ≥500 to <1000	◇
□ ≥1000 to <2000	◇
□ ≥2000 to <3000	◇
□ ≥3000	◇

Fig. 34 (cont.)

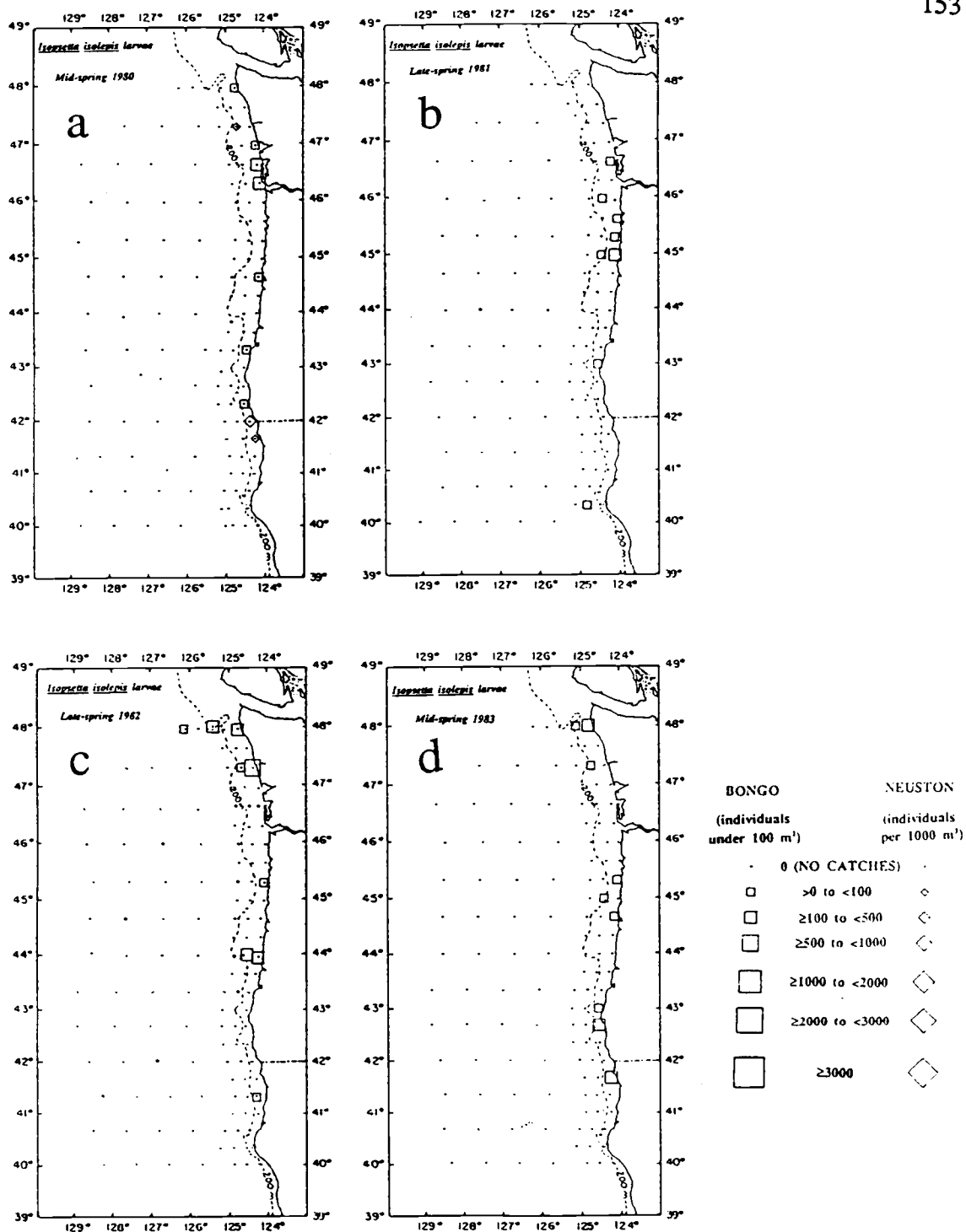


Fig. 35. Distribution of larval abundances of *I. isolepis* off Washington, Oregon and northern California, between 1980 and 1983.

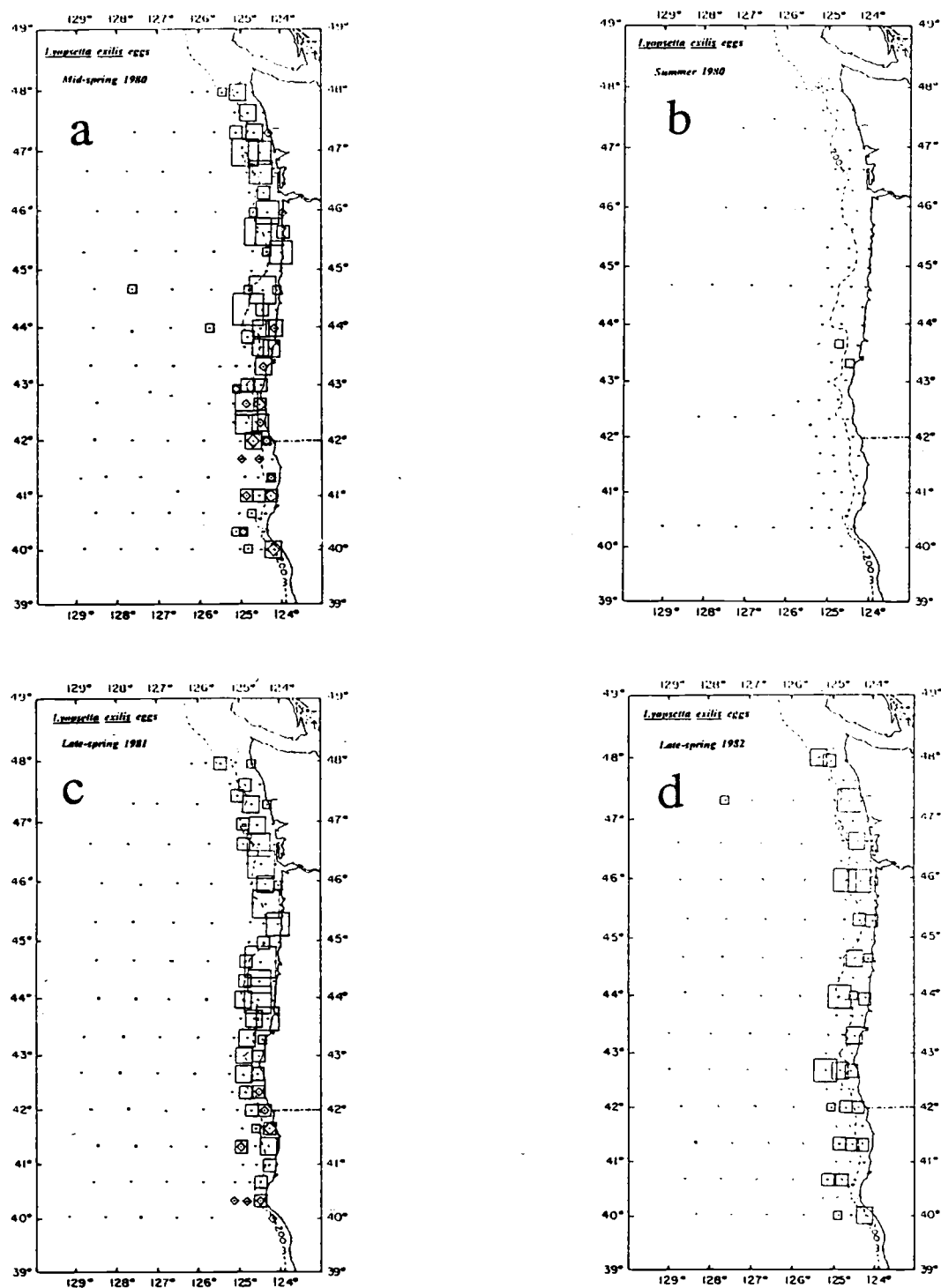


Fig. 36. Distribution of egg abundances of *L. exilis* off Washington, Oregon and northern California, between 1980 and 1983.

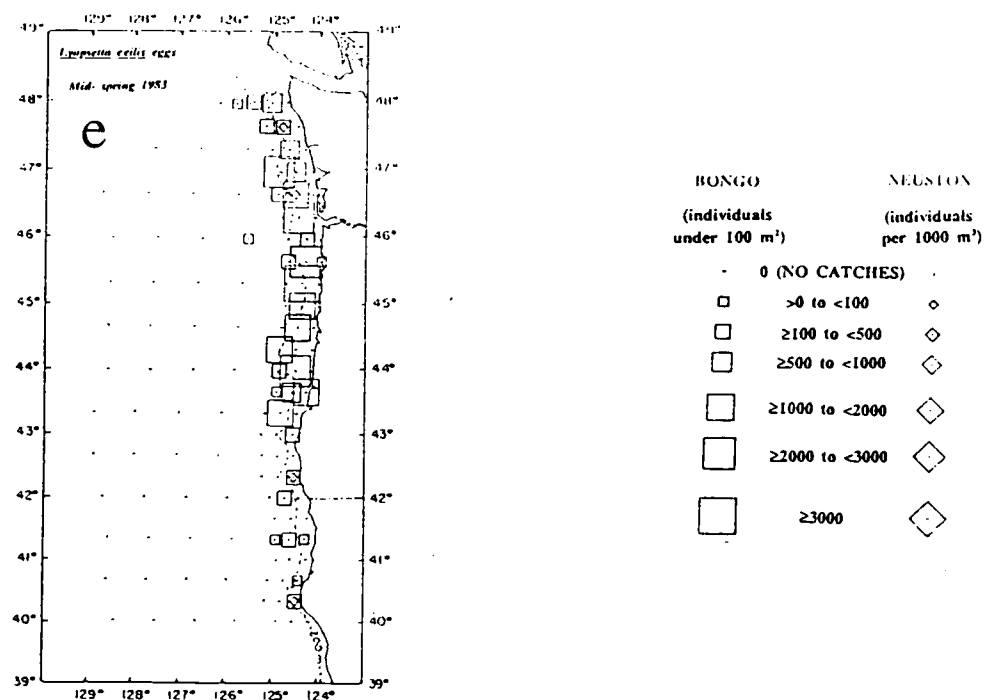


Fig. 36 (cont.)

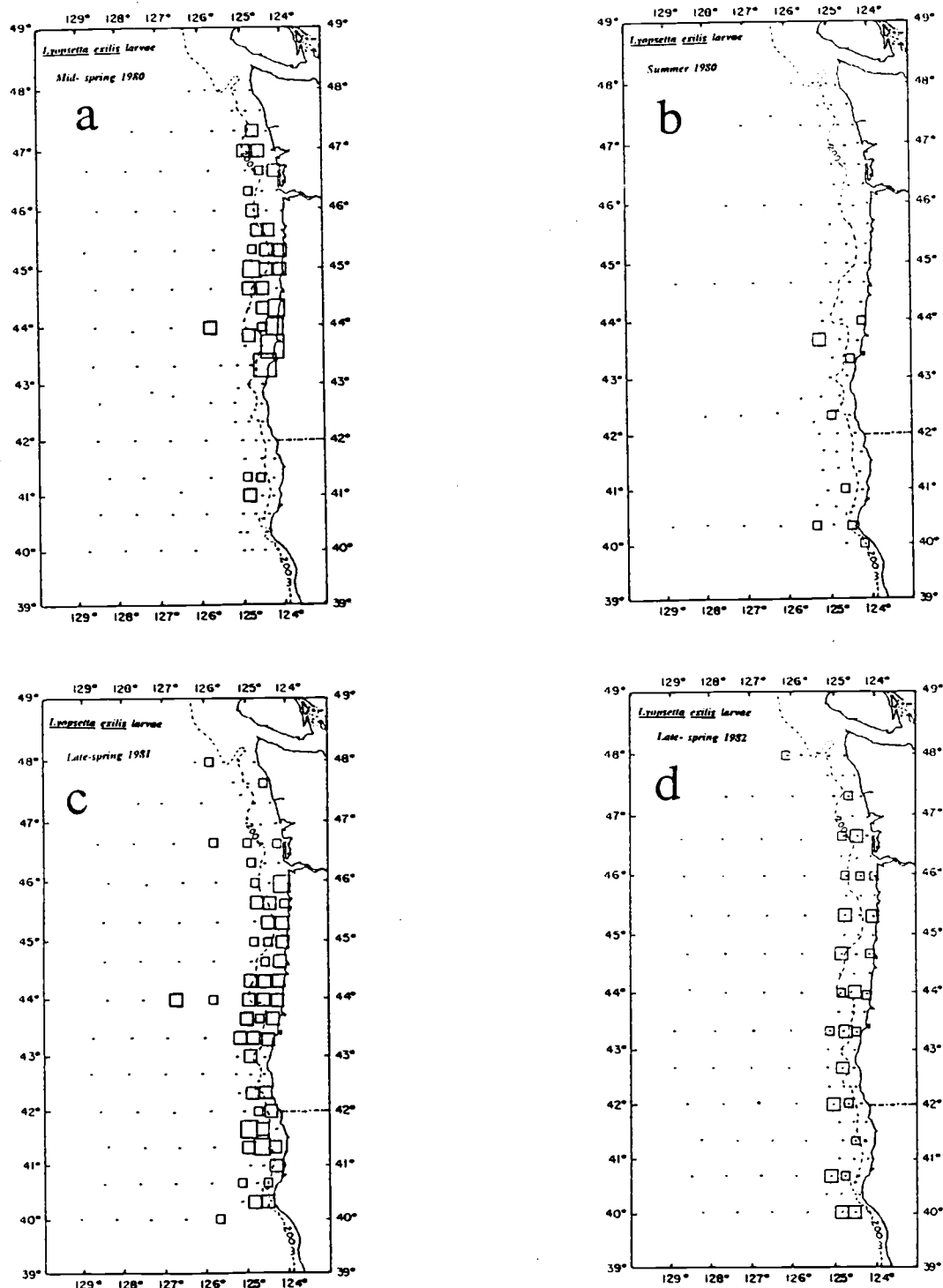


Fig. 37. Distribution of larval abundances of *L. exilis* off Washington, Oregon and northern California, between 1980 and 1983.

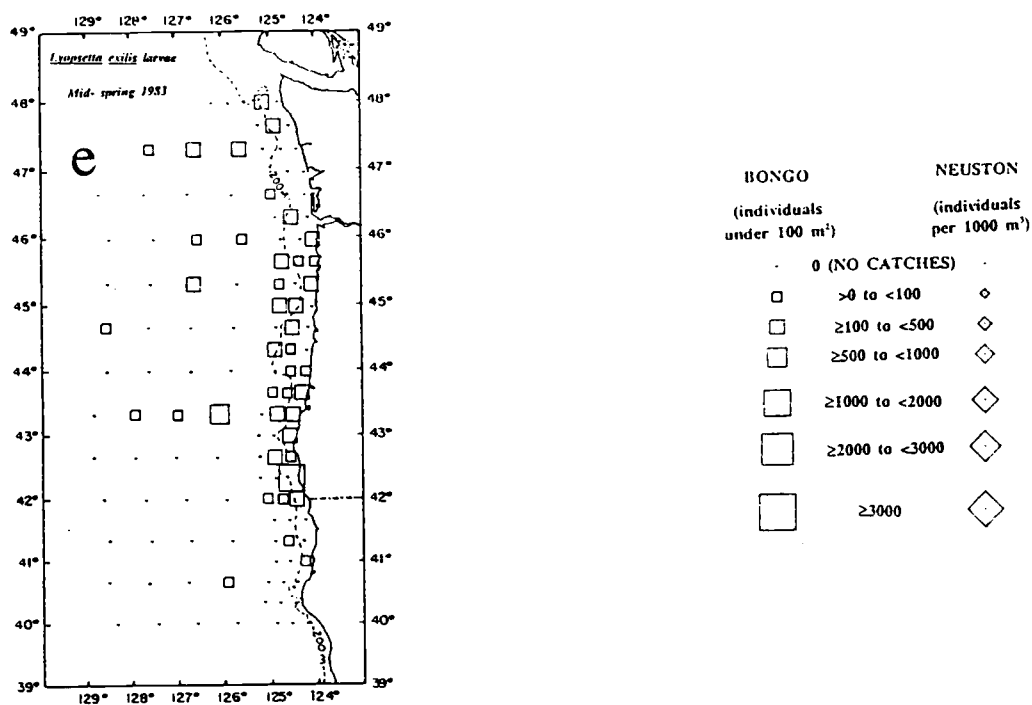


Fig. 37 (cont.)

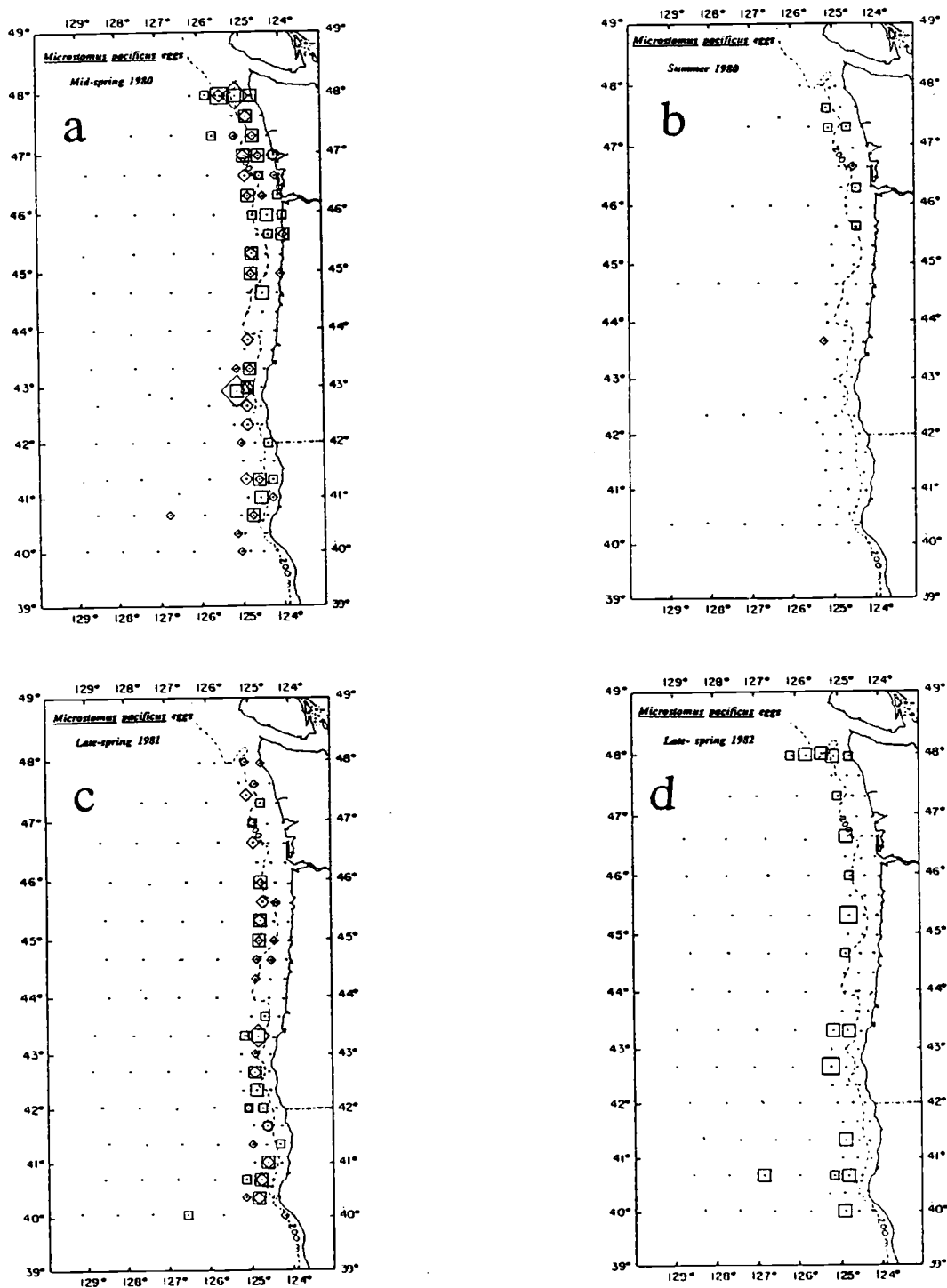


Fig. 38. Distribution of egg abundances of *M. pacificus* off Washington, Oregon and northern California, between 1980 and 1983.

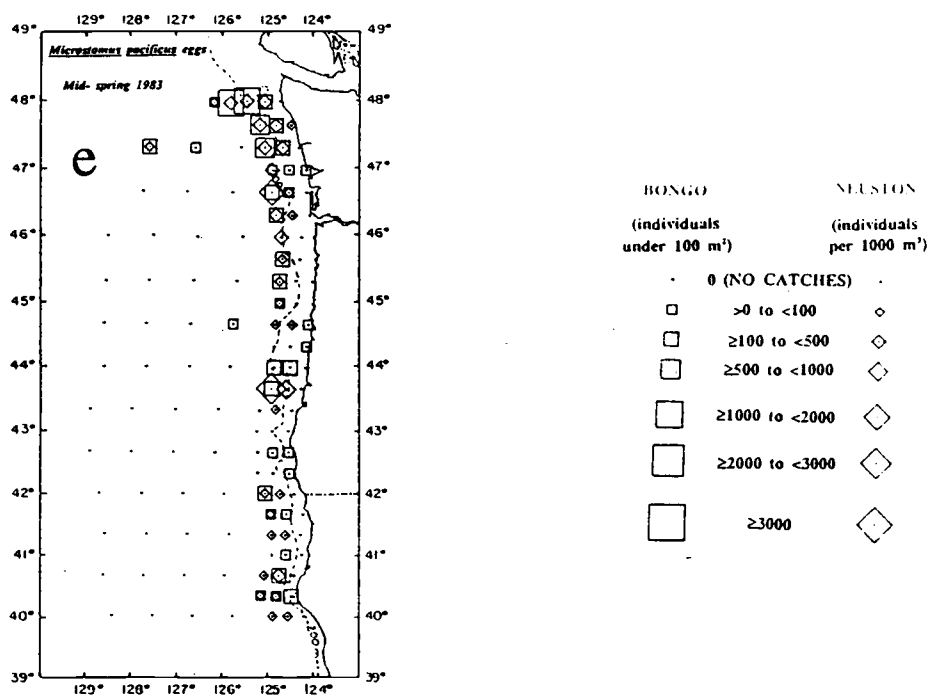


Fig. 38 (cont.)

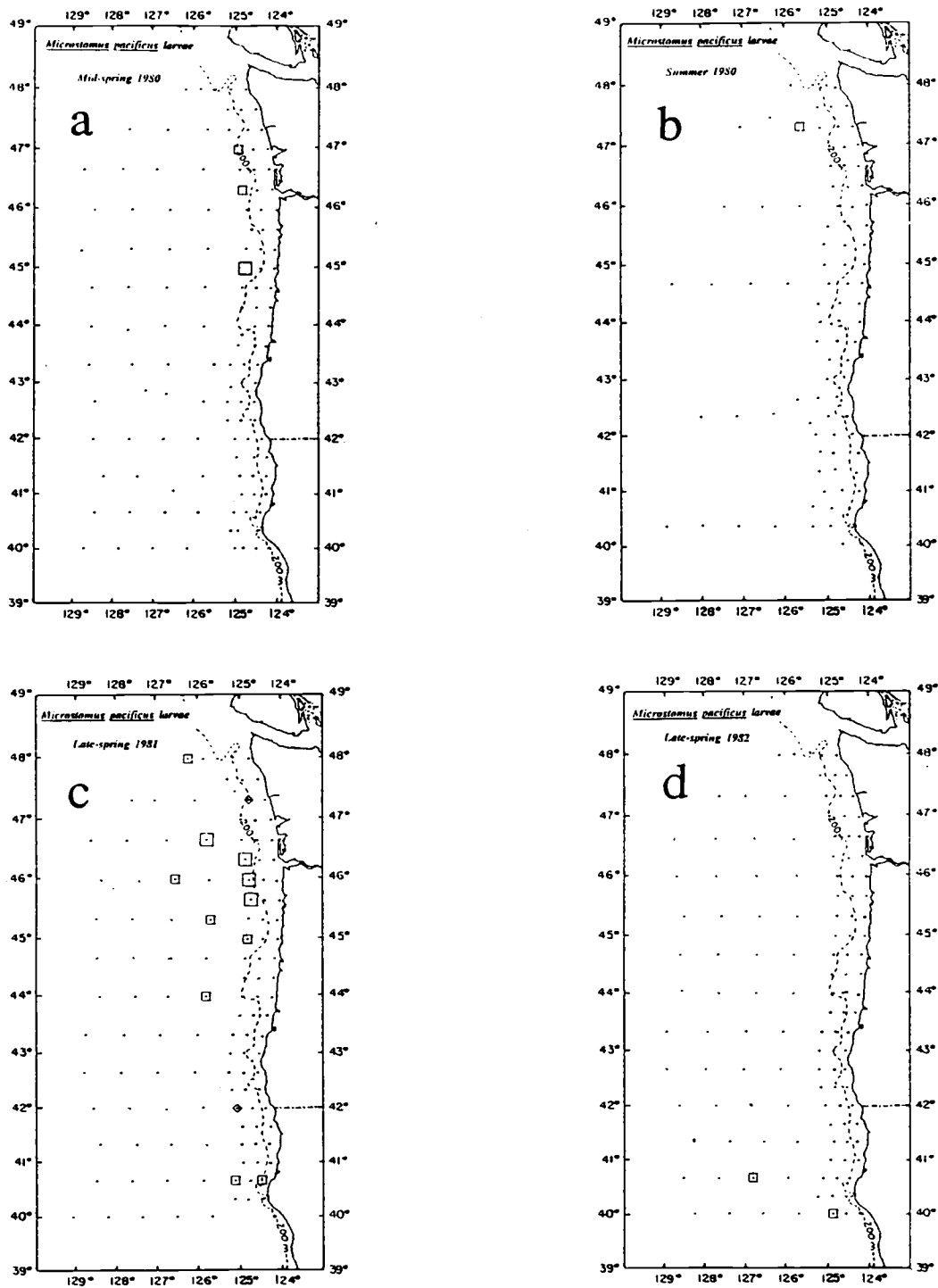


Fig. 39. Distribution of larval abundances of *M. pacificus* off Washington, Oregon and northern California, between 1980 and 1983.

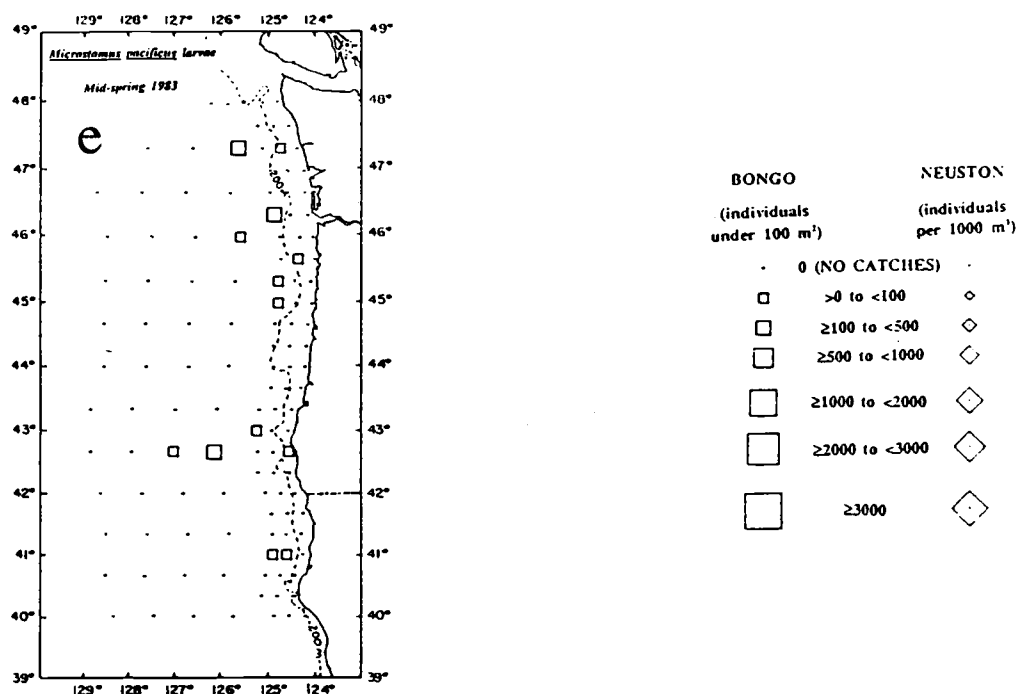


Fig. 39 (cont.)

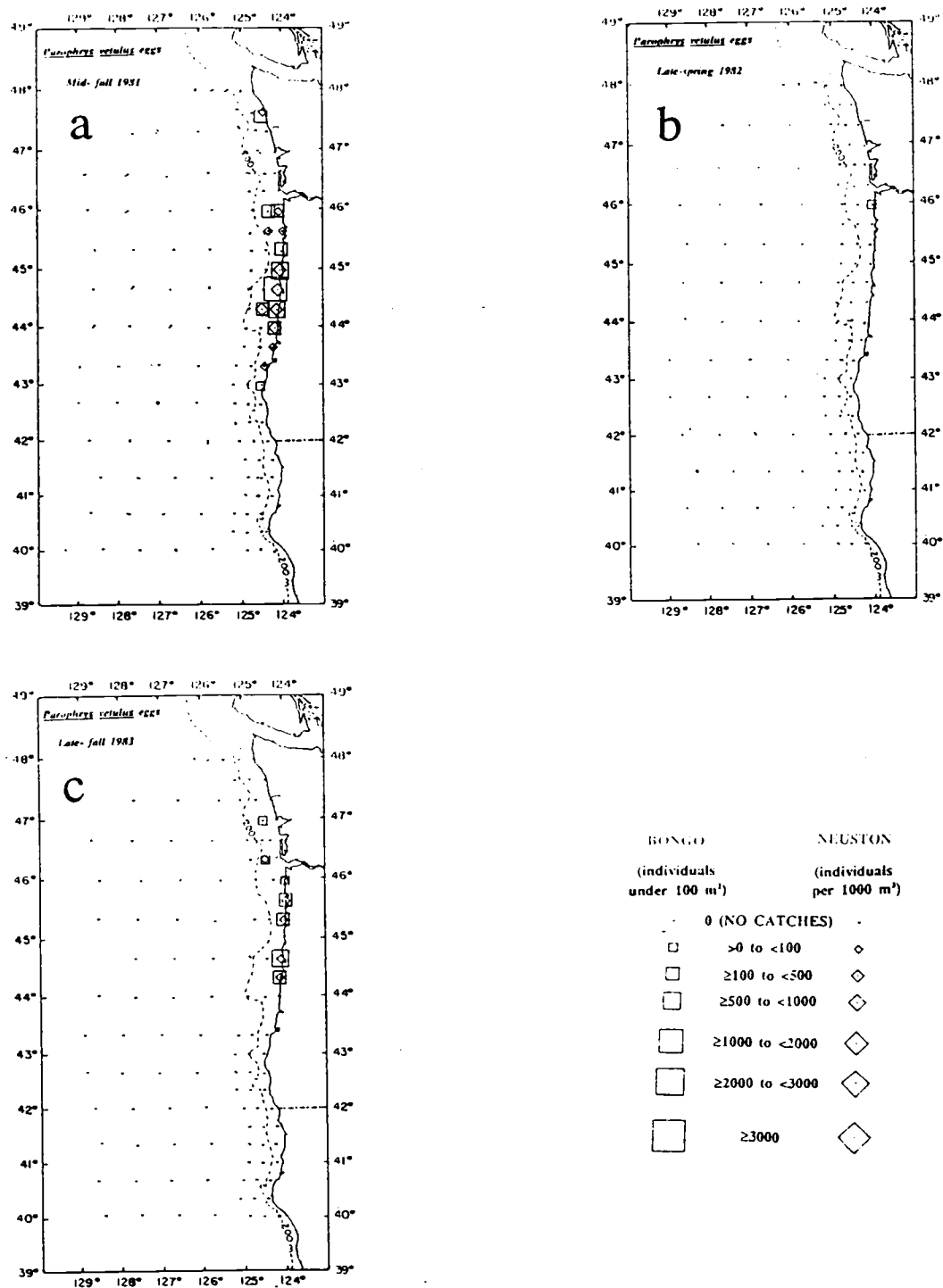


Fig. 40. Distribution of egg abundances of *P. vetulus* off Washington, Oregon and northern California, between 1980 and 1983.

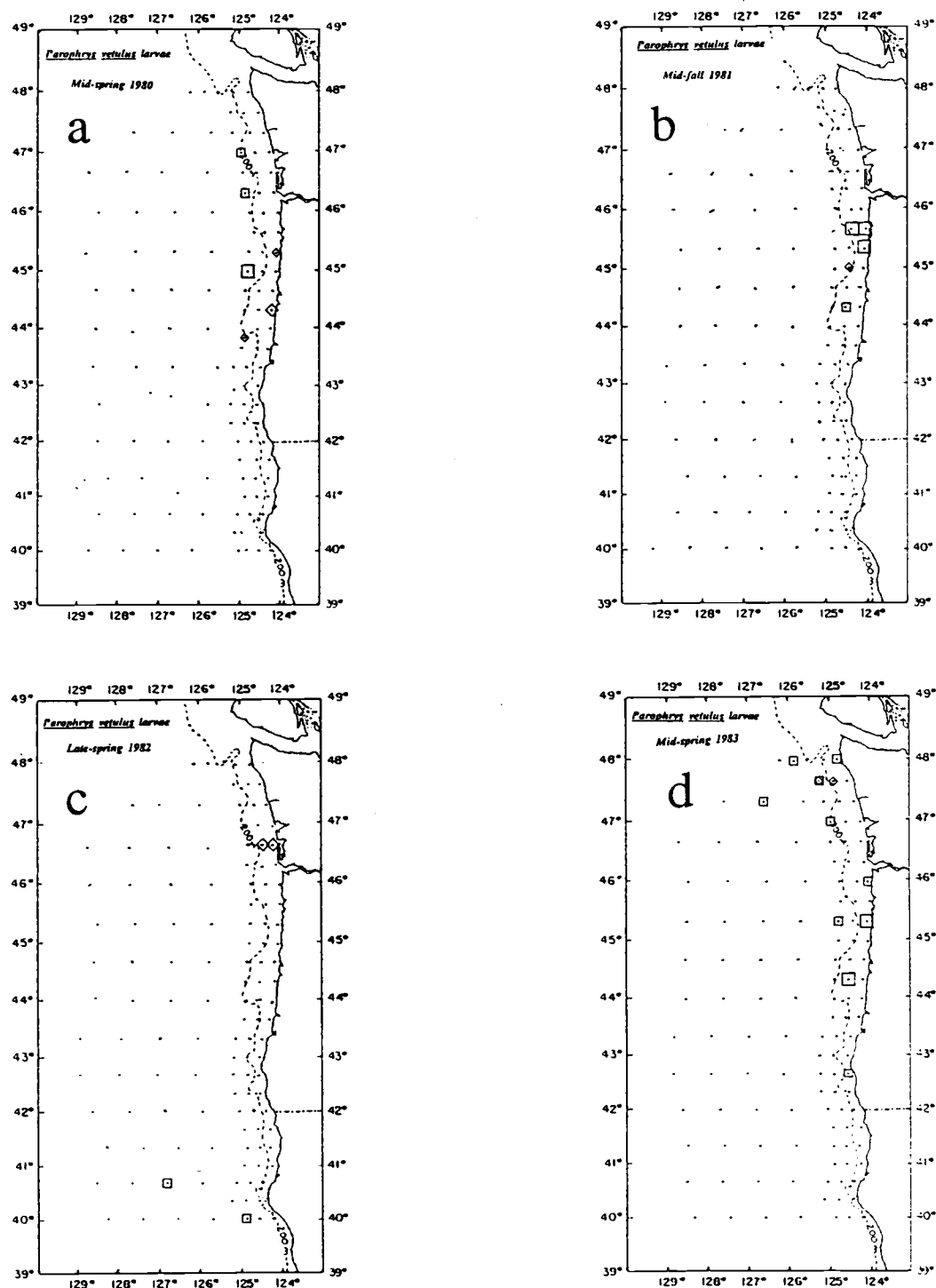


Fig. 41. Distribution of larval abundances of *P. vetulus* off Washington, Oregon and northern California, between 1980 and 1983.

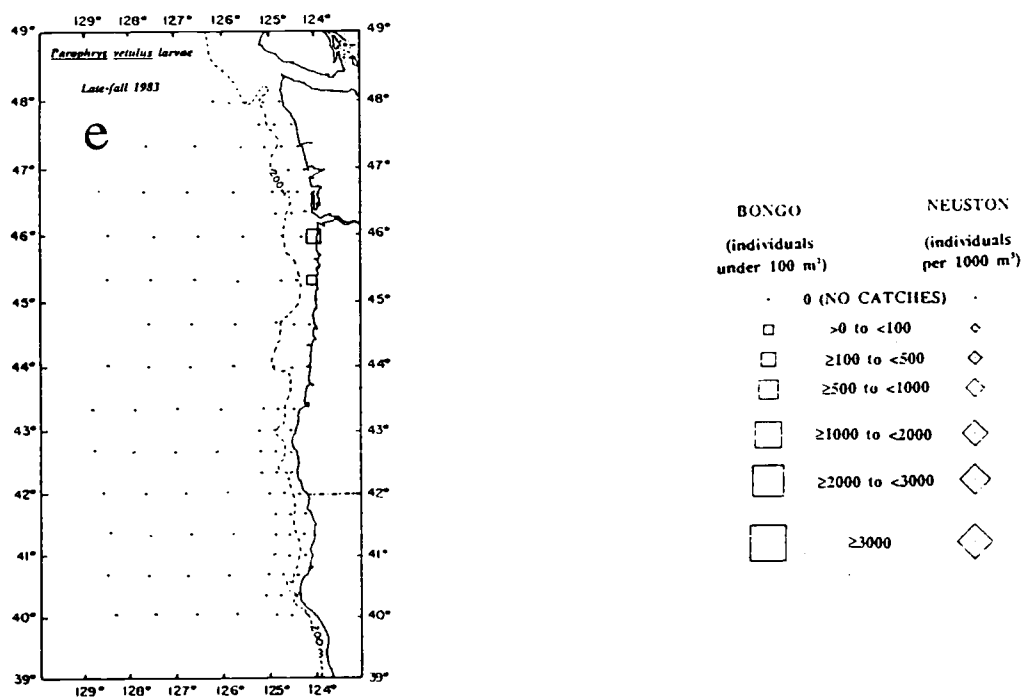


Fig. 41 (cont.)

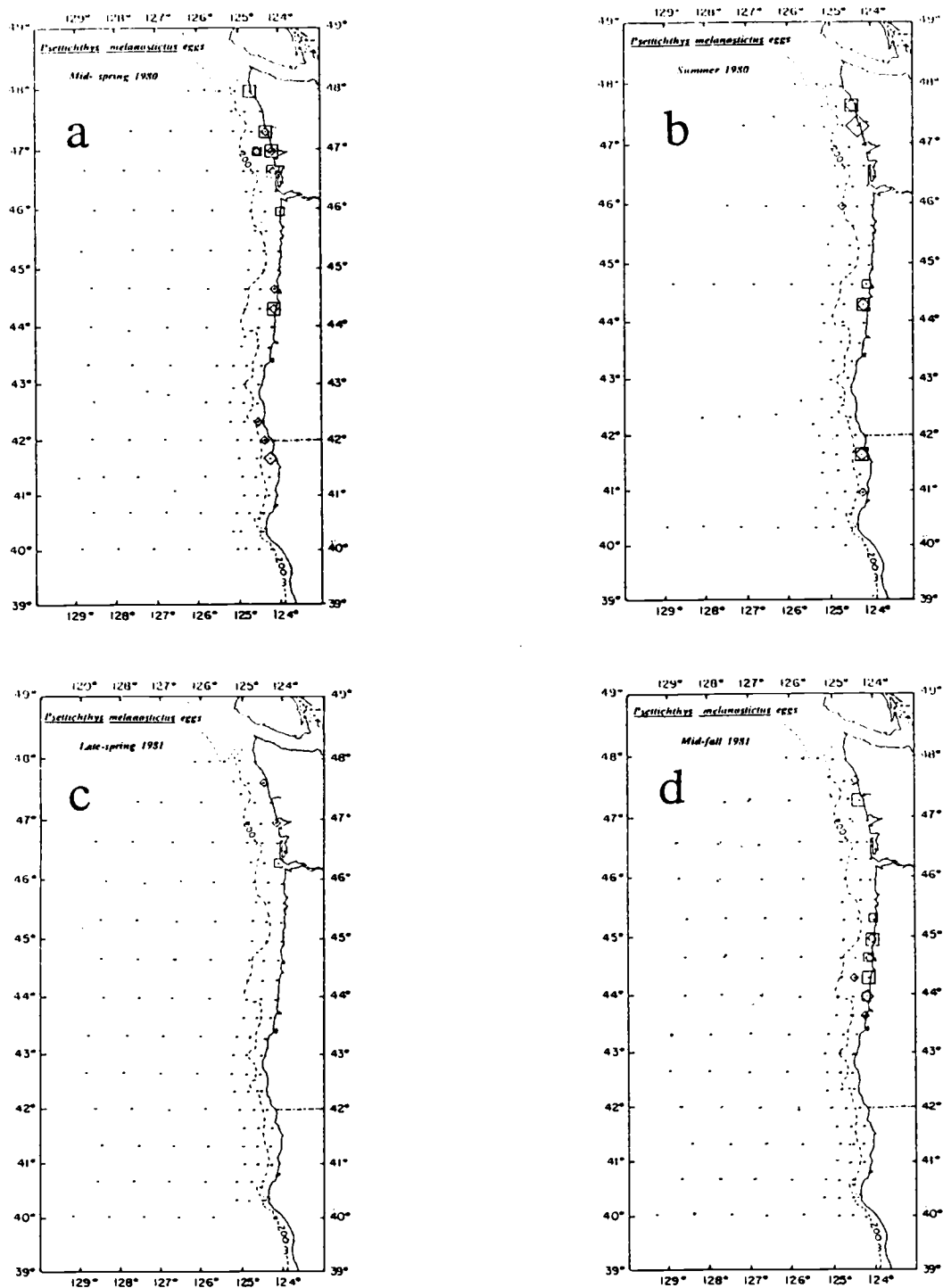


Fig. 42. Distribution of egg abundances of *P. melanostictus* off Washington, Oregon and northern California, between 1980 and 1983.

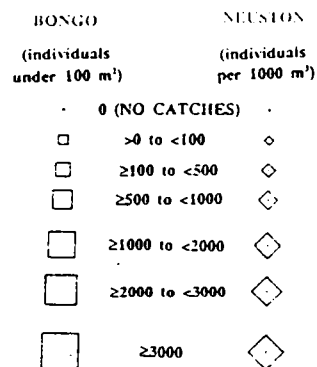
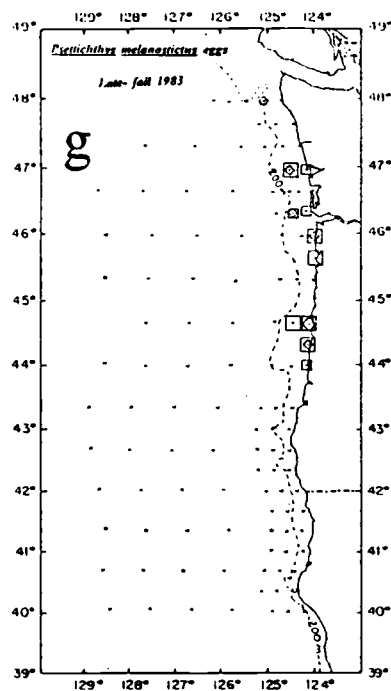
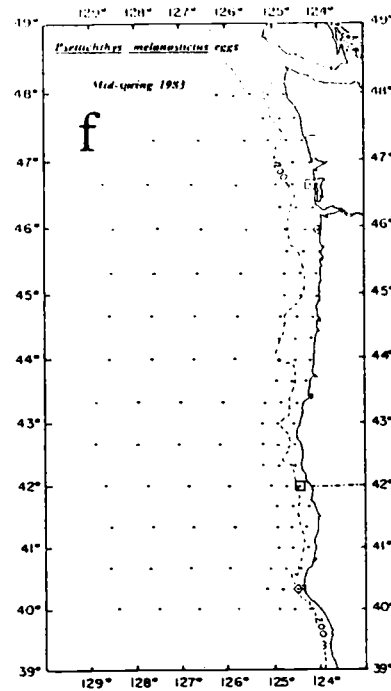
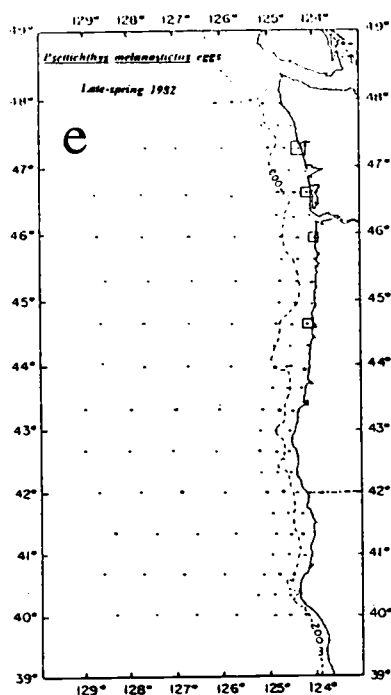


Fig. 42 (cont.)

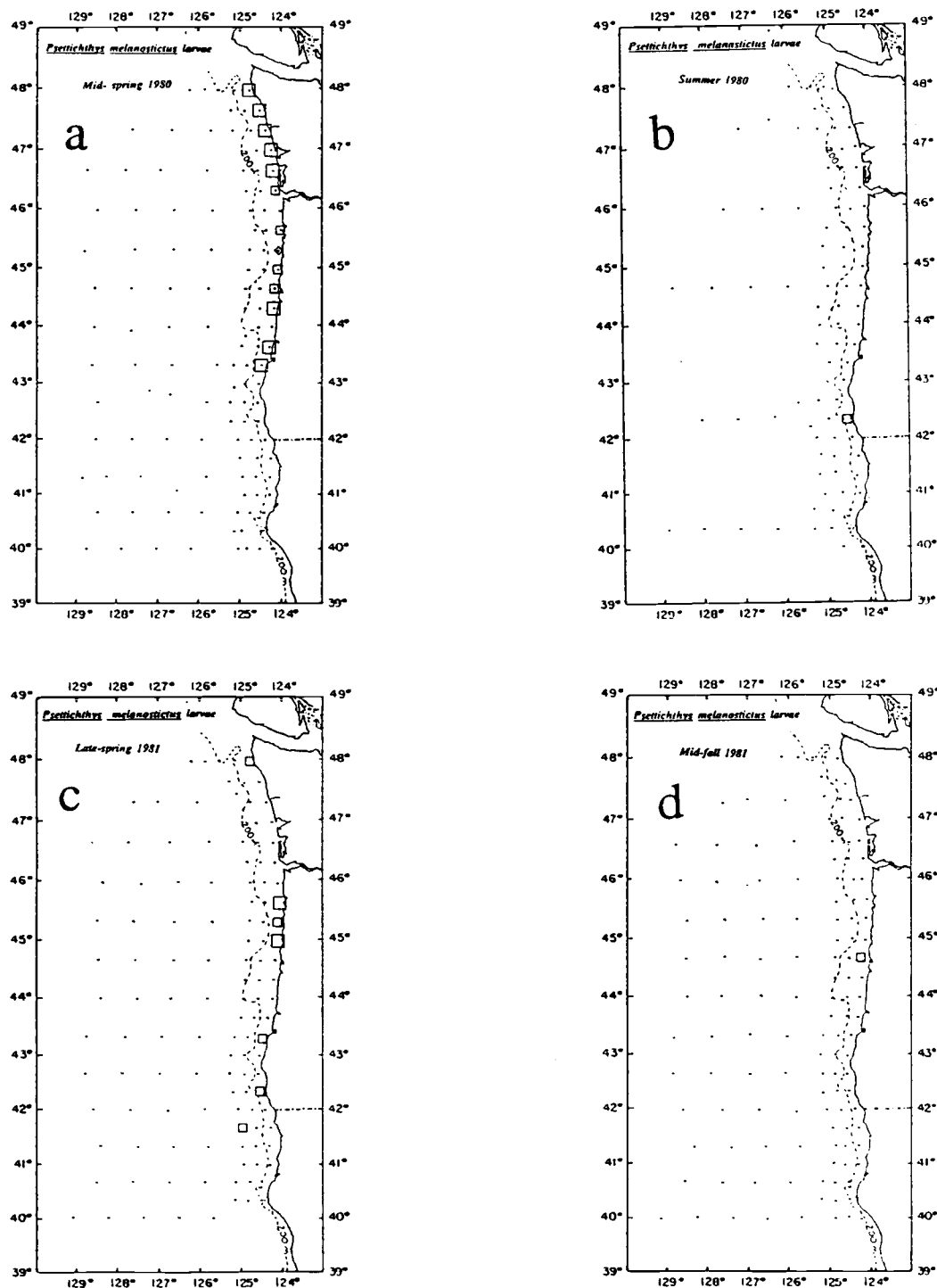


Fig. 43. Distribution of larval abundances of *P. melanostictus* off Washington, Oregon and northern California, between 1980 and 1983.

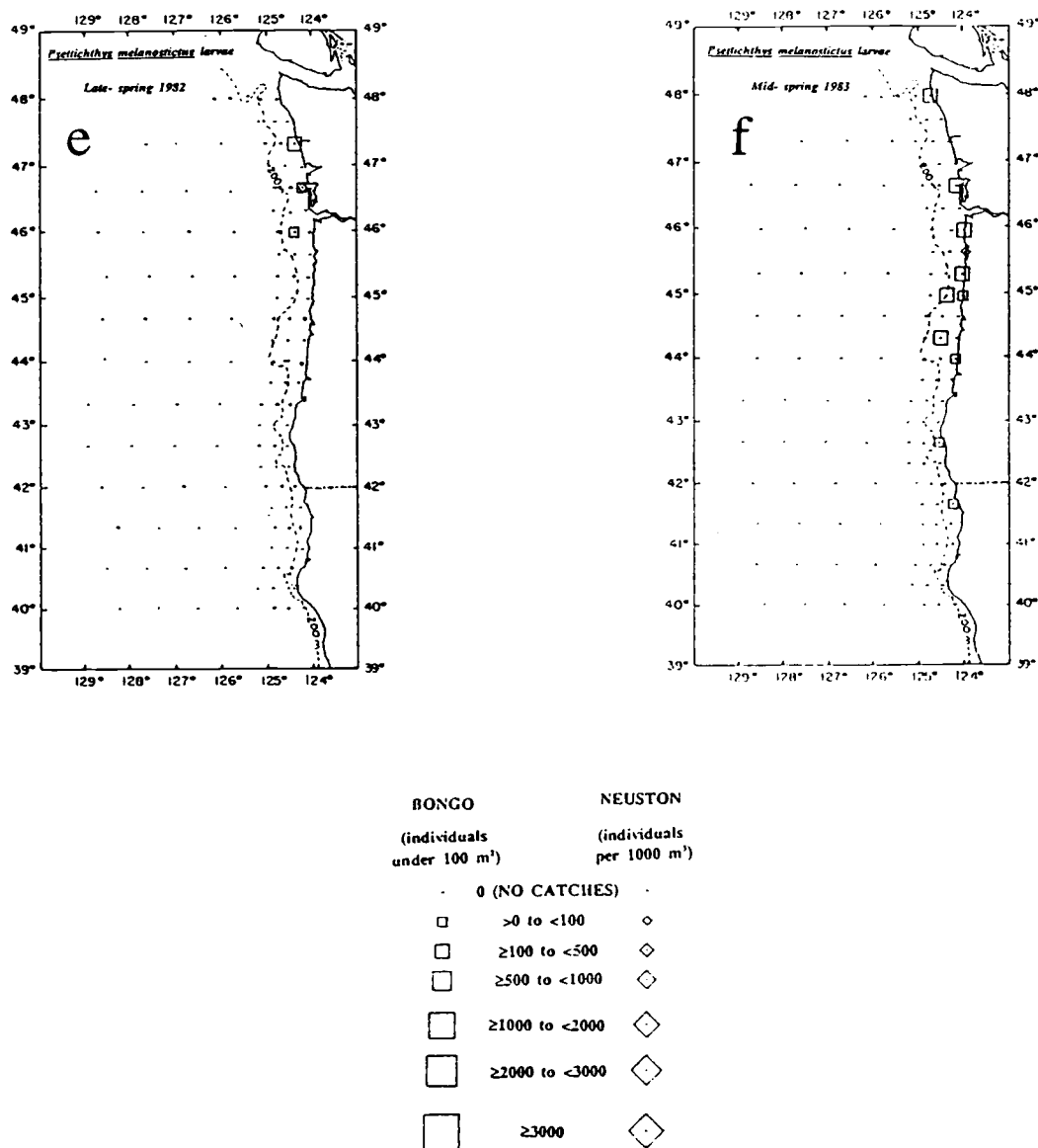
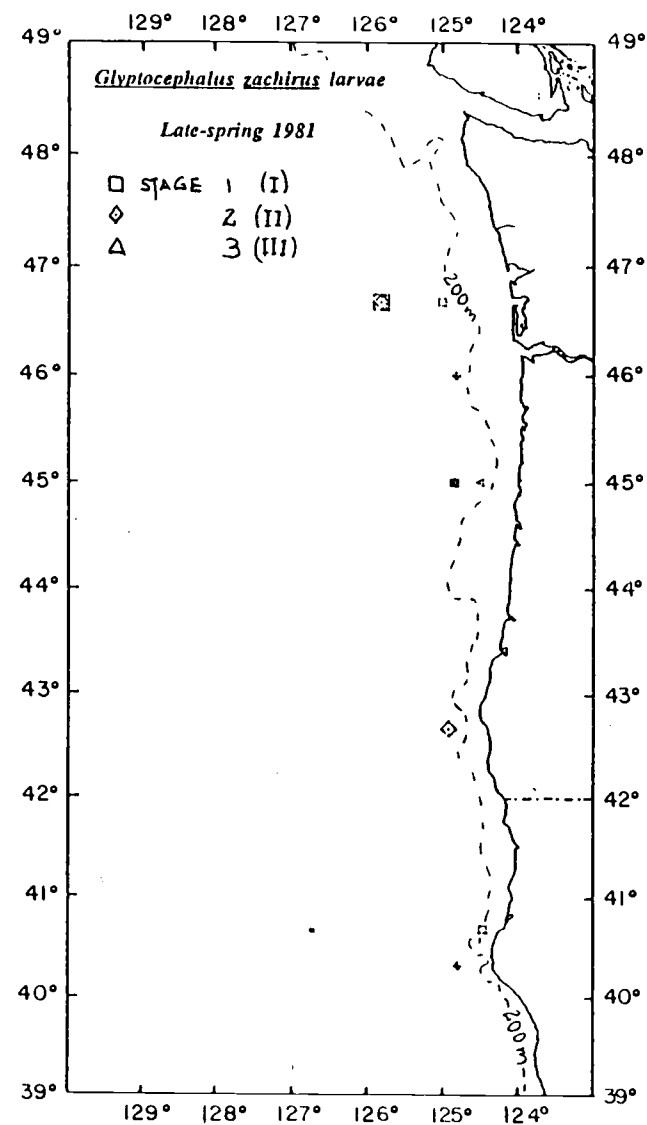
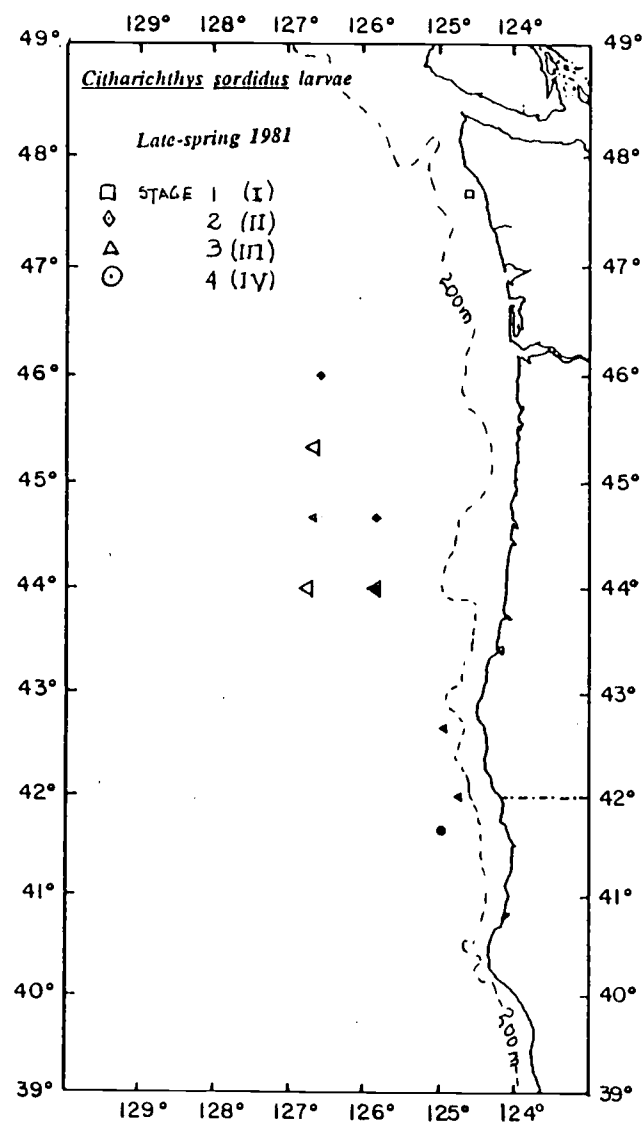


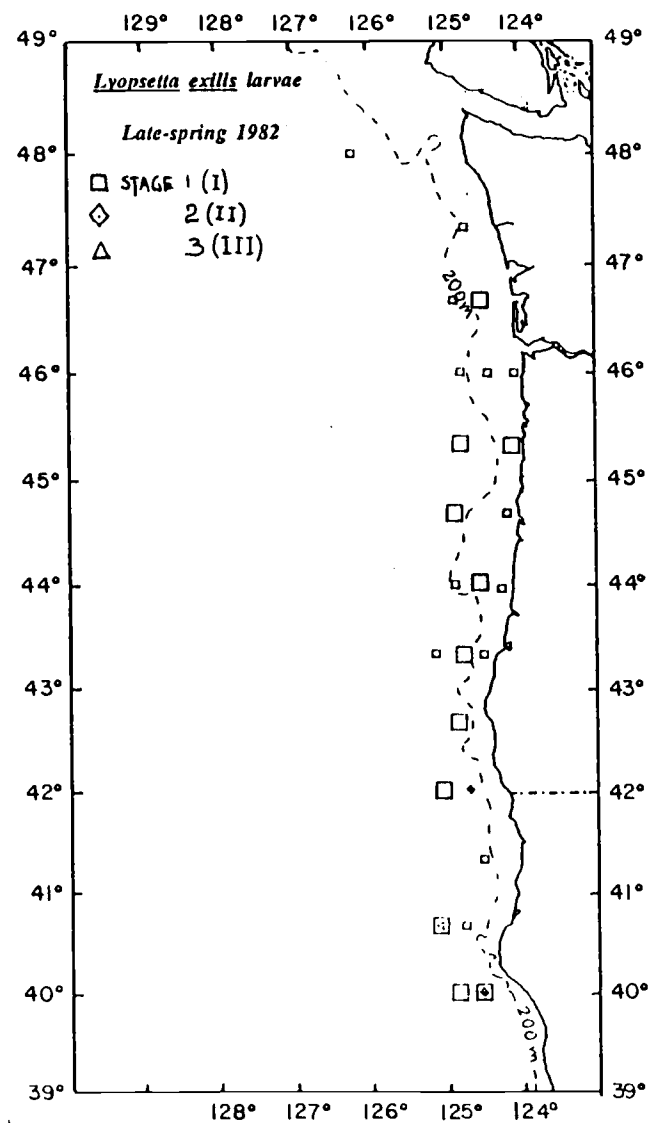
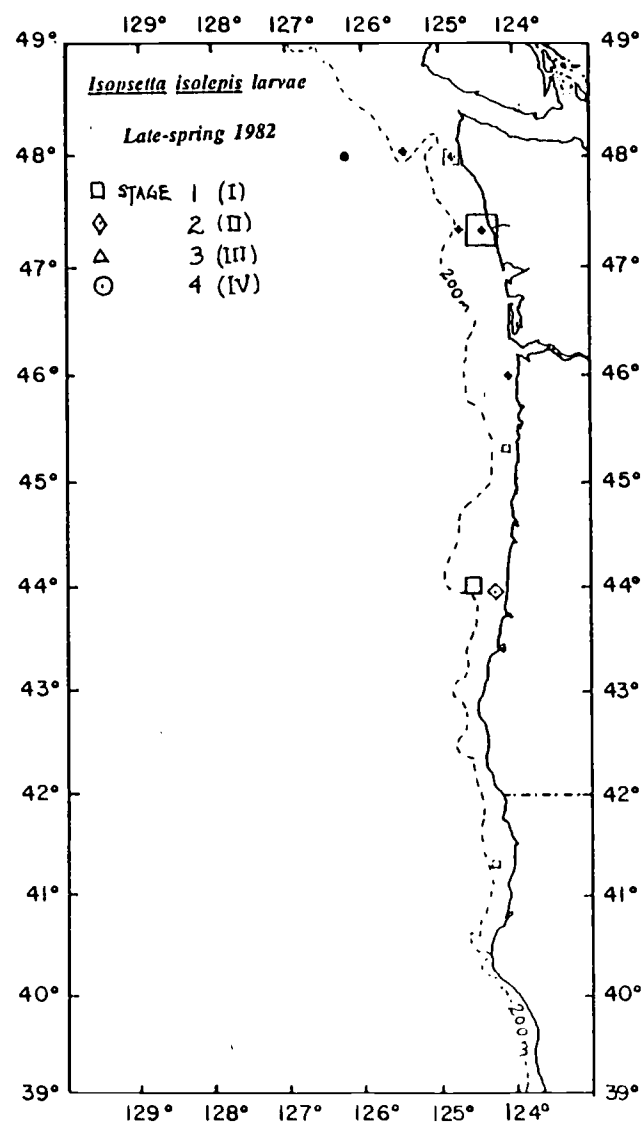
Fig. 43 (cont.)

Fig. 44. Distribution of larval abundances by stage of some flatfishes off the Washington, Oregon and northern California coasts during: (a) late-spring 1981; (b) late-spring 1982; (c) mid-fall 1981; (d) late-fall 1983.



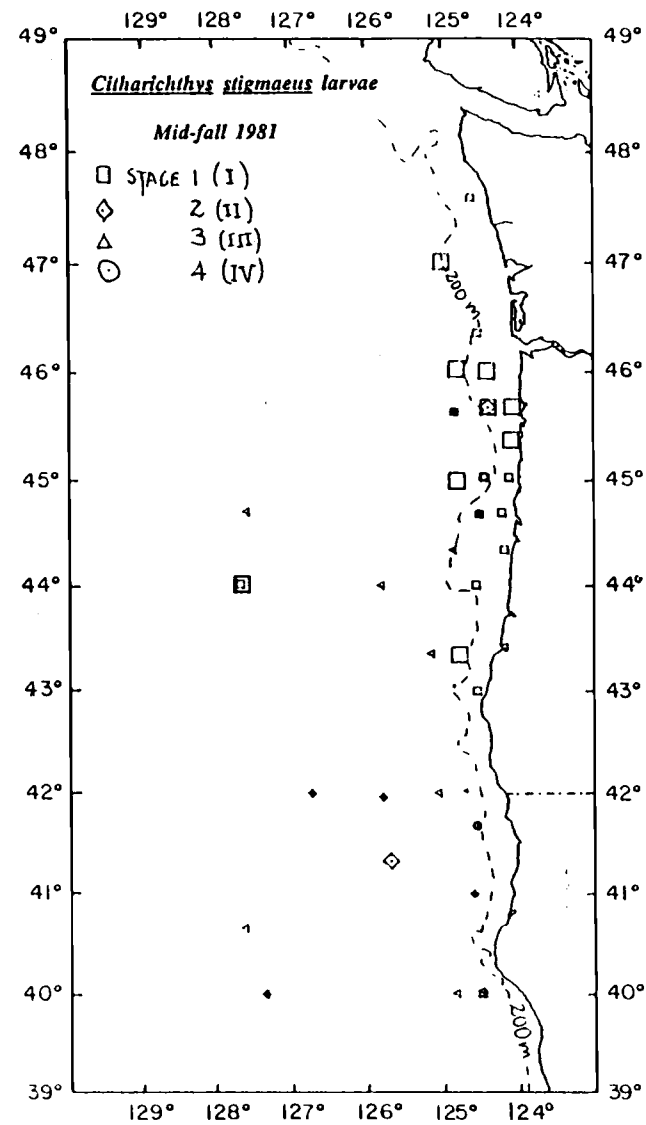
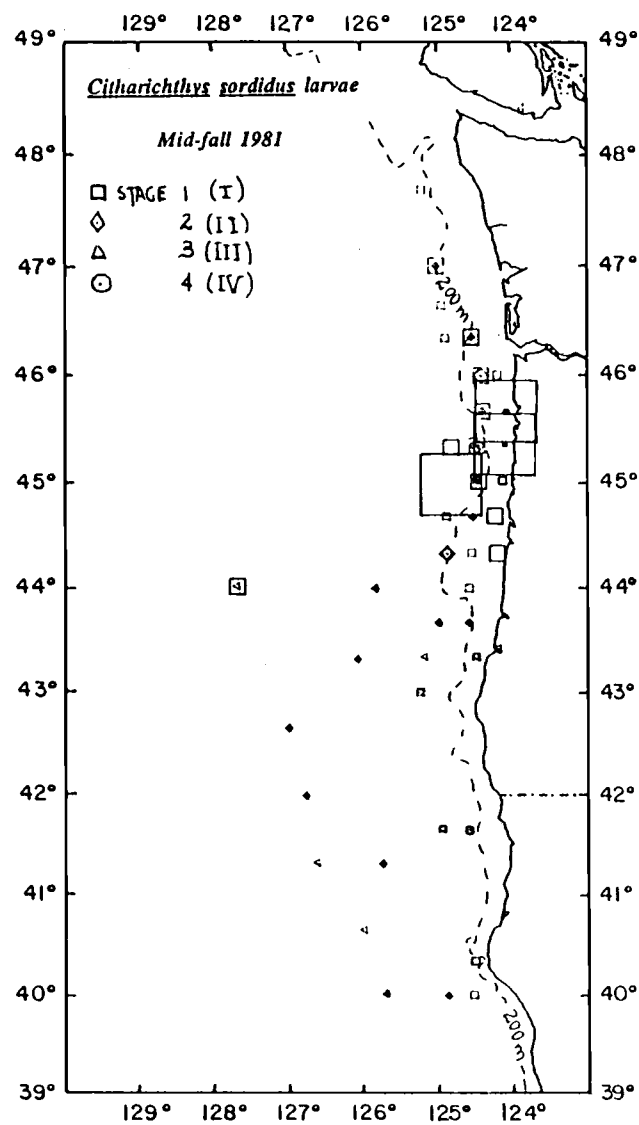
a

Fig. 44 (cont.)



b

Fig. 44 (cont.)



C

Fig. 44 (cont.)

d

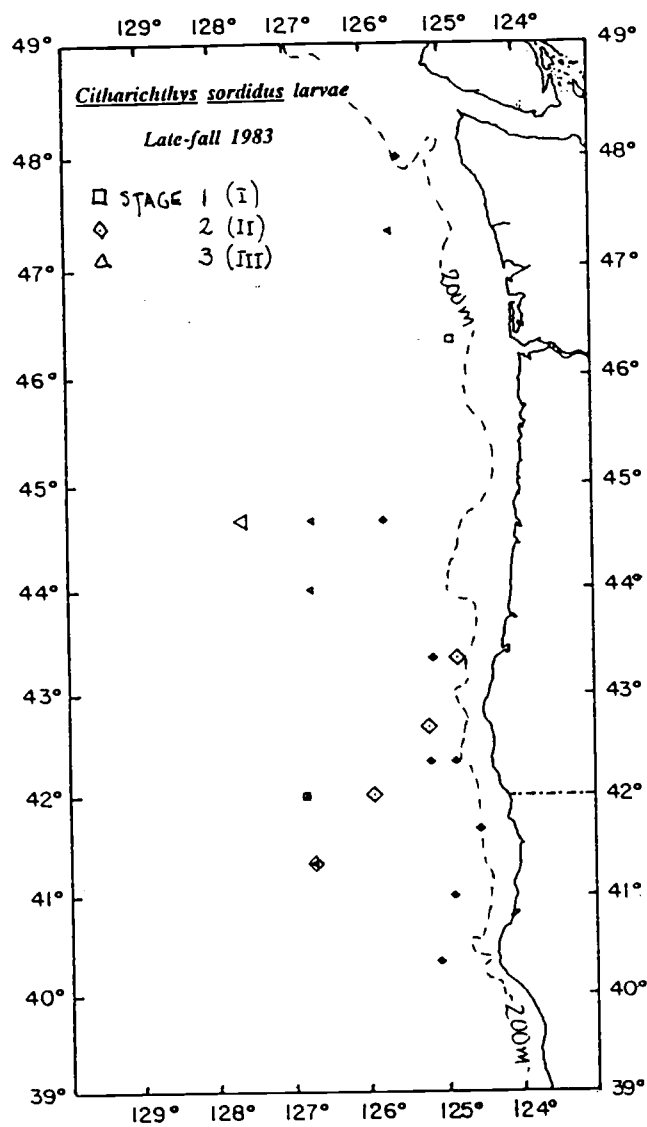


Fig. 44 (cont.)

TABLE 1. Summary of U.S.-U.S.S.R. cruises used for ichthyoplankton surveys in waters off Washington, Oregon and northern California, between 40 and 48°N lat and 3 to 200 miles offshore.

CRUISE	VESSEL	DATES	SEASON	# BONGO/NEUSTON SAMPLES	REPORT
1TK80	Tikhookeanskiy	April 20- May 15, 1980	Mid-spring	125/125	Kendall & Clark, 1982b.
1PO80	Poseydon	Aug 1-20, 1980	Summer	91/91	Kendall & Clark, 1982a.
1PO81	Poseydon	May 9-June 2, 1981	Late-spring	122/123	Clark, 1984.
1DA81	Mis Dalnyi	October 24- Nov. 19, 1981	Mid-fall	125/125	Bates, 1984.
1PO82	Poseydon	May 3-June 1, 1982	Late-spring	49/124	Clark, 1986a.
1EQ83	Equator	April 23- May 15, 1983	Mid-spring	124/124	Clark & Kendall, 1985.
1MF83	R/V Miller Freeman	November 11- Dec. 2, 1983	Late-fall	113/113	Clark, 1986b.

TABLE 2a. Egg densities (number of eggs under 1000 m² of sea surface) (number of eggs under 1000 m² of sea surface) of seven taxa of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	TOTAL	
TAXA								No.	%
<u>Citharichthys</u> spp.	58	667	189	584	243	590	168	2499	10.3
<u>G. zachirus</u>	258	30	419	0	1456	1453	0	3616	14.9
<u>I. isolepis</u>	164	194	13	0	41	10	5	427	1.8
<u>L. exilis</u>	2756	10	2174	0	3046	5687	0	13673	56.5
<u>M. pacificus</u>	479	29	234	0	744	1646	0	3132	12.9
<u>P. vetulus</u>	0	0	0	342	6	0	118	466	1.9
<u>P. melanostictus</u>	73	75	6	67	74	29	92	416	1.7
TOTAL	3788	1005	3035	993	5610	9415	383	24229	

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 2b. Egg densities (number of eggs per 10^5 m³ of sea water) of seven taxa of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	TOTAL	
TAXA									
									No. %
<u>Citharichthys</u> spp.	614	9092	325	4667	0	790	1156	16644	39.2
<u>G. zachirus</u>	3084	108	880	0	0	178	0	4250	10.0
<u>I. isolepis</u>	140	0	10	0	0	0	32	182	0.4
<u>L. exilis</u>	1060	0	230	0	0	57	0	1347	3.2
<u>M. pacificus</u>	11344	43	329	0	0	4468	0	16184	38.1
<u>P. vetulus</u>	0	0	0	1291	0	0	130	1421	3.3
<u>P. melanostictus</u>	377	1519	31	224	0	29	292	2472	5.8
TOTAL	16619	10762	1805	6182	0	5522	1610	42500	

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 3. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on abundance of eggs of seven taxa of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. ($\alpha=0.05$) m = number of cruises compared

	BONGO		NEUSTON		
	W	P-value	W	P-value	m
All cruises combined	0.21	0.10<P<0.20	0.32	0.01<P<0.05	7
Spring (1980-1983)	0.92	<0.01	0.70	<0.01	4
Mid-spring (1980,83)	0.93		0.94		2
Late-spring (1981,82)	0.98		0.50		2
Fall (1981,83)	0.97		0.95		2

NOTE: When only two sets of rankings (i.e., cruises) are compared, the test is inappropriate. However, the W value is shown to indicate trends (Tate and Clelland, 1959).

TABLE 4. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on frequency of occurrence of eggs of seven taxa of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. ($\alpha=0.05$) m = number of cruises compared

	BONGO		NEUSTON		
	W	P-value	W	P-value	m
All cruises combined	0.29	0.05	0.29	0.05	7
Spring (1980-1983)	0.92	<0.01	0.28	>0.20	4
Mid-spring (1980,83)	0.95		0.96		2
Late-spring (1981,82)	0.98		0.50		2
Fall (1981,83)	0.95		0.96		2

NOTE: When only two sets of rankings (i.e., cruises) are compared, the test is inappropriate. However, the W value is shown to indicate trends (Tate and Clelland, 1959).

TABLE 5a. Egg frequency of occurrences (in percentages) of seven taxa of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	AVERAGE F.O.
TOTAL NUMBER OF STATIONS	125	91	122	125	49	124	113	
SPECIES								
<u>Citharichthys</u> spp.	3.2	12.1	2.5	12.0	12.2	8.1	9.7	8.5
<u>G. zachirus</u>	20.0	4.4	23.8	0	51.0	26.6	0	17.9
<u>I. isolepis</u>	3.2	1.1	1.6	0	4.1	0.8	0.7	1.6
<u>L. exilis</u>	38.4	2.2	33.6	0	59.2	27.4	0	22.9
<u>M. pacificus</u>	23.2	5.5	15.5	0	36.7	29.0	0	15.6
<u>P. vetulus</u>	0	0	0	8.0	2.0	0	6.2	2.3
<u>P. melanostictus</u>	5.6	4.4	0.8	4.8	8.2	1.6	8.8	4.8

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 5b. Egg frequency of occurrences (in percentages) of seven taxa of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	AVERAGE F.O.
TOTAL NUMBER OF STATIONS	125	91	123	125	124	124	113	
SPECIES								
<u>Citharichthys</u> spp.	7.2	27.5	6.5	14.4	0	7.3	6.2	9.8
<u>G. zachirus</u>	16.0	5.5	6.5	0	0	18.5	0	6.6
<u>I. isolepis</u>	4.0	0	0.8	0	0	0	1.8	0.9
<u>L. exilis</u>	13.6	0	6.5	0	0	3.2	0	3.3
<u>M. pacificus</u>	25.6	2.2	21.1	0	0	25.8	0	10.6
<u>P. vetulus</u>	0	0	0	8.8	0	0	5.36	2.0
<u>P. melanostictus</u>	7.2	6.6	1.6	4.8	0	1.6	5.3	3.8

MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 6a. Larval densities (individuals under 1000 m² of sea surface) of eight species of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	TOTAL	
SPECIES									
									No. %
<u>C. sordidus</u>	13	13	82	1163	0	193	145	1609	21.6
<u>C. stigmaeus</u>	25	0	0	241	15	111	210	602	8.1
<u>G. zachirus</u>	69	23	60	4	193	365	0	714	9.6
<u>I. isolepis</u>	80	0	58	0	352	120	0	610	8.2
<u>L. exilis</u>	786	61	820	0	719	657	0	3043	40.8
<u>M. pacificus</u>	25	4	95	0	3	119	0	246	3.3
<u>P. vetulus</u>	50	0	0	39	41	82	19	231	3.1
<u>P. melanostictus</u>	148	4	48	4	62	130	0	396	5.3
TOTAL	1196	105	1163	1451	1385	1777	374	7451	

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 6b. Larval densities (individuals per 10^5 m³ of sea water) of eight species of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	TOTAL	
SPECIES								No.	%
<u>C. sordidus</u>	14	0	0	142	0	0	0	156	16.8
<u>C. stigmaeus</u>	56	0	10	81	10	0	32	189	20.3
<u>G. zachirus</u>	0	0	0	0	0	0	0	0	0
<u>I. isolepis</u>	251	0	0	0	0	0	0	251	27.0
<u>L. exilis</u>	0	0	0	0	0	0	0	0	0
<u>M. pacificus</u>	0	0	21	0	0	0	0	21	2.2
<u>P. vetulus</u>	200	0	0	10	20	29	0	259	28.0
<u>P. melanostictus</u>	28	0	0	0	10	14	0	52	5.6
TOTAL	549	0	31	233	40	43	32	928	

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 7. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on larval abundance of eight species of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. ($\alpha=0.05$) m = number of cruises compared

	BONGO		NEUSTON		
	W	P-value	W	P-value	m
All cruises combined	0.19	>0.20	0.31	0.01<P<0.05	7
Spring (1980-1983)	0.61	<0.01	0.37	0.10<P<0.20	4
Mid-spring (1980,83)	0.71		0.70		2
Late-spring (1981,82)	0.63		0.50		2
Fall (1981,83)	0.93		0.72		2

NOTE: When only two sets of rankings (i.e., cruises) are compared, the test is inappropriate. However, the W value is shown to indicate trends (Tate and Clelland, 1959).

TABLE 8a. Larval frequency of occurrences (in percentages) of eight species of flatfishes collected in bongo tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	AVERAGE F.O.
TOTAL NUMBER OF STATIONS	125	91	122	125	49	124	113	
SPECIES								
<u>C. sordidus</u>	1.6	2.2	8.2	30.4	0	9.7	15.9	9.7
<u>C. stigmaeus</u>	3.2	0	0	24.8	2.0	9.7	23.9	9.0
<u>G. zachirus</u>	5.6	3.3	5.7	0.8	10.2	26.6	0	7.5
<u>I. isolepis</u>	5.6	0	6.6	0	18.4	7.3	0	5.4
<u>L. exilis</u>	23.2	8.8	39.3	0	51.0	33.9	0	22.2
<u>M. pacificus</u>	2.4	1.1	9.0	0	4.1	10.5	0	3.8
<u>P. vetulus</u>	5.6	0	0	3.2	4.1	8.1	1.8	3.2
<u>P. melanostictus</u>	9.6	1.1	5.7	0.8	6.1	8.1	0	4.4

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 8b. Larval frequency of occurrences (in percentages) of eight species of flatfishes collected in neuston tows off Washington, Oregon and northern California, during 1980-1983.

CRUISE	MS80 ¹	SU80	LS81	MF81	LS82	MS83	LF83	AVERAGE F.O.
TOTAL NUMBER OF STATIONS	125	91	123	125	124	124	113	
SPECIES								
<u>C. sordidus</u>	0.8	0	0	3.2	0	0	0	0.6
<u>C. stigmaeus</u>	2.4	0	0.8	4.8	0.8	0	2.7	1.6
<u>G. zachirus</u>	0	0	0	0	0	0	0	0
<u>I. isolepis</u>	2.4	0	0	0	0	0	0	0.3
<u>L. exilis</u>	0	0	0	0	0	0	0	0
<u>M. pacificus</u>	0	0	1.6	0	0	0	0	0.2
<u>P. vetulus</u>	2.4	0	0	0.8	1.6	1.6	0	0.9
<u>P. melanostictus</u>	0.8	0	0	0	0.8	0.8	0	0.3

¹MS80 = MID-SPRING 1980
 SU80 = SUMMER 1980
 LS81 = LATE-SPRING 1981
 MF81 = MID-FALL 1981

LS82 = LATE-SPRING 1982
 MS83 = MID-SPRING 1983
 LF83 = LATE-FALL 1983

TABLE 9. Kendall's Concordance Coefficient (W) and corresponding P values (when applicable) for the ranking based on larval frequency of occurrence of eight species of flatfishes off Washington, Oregon and northern California in different seasons and years, during the 1980-1983 period. ($\alpha=0.05$) m = number of cruises compared

	BONGO		NEUSTON		
	W	P-value	W	P-value	m
All cruises combined	0.16	>0.20	0.35	<0.01	7
Spring (1980-1983)	0.49	0.01<P<0.05	0.43	0.05<P<0.10	4
Mid-spring (1980,83)	0.52		0.66		2
Late-spring (1981,82)	0.67		0.50		2
Fall (1981,83)	0.93		0.80		2

NOTE: When only two sets of rankings (i.e., cruises) are compared, the test is inappropriate. However, the W value is shown to indicate trends (Tate and Clelland, 1959).

TABLE 10. Summary of the F tests for differences in egg and larval abundances among cruises in bongo and neuston collections for eight species of flatfishes off Washington, Oregon and northern California, in the period 1980-1983.

* indicates $P \leq 0.05$; ** indicates $P \leq 0.01$

B = present only in bongo tows

N/A = Sanddab eggs were identified only to the genus (Citharichthys spp.) level, while larvae were identified to the species level.

TAXA	EGGS		LARVAE	
	BONGO ind/10 m ²	NEUSTON ind/10 ³ m ³	BONGO ind/10 m ²	NEUSTON ind/10 ³ m ³
<u>Citharichthys</u> spp.	*	**	N/A	N/A
<u>C. sordidus</u>	N/A	N/A	**	**
<u>C. stigmaeus</u>	N/A	N/A	**	*
<u>G. zachirus</u>	**	**	**	B
<u>I. isolepis</u>	*	**	**	**
<u>L. exilis</u>	**	**	**	B
<u>M. pacificus</u>	**	**	**	
<u>P. vetulus</u>	**	**	**	
<u>P. melanostictus</u>		**	**	

TABLE 11. Means \pm (standard deviations) and ranges (in parenthesis) of the standard length, and number of specimens in five developmental stages of larval flatfishes of eight species collected off Washington, Oregon and northern California during the 1980-1983 period.

SPECIES	STAGES				
	I	II	III	IV	V
<u>C. sordidus</u>	4.6 \pm 1.4 (2.3-9.5) 243	10.6 \pm 1.6 (6.8-14.5) 51	16.7 \pm 7.6 (9.7-42.7) 31	38.5 \pm 5.3 (33.2-43.7) 2	
<u>C. stigmaeus</u>	6.1 \pm 1.6 (3.3-9.5) 64	10.9 \pm 1.3 (9.2-14.8) 41	22.3 \pm 7.6 (10.4-36.5) 32	29.7 \pm 4.7 (25.0-34.3) 2	
<u>G. zachirus</u>	9.9 \pm 3.2 (5.5-21.1) 63	26.7 \pm 8.6 (13.4-46.8) - 26	32.6 \pm 14.0 (12.5-65.5) 10		
<u>I. isolepis</u>	5.3 \pm 1.9 (2.0-10.0) 51	10.1 \pm 1.8 (8.0-16.1) 23	16.9 \pm 2.4 (12.2-21.8) 10	19.7 \pm 1.7 (16.4-22.6) 17	21.1 \pm 0.7 (20.4-21.7) 2
<u>L. exilis</u>	6.8 \pm 1.8 (2.3-13.9) 350	12.5 \pm 1.9 (7.2-16.8) 76	16.6 \pm 1.8 (11.2-19.8) 21	21.6 \pm 2.3 (19.0-25.0) 5	
<u>M. pacificus</u>	7.9 \pm 2.0 (4.7-12.5) 31	11.5 \pm 0.9 (10.1-12.9) 10	14.6 \pm 3.7 (10.3-22.3) 7	23.7 \pm 3.6 (18.7-26.2) 3	
<u>P. vetulus</u>	4.7 \pm 1.1 (3.3-7.3) 11	11.5 \pm 3.1 (7.2-17.2) 6	18.7 \pm 2.1 (12.9-21.8) 25	20.2 \pm 1.4 (18.9-22.2) 4	
<u>P. melanostictus</u>	4.9 \pm 1.5 (2.3-7.8) 40	8.9 \pm 0.3 (8.6-9.2) 2	13.5 \pm 3.0 (9.5-19.8) 7	19.2 \pm 5.1 (12.5-26.4) 6	

TABLE 12. Boundaries of the (a) latitudinal, (b) on/offshore and (c) geographic regions of the study area.

(a) LATITUDE

REGION	AREA	LATITUDE	LOCATION
1	Northern California	40 to 42	Cape Mendocino, Ca. to Brookings, Or.
2	Southern Oregon	42 to 44	Brookings, Or. to Siuslaw River, Or.
3	Northern Oregon	44 to 46	Siuslaw River, Or. to Columbia River, Or.
4	Washington	46 to 48	Columbia River to Juan de Fuca Strait, Wa.

(b) BOTTOM DEPTH

REGION	AREA	BOTTOM DEPTH	LOCATION
1	Onshore	≤ 200 m.	Over continental shelf
2	Offshore	> 200 m.	Off continental break

(c) GEOGRAPHIC REGION

REGION	AREA	LATITUDE	LOCATION
I	Northern California onshore	40 to 42	Cape Mendocino, Ca. to Brookings, Or. Bottom depth \leq 200 m
II	Northern California offshore	40 to 42	Cape Mendocino, Ca. to Brookings, Or. Bottom depth \geq 200 m
III	Southern Oregon onshore	42 to 44	Brookings, Or. to Siuslaw River, Or. Bottom depth \leq 200 m
IV	Southern Oregon offshore	42 to 44	Brookings, Or. to Siuslaw River, Or. Bottom depth \geq 200 m
V	Northern Oregon onshore	44 to 46	Siuslaw River, Or. to Columbia River, Or. Bottom depth \leq 200 m
VI	Northern Oregon offshore	44 to 46	Siuslaw River, Or. to Columbia River, Or. Bottom depth \geq 200 m
VII	Washington onshore	46 to 48	Columbia River, Wa. to Juan de Fuca Strait, Wa. Bottom depth \leq 200 m
VIII	Washington offshore	46 to 48	Columbia River, Wa. to Juan de Fuca Strait, Wa. Bottom depth \geq 200 m

TABLE 13: Summary of the ANOVA tests for differences in abundances of larvae and eggs in bongo (B) and neuston (N) tows among four latitudinal regions, between onshore/off-shore stations and among eight geographic regions, for eight species of flatfishes off Washington, Oregon and northern California, in the period 1980-1983.

* indicates P 0.05; ** indicates P 0.01

1 = Sanddab eggs were identified only to the genus (*Citharichthys* spp.) level, while larvae were identified to the species level
I = significant interaction (ANOVA p 0.05) between latitude and bottom depth, which detracts from analysis of main effects of each factor separately.
- = no eggs or larvae collected during that cruise.

a) LATITUDE

	<u>Citharichthys</u> spp.		<u>C.</u> <u>sordidus</u>		<u>C.</u> <u>stigmaeus</u>		<u>G. zachirus</u>		<u>I. isolepis</u>				<u>L.</u> <u>exilis</u>		<u>M.</u> <u>pacificus</u>		<u>P.</u> <u>vetulus</u>		<u>P.</u> <u>melanostictus</u>			
	EGGS ¹		LARVAE ¹		LARVAE ¹		EGGS		LARVAE		EGGS		LARVAE		EGGS		LARVAE		EGGS		LARVAE	
	B	N	B	N	B	N	B	N	B		B	N	B		B	N	B	N	B	N	B	N
Among cruises	I	I	**	**	*		I	I	I		I		I				I	I		I	I	
Within cruises																						
MS80		I					I	I			I		I		-	-	-	I	I	I		*
SU80				-	-	-	I	I	I		-	-	-		-	-	-	-	-		I	-
LS81		I		-	-		I	I							-	-	-	-		I	I	-
MF81	I	I	**		**		-	-			-	-	-	-	I	I	I		I	I		-
LS82		-	-	-				-			-	-	-			-				-		
MS83			I	-	I	-	**	**	I		-	-	-		-	-	-					
LF83	I			-			-	-	-		I		-	-	-	-	I	I		I	I	-

b) BOTTOM DEPTH

Among cruises	I	I					I	I	I		I		I				I	I		I	I	I
Within cruises																						
MS80	**	I					I	I	*		I	**	**	I		-	-	-	I	I	I	**
SU80	**	**		-	-	-	I	I	I		-	-	-		-	-	-	-	**	*	I	-
LS81	**	I		-	-		I	I			*		**	-		-	-	-		I	I	-
MF81	I	I					-	-			-	-	-	-	I	I	I		I	I		-
LS82	*	-	-	-			*	-			-	**	-			-				-		
MS83	**	**	I	-	I	-	**	**	I		-	**	-		-	-	-		*	*	**	
LF83	I	**		-			-	-	-		I	*	-	-	-	-	I	I		I	I	-

TABLE 13: Summary of the ANOVA tests for differences in abundances of larvae and eggs in bongo (B) and neuston (N) tows among four latitudinal regions, between onshore/off-shore stations and among eight geographic regions, for eight species of flatfishes off Washington, Oregon and northern California, in the period 1980-1983.

* indicates P 0.05; ** indicates P 0.01

1 = Sanddab eggs were identified only to the genus (*Citharichthys* spp.) level, while larvae were identified to the species level
 I = significant interaction (ANOVA p 0.05) between latitude and bottom depth, which detracts from analysis of main effects of each factor separately.
 - = no eggs or larvae collected during that cruise.

(cont.)

c) GEOGRAPHIC REGIONS

	<u>Citharichthys</u> <u>spp.</u>		<u>C.</u> <u>sordidus</u>		<u>C.</u> <u>stigmaeus</u>		<u>G. zachirus</u>		<u>I. isolepis</u>				<u>L.</u> <u>exilis</u>		<u>M.</u> <u>pacificus</u>				<u>P.</u> <u>vetulus</u>				<u>P.</u> <u>melanostictus</u>			
	EGGS		LARVAE		LARVAE		EGGS		LARVAE		EGGS		LARVAE		EGGS		LARVAE		EGGS		LARVAE		EGGS		LARVAE	
	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N
Within cruises																										
MS80	*	**					*	**		*		**	**	**	**			-	-	-	**	*	**	**	**	
SU80	*	**		-	-	-	**	**			-	-	-				-	-	-	-	-			**	-	
LS81	**	**		-	-		**	**		*	-			**		*		-	-	-	-		**	**	-	
MF81	**	**	**		*		-	-		-	-	-	-		-	-	-	-	**	**	**		**		-	
LS82		-	-	-				-			-		-		-		-				*		-			
MS83	**	*	**	-	**	-	**	**			-	*	-		MS83	*	**	*	*	-	-	-			**	
LF83	**	**		-			-	-		-		*	-	-	LF83	-	-	-	-	**	**	-	**	**	-	