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English Sole Transport During Pelagic Stages on the Pacific Northwest Coast, and Habitat Use by Juvenile Flatfish in Oregon and Washington Estuaries

Christopher Nethercote Rooper

A dissertation submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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Abstract

English Sole Transport During Pelagic Stages on the Pacific Northwest Coast, and
Habitat Use by Juvenile Flatfish in Oregon and Washington Estuaries

Christopher Nethercote Rooper

Chairperson of the Supervisory Committee:
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Trawl surveys of four West Coast estuaries were conducted to determine the spatial and temporal patterns of juvenile English sole residence during 1998-2000. Additional data from 1983-1988 was also analyzed. Juvenile English sole were present in both June and August with densities in the range of 1000-2000 fish*ha^{-1} across all estuaries.

The occurrence of interannual variability in juvenile English sole abundance and the appearance of multiple cohorts in nursery estuaries were addressed by examining transport in the California Current. The larval trajectories for English sole demonstrated that passive larval drift does not account for the patterns in sole distribution in estuaries.

In most cases cohorts of English sole larvae were transported north or south off the Oregon-Washington shelf prior to the conclusion of development. However, based on model trajectories, egg stage was carried offshore before hatching in only 6 of 19 cases, and it is suspected that spawn timing occurs during periods of onshore transport to insure that eggs move inshore where they may be retained in local hydrographic features.

The relationship of large (TL > 50-mm) and small (TL <50-mm) English sole cohorts to estuarine habitat were also examined. Both small and large cohort English sole utilized lower side channel locations at significantly higher densities than other estuarine areas. Small English sole also showed significant relationships with both bottom temperature and depth. These patterns in habitat use were consistent across all estuaries and indicate that English sole utilized shallow depth areas where temperatures were optimal for growth, and more extensive tidal flats were available. The analysis also indicated a carrying capacity may exist for large English sole in nursery estuaries.

The distribution of additional flatfish species was analyzed to examine spatial partitioning of nursery estuaries. The analysis of density anomalies indicated that the four flatfish species were exploiting different sections of each estuary. Densities of sanddab and sand sole were higher in lower main channel sites close to the estuary mouth, that were more oceanic than other parts of the estuary, while starry flounder were more common in the upper sections of the estuary where salinity was typically lower and temperature warmer.

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Acknowledgements

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Dedication

This dissertation is dedicated to my grandparents Frederick Manson and Ethel Anne Wilson, the best grandparents we could ever have.

Chapter 1. Introduction and life history of English sole

1.1. Introduction

Commercial exploitation of flatfish on the Pacific coast began prior to World War II, and the English sole (*Pleuronectes vetulus*) has been an important component of the bottom trawl fishery on the Oregon and Washington coasts. The English sole has been the second most important flatfish species in terms of pounds landed for the fishery over the last 10 years. Because of the sexual dimorphism and larger size of female English sole, the landings consist almost exclusively of females, while the smaller males and females are discarded (Sampson 1993). The total ex-vessel value of English sole landings has averaged $1.19 million from 1990-2000 (Pacific Fisheries Information Network, PacFin, unpublished data). Landings of English sole have declined in recent years, with recent landings of around 1,300 mt (Figure 1.1).

1.2. English Sole Life History

English sole, as with most other flatfish species have a complex life cycle. Adult English sole stocks are found in the coastal ocean and are separated geographically from juvenile nursery areas in coastal estuaries. The English sole has prolonged pelagic egg and larval stages that connect the juvenile population in estuaries and the spawning populations on the open coast. Adult English sole are distributed from Baja California to southwestern Alaska along the shallow continental shelf, and can be found at depths ranging from the surface to 550 m, although commercially exploitable abundance generally occurs at depths less than 130 m (Hart 1973).

Oregon and Washington English sole stocks are believed to spawn over sandy substrates from 44 to 46^0 N. latitude (Hewitt 1980, Kruse and Tyler 1989). Spawning can occur from September to April, with peak spawning typically occurring in January or February (Kruse and Tyler 1983). Previous modeling indicates that water temperature and current patterns influence spawning behavior (Kruse and Tyler 1983). Tagging studies have shown that adults can make extensive along-shelf migrations during winter to suitable spawning habitat on mud and sandy bottoms (Ketchen 1956, Jow 1969).

The eggs and larvae of English sole are at the mercy of oceanographic conditions for an extended period during the pelagic phase. Fertilized eggs typically float at the surface after release (Ketchen 1956, Orsi 1968), where the egg stage lasts 3.5 to 12 days dependent on water temperature (Ketchen 1956, Alderdice and Forrester 1968). The yolk-sac larvae also float at the surface (Budd 1940, Orsi 1968), and the total pelagic phase including both egg and larvae can last from 8-10 weeks (Laroche et al. 1982). Kruse and Tyler (1989) hypothesized, based on data from a number of sources, that over 95% of English sole larvae are found in the top 50-m of the water column and over 50% of larvae are found in the top 10-m after yolk sac depletion.

During the egg and larval stages onshore movement occurs since metamorphosing larvae are found in shallow nearshore waters. Late stage larvae are also more common in nearshore areas during transformation (Krygier and Pearcy 1986). During or shortly after transformation and settlement, the juveniles move into estuaries to continue development (Krygier and Pearcy 1986, Boehlert and Mundy 1987, Gunderson et al. 1990). Metamorphosis begins at an age of 60 to 75 days (Rosenberg 1982) and length of 14 to 21-mm (Rosenberg and Laroche 1982, Botsford et al. 1989). Metamorphosis is completed at a length of 20 to 26-mm (Rosenberg and Laroche 1982, Botsford et al. 1989).

Studies of English sole distribution have indicated that the juvenile stage is estuarine dependent, and that most if not all juveniles enter estuaries during their first year (Olson and Pratt 1973, Krygier and Pearcy 1986, Gunderson et al. 1990). Estuarine residence of English sole is usually limited to age 0+ juveniles (Gunderson et al. 1990). Gunderson et al. (1990) observed small fish moving from coastal areas into estuaries and large fish moving from estuaries all in the first year of life. They found that most juveniles had settled in estuaries by 55-mm length, and migrated from the estuary beginning at 75 to 80-mm. By the time the sole reach 125 to 154-mm 86 to 94% of them have moved into coastal waters. However, interannual differences were found in these migration patterns.

At the conclusion of estuarine residence, juvenile English sole move into coastal and offshore waters where they eventually join the adult population completing their life cycle. Male English sole have been found to reach sexual maturity as early as age 2, while females mature at age 3 to 4 (Ketchen 1956). Recruitment levels for each year are probably determined at some time prior to movement out of the estuaries, although this is not known for certain.

The passively drifting egg and larval phases of English sole, the centralized spawning location and the dependence on current dispersal of the eggs and larvae make this species a good candidate for exploring the mechanisms by which oceanographic conditions control survival and recruitment. The estuarine dependence of the species provides an easily accessible population of juveniles for whom abundance and spatial patterns in habitat usage are easily studied.

1.3. Dissertation organization

This dissertation is organized into four main chapters with an introduction at the beginning and overall summary and discussion at the end. The first of the main chapters (Chapter 2) describes the results of nine years of trawl surveys of Pacific Northwest estuaries from 1983-1988 and more recently from 1998-2000. The results presented in Chapter 2 are meant to set the stage for the analyses that follow, in that patterns observed during trawl surveys provided the basis for further hypotheses and analyses in Chapters 3-5. In Chapter 3 the role of alongshore transport in determining the density and abundance of juvenile English sole in nursery estuaries is explored in detail. In Chapter 4 the distribution of juvenile English sole within nursery estuaries is framed in the context of underlying habitat use. In Chapter 5 the distributions of three additional species of flatfish, sand sole (*Psettichthys melanostictus*), starry flounder (*Platichthys stellatus*) and Pacific sanddab (*Citharichthys stigmaeus*) are compared to English sole distribution to determine how these co-occurring juvenile flatfish species partition nursery estuaries.

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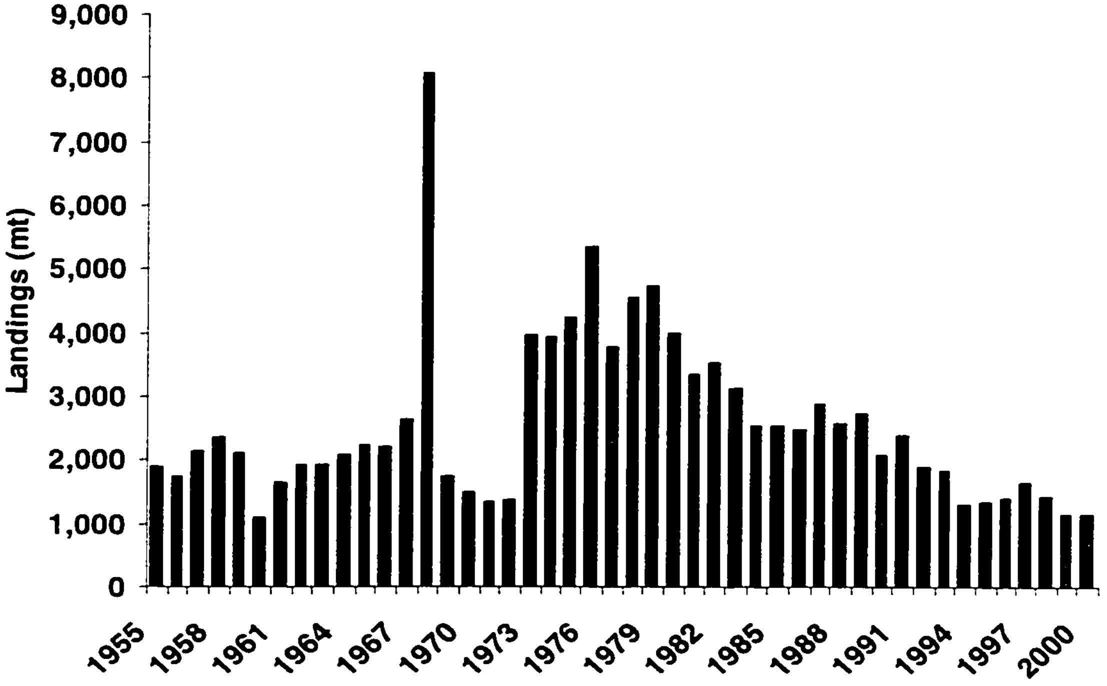

Figure 1.1. Time series of combined landings of English sole for Oregon and Washington commercial trawl fisheries from 1955-2000 (Pacific Fisheries Information Network, PacFIN unpublished data).

Chapter 2. Young-of-the-year English sole distribution and abundance in four coastal nursery estuaries

2.1. Introduction

Nursery areas for juvenile fishes form an important link between early life history stages and adult populations. In fish species that exhibit the classic triangular life history pattern, dispersal to an appropriate nursery area is an especially important process (Harden-Jones 1968). Larval dispersal typically entails pelagic egg and/or larval stages. Survival through these stages is influenced by oceanic conditions, including prevailing current patterns and the physical character of the water column (Lasker 1975, Iles and Sinclair 1987). Larval survival is also influenced by the abundance of predators and appropriate prey species in the water column (Cushing 1975, Bailey and Houde 1989). Species with pelagic egg and larval stages seem to be especially susceptible to dramatic fluctuations in population abundance both over long and short time periods (Cushing 1971, Soutar and Isaacs 1974, Botsford et al. 1989). Thus, many species such as Walleye pollock (*Theragra chalcogramma*), English sole (*Pleuronectes vetulus*), Dungeness crab (*Cancer magister*), capelin (*Mallotus villosus*), northern anchovy (*Engraulis mordax*), and Pacific herring (*Clupea pallasi*) have demonstrated strong correlation between physical variables and recruitment (Ketchen 1956, Hayman and Tyler 1980, Leggett et al. 1984, Peterman and Bradford 1987, McConnaughey et al. 1994, Quinn and Niebauer 1995, Schweigert 1995, Zebdi and Collie 1995).

In addition to variability in larval supply due to oceanic conditions during pelagic stages, the available habitat will also effect the abundance of a species within a nursery area. The amount and type of habitat available can influence survival (Fernandez et al. 1993, Lipcius et al. 1997), growth (Tupper and Boutilier 1995) and distribution (Norcross et al. 1997, Howell et al. 1999) of juvenile fishes. Ultimately the amount of available nursery habitat can dampen recruitment variation in years when large settlement events occur (Iles and Beverton 2000). Therefore, for fish species that utilize nursery areas two critical components, pelagic conditions and available nursery habitat, act to influence eventual recruitment to the adult population.

English sole are a flatfish species with pelagic egg and larval stages, followed by an estuarine dependent juvenile stage. Adult English sole are distributed from Baja California to southwestern Alaska along the shallow continental shelf, and can be found at depths ranging from the surface to 130-m (Hart 1973). Oregon and Washington stocks are believed to spawn over sandy substrates from 44 to 46^0 N. latitude (Hewitt 1980, Kruse and Tyler 1989). Spawning can occur from September to April, with peak spawning typically occurring in January or February (Kruse and Tyler 1983). Fertilized eggs and yolk sac larvae float at the surface after release (Budd 1940, Ketchen 1956, Alderdice and Forrester 1968, Orsi 1968), and later stage larvae are typically found in the top 50-m of the water column (Kruse and Tyler 1989). The total pelagic phase including both egg and larvae can last from 8-10 weeks (Laroche et al. 1982). During the egg and larval stages, onshore movement occurs and metamorphosing larvae are found in shallow nearshore waters. Metamorphosis is completed at a length of 20 to 22-mm (Rosenberg and Laroche 1982). Studies of English sole distribution have indicated that the juvenile stage is estuarine dependent, and most if not all juveniles enter estuaries during their first year (Olson and Pratt 1973, Krygier and Pearcy 1986, Gunderson et al. 1990). Estuarine residence is usually limited to age 0+ juvenile for English sole (Gunderson et al. 1990).

Because of their dependence on coastal estuaries along Oregon and Washington for rearing habitats, the abundance of juveniles in these areas should reflect patterns in larval supply, habitat suitability within estuaries and mortality of early life history stages. The objectives of this study were to compare juvenile English sole distribution among four Pacific coast nursery areas. Special emphasis was placed on identifying estuarine patterns of interannual variability in English sole density and length, as well as within-estuary spatial distribution.

2.2. Methods

Study area

This study was carried out at four estuaries on the Oregon and Washington coast; Grays Harbor, Willapa Bay, Coos Bay, and Yaquina Bay (Figure 2.1). The subtidal area for each estuary was estimated from digitized NOAA nautical charts. All four estuaries were originally divided into 4-5 strata based on degree of oceanic influence (i.e. distance from estuary mouth). Random sampling stations were originally chosen within the strata with the caveat that no two stations were adjacent (see Shi et al. 1997 for detailed description of survey design; Figure 2.2). The northernmost estuary, Grays Harbor, has approximately 8,545 ha of subtidal habitat and was divided into four strata (GH-1, GH-2, GH-3, and GH-4). Within Grays Harbor eighteen trawl survey sites were chosen. The largest estuary, Willapa Bay, has 11,200 ha in subtidal area, and twenty trawl survey sites were allocated within five strata (WB-1, WB-2, WB-3, WB-4 and WB-5) in Willapa Bay. The study sites in Willapa Bay and Grays Harbor were the same in all years. Yaquina Bay was the smallest estuary studied in this project with just 470 ha of subtidal area. Seventeen sites were chosen in Yaquina Bay within four strata (YB-1, YB-2, YB-3 and YB-4). In Coos Bay 18 study sites were chosen in four strata (CB-1, CB-2, CB-3 and CB-4). The total amount of subtidal area estimated for Coos Bay was 1,187 ha.

Survey data collection

Trawl surveys of all four estuaries were conducted in both June and August from 1998-2000. During 1983-1988 trawl surveys were conducted at least monthly from May to September in Grays Harbor. In Willapa Bay, monthly trawl surveys were conducted from 1985-1988 throughout the summer. For ease of comparison between early and late year surveys, data from only the June and August surveys of Willapa Bay and Grays Harbor were used in the analysis (Table 2.1). A detailed description of the methods used in the 1983-1988 trawling can be found in Shi et al. (1994).

English sole were collected during daylight using a 3-m beam trawl described in Gunderson and Ellis (1986). The beam trawl had an effective opening width of 2.3-m and a height of 0.6-m. The net was towed at a speed of 2.8 to 3.3 km*hr^{-1} behind a 6.4-m research vessel with a minimum 5:1 scope of line out to depth. The distance towed averaged 260 m during the 1983-1988 surveys, and 139 m in 1998-2000. Trawls were made over a variety of tide stages, although efforts were made to conduct most trawling near the time of daylight low tides. Only about 4.5% of all trawls were conducted during high tide. Sampling was not conducted at high current velocities to allow maximum adherence of the beam trawl to the substrate. All fish and invertebrates captured were identified, and all English sole caught during the surveys were measured for total length to the closest mm.

Densities of juvenile English sole were calculated using the area swept method

$$A = W * D$$

where W is the net mouth opening width and D is the distance towed. Distance for each tow was measured from differential global positioning system (GPS) readings in 1998-2000, and an optical range finder between beginning and end buoy marks from 1983 to 1988. Specific descriptions of the methods used to calculate the distance towed for 1998-2000 can be found in Appendix 1. Mean density and abundance for each stratum and estuary were calculated separately, and then combined using stratified random sampling formulae (Thompson 1992, Shi et al. 1994).

Data Analysis

Three separate data sets were analyzed, the full time series of Grays Harbor English sole densities, the full time series of Willapa Bay densities, and the final three years of density (1998-2000) for all four estuaries. For the first two data sets, analysis of variance (ANOVA) was used to detect patterns in each estuary with month, stratum and year of survey as factors. Because stratum designations were not comparable across estuaries, the analysis of English sole density from 1998-2000 included only estuary, month and year as factors. A Kolmogorov D test for normality of the English sole density data indicated that a square-root data transformation would best meet the assumptions of ANOVA. All interaction terms were included in the ANOVA, and statistically significant effects in these analyses were examined using the least squares means approach (SAS 1987), with a Tukey adjustment for multiple comparisons to determine significant pairwise differences in density among levels of each effect (Zar 1974).

The length data collected in each estuary were analyzed in a similar fashion. Lengths from the Grays Harbor and Willapa Bay time series were analyzed separately from the data from all four estuaries. Kolmogorov D tests for normality of English sole length data indicated a log-transformation would best meet the assumptions of ANOVA. Length frequency histograms of measured English sole were also compiled for each survey period in each estuary, and scaled to total abundance in 5-mm length classes. Scaling length frequencies to total abundance was performed using the appropriate stratified sampling formulae. Length frequency plots were compared across estuaries, years and months to determine patterns in settlement events that were reflected in the length data.

2.3. Results

In 1998-2000 a total of 431 trawls were completed in the four estuaries. In Grays Harbor, 319 trawls were completed through nine years of surveys, and in seven years of surveys in Willapa Bay 280 trawls were completed. The dominant species caught in all estuaries in all years were age 0+ and age 1+ Dungeness crab and young of the year English sole. Also represented in the catch were other estuarine species or groups of fish and invertebrates, including staghorn sculpin (*Leptocottus armatus*), gunnels (family Pholidae) and crangonid shrimp species. In all the years of trawl surveys across all four estuaries, estimated densities of English sole captured in a single haul ranged from 0 to $>35{,}000*\text{ha}^{-1}$.

English sole density

There was a significant interaction ($p < 0.05$) between estuary and year in the analysis of the 1998-2000 data set, meaning that densities in some year-estuary combinations were significantly different than others (Table 2.2). This result was driven primarily by the average densities in Grays Harbor in 1999 which were lower than most of the other year-estuary combinations, and by Yaquina Bay in 2000 which had significantly higher densities than most other year-estuary combinations (Figure 2.3). Mean English sole density was typically between 1,200-1,800/ha in the estuaries, but was less than half this range (600/ha) in Grays Harbor during 1999, and double this range (4,000/ha) in Yaquina Bay during 2000. Analysis of variance showed that densities were significantly lower in August (mean = 958/ha, SE = 130) than June (mean = 2,189/ha, SE = 376), although this trend was most conspicuous in 1998 and 2000. Densities of English sole in August of all years were relatively constant (Figure 2.4).

Results of analysis of English sole density in the Grays Harbor data set (1983-1988 and 1998-2000) were similar to those found for the 1998-2000 data set over all estuaries (Table 2.2). Density of English sole in Grays Harbor varied with year ranging from 271*ha^{-1} in 1986 to 1,662*ha^{-1} in 2000 (Figure 2.3). Density in 1986 was lower than other years, although the difference was not significant in most cases. Densities in 2000 were significantly higher than all years except 1984 and 1998. June densities of English sole were significantly higher (mean = 1,016, SE = 276) than August densities (mean = 588, SE = 119). There was no significant interaction between year and month. English sole density was significantly different among the four different strata, with densities in GH-3 significantly lower than all other stratum. However, there was also a significant month*stratum interaction, and this was also driven primarily by the large decrease in density between June and August in GH-2 (Figure 2.5). The average density in GH-3 was low, and relatively high in GH-1 and GH-4 in both June and August. There was no significant year-strata interaction in the analysis, implying that the spatial patterns in density were fairly constant in all years of the study.

English sole density varied significantly among strata, month and year of survey in Willapa Bay from 1985-1988 and 1998-2000 (Table 2.2). No interaction terms were significant in the analysis of the Willapa Bay data set. Density in June was significantly higher (mean = 1,514, SE = 281) than in August surveys (mean = 873, SE = 150).

Densities in 1986 were significantly less than in the two highest years (1987 and 1998), but in all other years densities of juvenile English sole were similar (Figure 2.3). These results were similar to Grays Harbor, where 1986 densities were lower than most years. Within Willapa Bay densities of English sole were significantly lower in the most upriver stratum (WB-5) than in all other strata (Figure 2.6). Densities were also lower in WB-4 than in most other strata, but not significantly. Across the remaining strata in Willapa Bay densities of English sole were similar. The absence of interaction terms in the analysis indicated the year, month and spatial patterns in Willapa Bay English sole density were consistent across the data set.

English sole length

The length of English sole caught ranged from 14 to 200 mm in the 19,398 fish measured from 1998-2000. Analysis of variance revealed that average length was significantly different among all combinations of years and months among estuaries (Table 2.3). English sole were significantly larger in August than in June, as would be expected. Average length was largest in Yaquina Bay and smallest in Grays Harbor. Within Grays Harbor, average length was significantly different among all combinations of stratum, year and month (Table 2.3). Average length was largest in GH-3 and smallest in GH-2 (Figure 2.7). The analysis of Willapa Bay data also revealed significant differences in English sole length among all combinations of year, stratum and month (Table 2.3). Strata in the upper estuary (WB-3, WB-4, and WB-5) all contained significantly larger English sole than lower estuary strata (WB-1 and WB-2; Figure 2.8).

The typical lengths of fish captured in any estuary during June trawl surveys exhibited a mode centered at 25-40 mm (Figures 2.9-2.12). Some notable exceptions occurred in Grays Harbor 1988, Willapa Bay in 1985 and 1988 and Yaquina Bay in 2000. In these cases the small fish were poorly represented during June trawl surveys. Although larger fish (> 50 mm) were observed in each estuary during most June surveys, distinct peaks of both large and small fish in June were observed for English sole in Grays Harbor in 1983-84, 1986-87 and 2000 (Figure 2.9). Distinct large and small cohorts were also observed in Willapa Bay in 1986, 1999 and 2000 (Figure 2.10), in Yaquina Bay in 1999 and 2000 (Figure 2.11) and in Coos Bay in 1998 and 2000 (Figure 2.12). The distinct second mode of fish typically exhibited lengths centered at 60 to 85-mm. The presence of larger fish during June surveys resulted in a bimodal length frequency pattern. During the August survey, the mode of fish lengths typically increased to about 60-100 mm (Figure 2.13-2.16) across all estuaries and years.

2.4. Discussion

The use of density in the analysis of variance assumes catchability for juvenile English sole was not different among the different sites and estuaries in this study. The beam trawl used in this study was of the same design throughout all years of surveying. The gear has been previously tested by Gunderson and Ellis (1986) who found it to be highly effective at sampling demersal fauna. Results of testing by Williams (1994) indicated the beam trawl was an efficient gear for capturing demersal crab and fish species over a variety of soft bottom substrates. Testing during this study indictated that bottom contact was consistent for the net across a range of trawling depths (Appendix 1). Since the sites sampled during this study were all composed of soft-bottomed substrates it was assumed that gear efficiency did not contribute to the observed differences in English sole density.

Density of English sole in all of our study areas varied significantly on an interannual basis, but were generally in the range of 1000-2000 fish*ha^{-1} across all estuaries studied. In both Willapa Bay and Grays Harbor, interannual variation was driven by low density in only one year, 1986, in both estuaries. For the 1998-2000 data set, Yaquina Bay in 2000 was the only estuary where significantly higher than average densities of English sole were observed. Across estuaries, densities of English sole were constant with few exceptions. Densities in the two southern estuaries were slightly higher in 1999 and 2000, while densities in the combined northern estuaries were highest in 1998.

Interannual differences in settlement timing were apparent from the analysis of modes in the length frequencies of English sole captured during the June surveys (Table 2.4). In some year-estuary combinations an early settling cohort dominated the catch in June (i.e. Yaquina Bay, 2000), while typical June surveys were dominated by a late settling cohort. Additionally, in twelve cases a bimodal pattern in English sole length frequencies were observed indicating two distinct settlement events occurred in the estuary that year. By August of each year similar densities of English sole were present in the estuaries, and a single mode of fish in the 60-100 mm length range was typically observed.

The patterns in juvenile English sole density observed in this study suggest that larval supply to these nursery estuaries can vary on an interannual basis. The modes of settlement suggest that the timing of pulses of recruits to the estuaries can vary both temporally and spatially. The supply of larvae, because of the pelagic nature of the stage, is dictated by current patterns over the shelf and mortality (presumably due to starvation or predation) occurring during this phase. Water movement over the Oregon and Washington shelf is dominated by the northward flowing Davidson current during the winter months (Hickey 1989). This northward flowing current is generally associated with Ekman transport onshore and downwelling at the coast. The spring transition in late March or April gives rise to southward flowing currents associated with offshore Ekman transport and upwelling along the coast. Periodic interruptions lasting days or weeks of these states with relaxation of current patterns can be observed at any time.

In conjunction with current patterns, the timing of English sole spawning determines the regime under which their eggs and larvae are transported. English sole have a very protracted spawning period, with spawning occurring between September and April of the following year (Kruse and Tyler 1983). Kruse and Tyler (1983) developed a relationship between timing of spawning and water temperature during summer gonadal development, with colder temperature indicating strong upwelling, high food production and thus fast development. Abrupt temperature changes occurring when the fish are ripe in the fall and winter was also found to influence spawn timing (Kruse and Tyler 1983). Therefore, the interaction between spawn timing and current patterns as well as natural mortality will most likely determine the supply of larvae to a given estuary during the spring. This interaction could also produce two modes of recruits to an estuary in years when favorable currents and spawn timing coincide. These issues will be further explored in Chapter 3.

Interestingly, the density of English sole in estuaries did not seem to be strongly effected by the El Nino conditions that occurred in 1982-83, 1987-88 and 1997-98. El Nino events have been shown to effect a number of groundfish species, in many cases producing larger or smaller than normal year classes (Hollowed and Wooster 1992, Hollowed et al. 2001). These El Nino events caused disruptions of the usual transport regimes, reduced upwelling and increased water temperatures off the coast (Hickey 1989). Mortality of English sole would be thought to increase due to reduced food availability over the shelf. These disruptions may have been offset by increases in water temperature that possibly reduced the length of the pelagic phase and increased growth rates.

However, it is known that seasonal variation in oceanographic conditions on the Oregon and Washington coasts is much larger than the variability from year to year (Hickey 1989). As a result, the response of English sole populations to seasonal changes may be more important than responses to interannual changes, and the effects of broad scale patterns such as El Nino and La Nina on English sole reproduction and survival may be relatively minor.

Patterns in spatial distribution of English sole were apparent in the Grays Harbor and Willapa Bay estuaries, as some strata had higher densities of English sole. The more upriver strata had significantly lower densities in both Willapa Bay and Grays Harbor. The juvenile English sole occupying these upriver regions were significantly larger than their lower river counterparts. These consistent distinctions in density among the different areas imply that downstream habitats are preferred areas for English sole. The patterns in English sole distribution within estuaries will be further explored in Chapters 4 and 5.

The concentration hypothesis (Iles and Beverton 2000) suggests that in fishes that concentrate during juvenile stages population size may be moderated by density dependent mechanisms when juvenile settlement is high. If the size classes of English sole are able to segregate spatially and temporally, producing multiple cohorts of settlers per year may be a way to maximize recruitment to the adult population. The spatial distributions of juvenile English sole found during this study suggest that this may occur to a limited extent. In years when two cohorts of fish occurred in estuaries, large fish were found in upriver areas. These areas may have been unsuitable or not preferred for residence by small juveniles. However, large juveniles were also found throughout the estuary in most cases. A feeding transition has been noted to occur at sizes of about 50-65 mm, as fish move from feeding on copepods to infaunal polychaetes (Toole 1980). This could potentially be a mechanism for preventing competition and the resulting density dependent compensation between large and small cohorts of young-of-the-year English sole.

It is still unclear at which early life history stage recruitment in English sole is determined. In other fish species, failure of larval and egg abundance to match recruitment in later years have led some to believe that recruitment levels are ultimately set at late stages such as the post-settlement juvenile stage (Peterman et al. 1988, Pepin and Myers 1991, Bradford 1992). The availability of suitable habitat at the time the larvae are settling out of the water column has been proposed as a determinant of recruitment levels (Sale 1991, McConnaughy et al. 1994). Our work in Pacific coast estuaries suggests that exploration of the interaction of spawn timing and larval transport patterns as well as the availability of habitat within nursery estuaries may be important avenues for further investigation into English sole recruitment variability.

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Table 2.1. Sampling dates for trawl surveys of each estuary in each year.

Year	Coos Bay	Yaquina Bay	Willapa Bay	Grays Harbor
1983				6/11-6/14 8/22-8/24
1984				6/29-7/1 8/10-8/12
1985			6/30-7/3 8/28-8/31	6/1-6/6 8/15-8/18
1986			6/19-6/21 8/19-8/21	6/7-6/8 8/5-8/6
1987			6/10-6/12 8/9-8/10	6/24-6/26 8/23-8/25
1988			6/28-6/30 8/27-8/29	6/13-6/15 8/10-8/11
1998	6/23-6/24 8/20-8/21	6/25-6/26 8/22-8/23	6/13-6/15 8/9-8/11	6/10-6/11 8/6-8/7
1999	6/26-6/28 8/24/8/25	6/29-7/1 8/26-8/27	6/14-6/16 8/12-8/14	6/11-6/12 8/9-8/11
2000	6/22-6/24 8/14-8/15	6/25-6/26 8/16-8/17	6/14-6/16 8/4-8/6	6/11-6/14 8/1-8/3

Table 2.2. Results of analysis of variance of juvenile English sole densities for each data set examined. Factors found to be significant ($p < 0.05$) are shown (*indicates $p < 0.01$), the sample size (n), and correlation coefficient (R^2) are shown.

Data set	Significant factors	n	R^2
Willapa Bay 1985-1988, 1998-2000	Month*, Year*, Strata*	280	0.37
Grays Harbor 1983-1988, 1998-2000	Month*, Year*, Strata*, Strata-month	319	0.41
All estuaries 1998-2000	Month*, Year, Estuary, Estuary-year*, Year-month	431	0.18

Table 2.3. Results of analysis of variance of juvenile English sole lengths for each data set examined. Factors found to be significant ($p < 0.05$) are shown (*indicates $p < 0.01$, ... indicates all interactions were estimated), the sample size (n), and correlation coefficient (r^2) are shown.

Data set	Significant factors	n	r^2
Willapa Bay 1985-1988, 1998-2000	Month*, Strata*, Year*, ..., Month-strata-year*	16,660	0.50
Grays Harbor 1983-1988, 1998-2000	Month*, Strata*, Year*, ..., Month-strata-year*	11,295	0.48
All estuaries 1998-2000	Month*, Strata*, Year*, ..., Month-strata-year*	19,398	0.36

Table 2.4. Length cohorts captured in trawl surveys during June of each year. Abbreviations are given for Grays Harbor (GH), Willapa Bay (WB), Coos Bay (CB) and Yaquina Bay (YB). * indicates surveys were conducted in Grays Harbor only. ** indicates surveys were conducted in Grays Harbor and Willapa Bay only.

Year	Late settlers only	Early settlers only	Both cohorts
1983*			GH
1984*			GH
1985**	GH	WB	
1986**			GH, WB
1987**	WB		GH
1988**		GH, WB	
1998	GH, WB, YB		CB
1999	GH, CB		WB, YB
2000			YB, CB, GH, WB

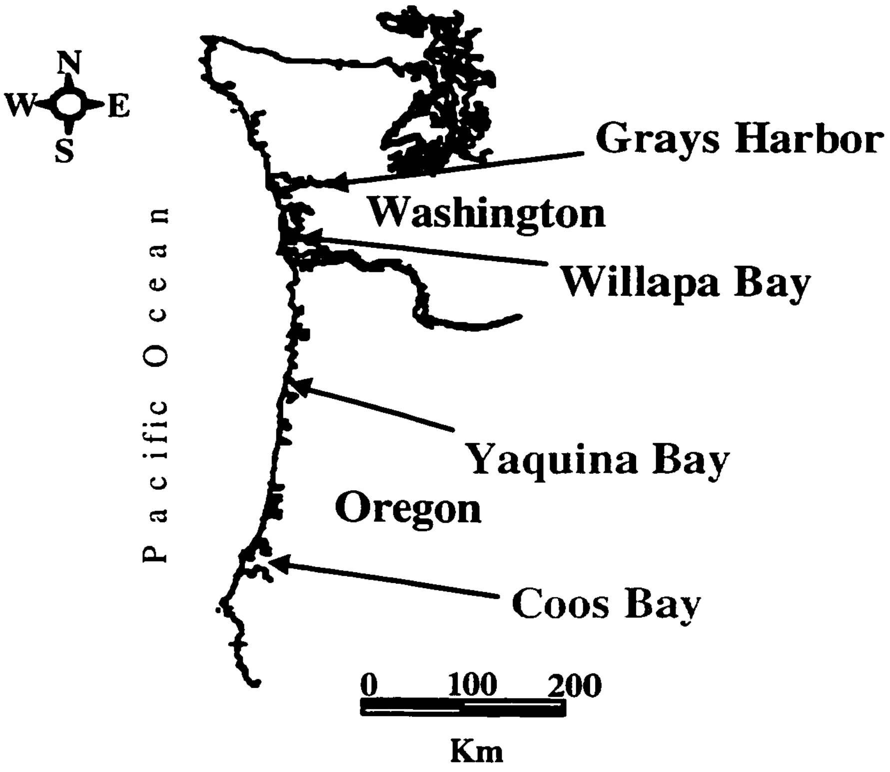

Figure 2.1. Map of the Oregon and Washington coast showing the four study estuaries, Grays Harbor, Willapa Bay, Yaquina Bay and Coos Bay.

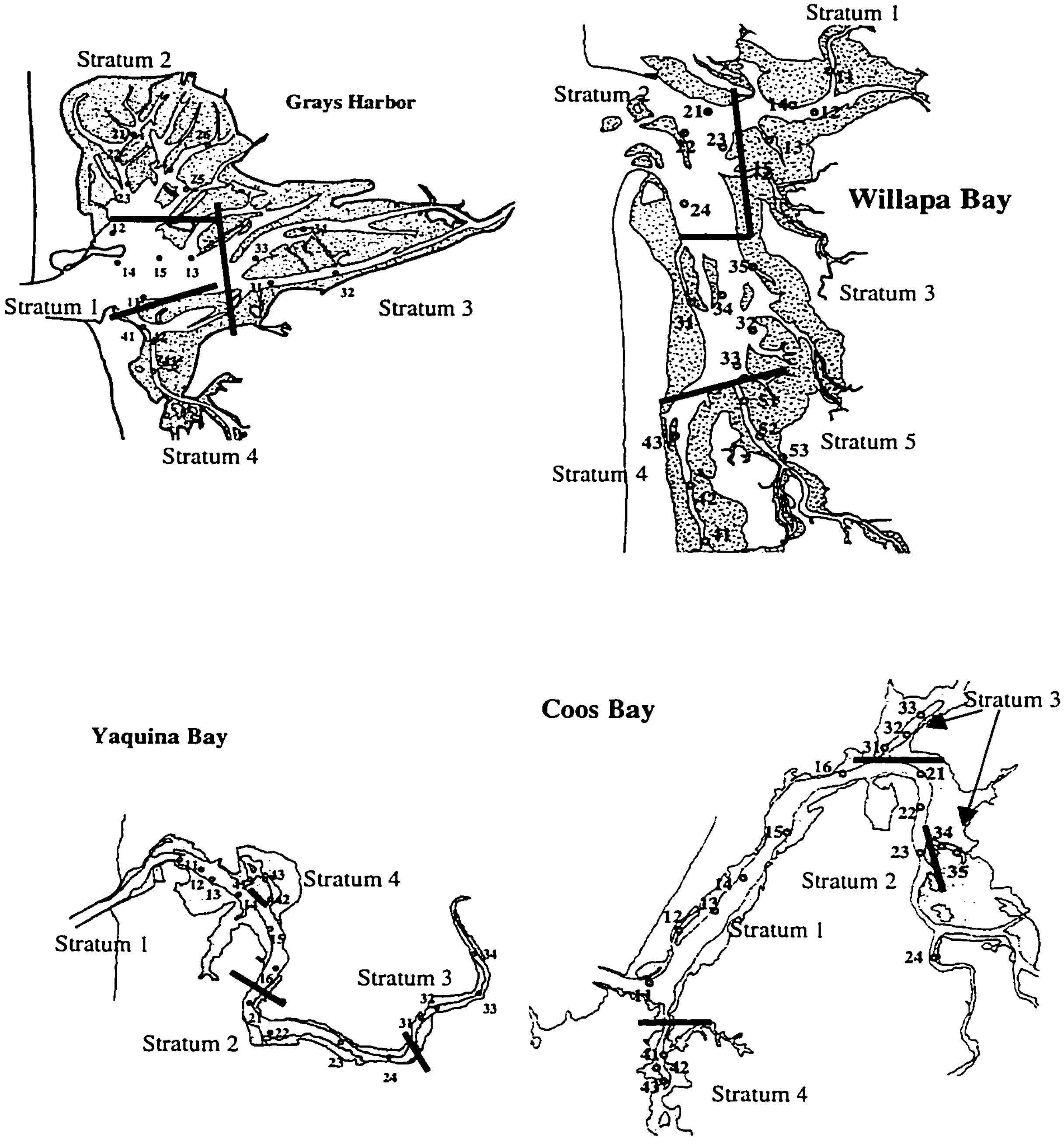

Figure 2.2. Individual maps of the study estuaries, Grays Harbor, Willapa Bay, Yaquina Bay and Coos Bay. Station location and stratum designations are shown for each estuary.

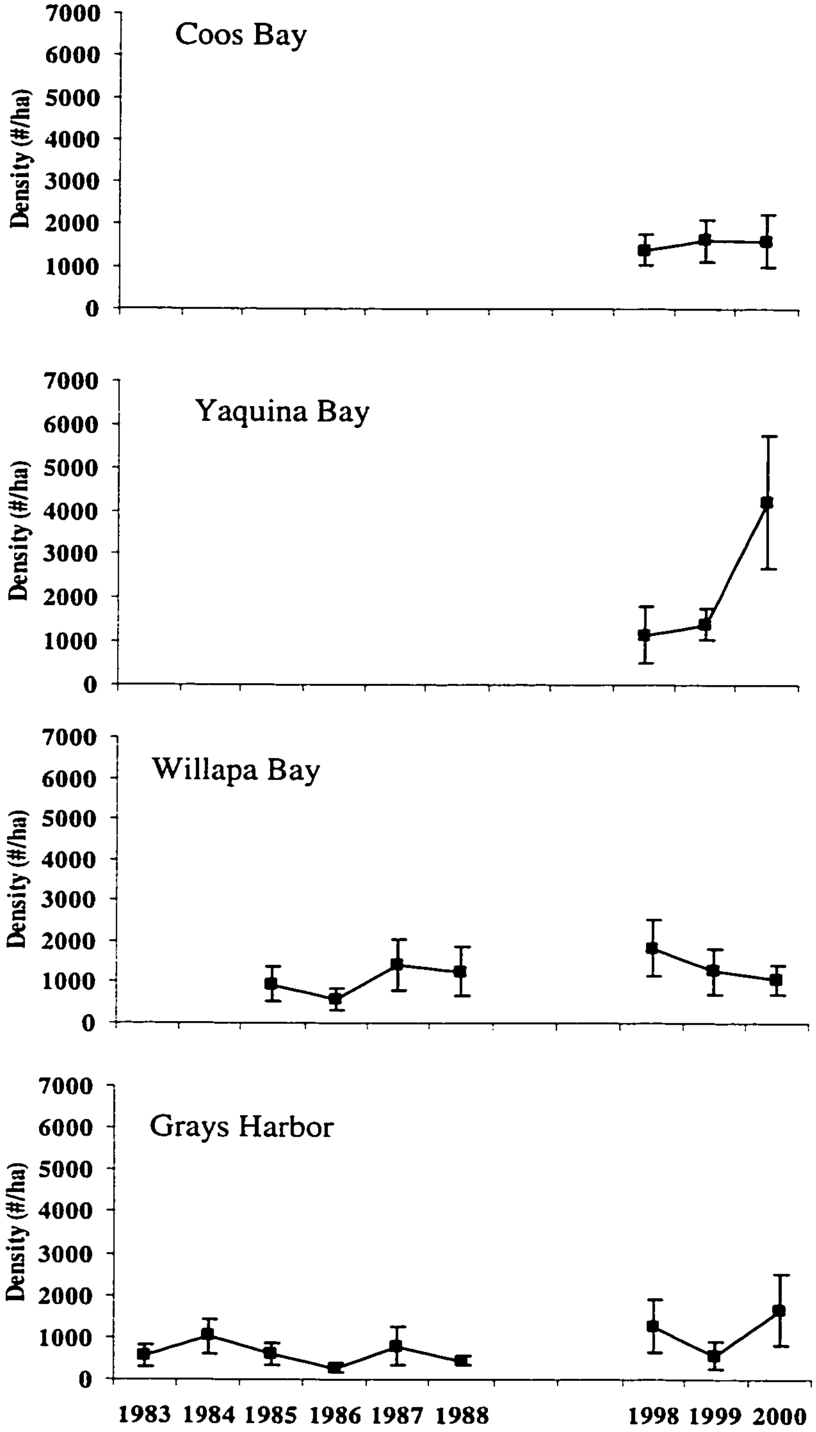

Figure 2.3. Mean density of English sole (+/- SE) for each estuary (months combined).

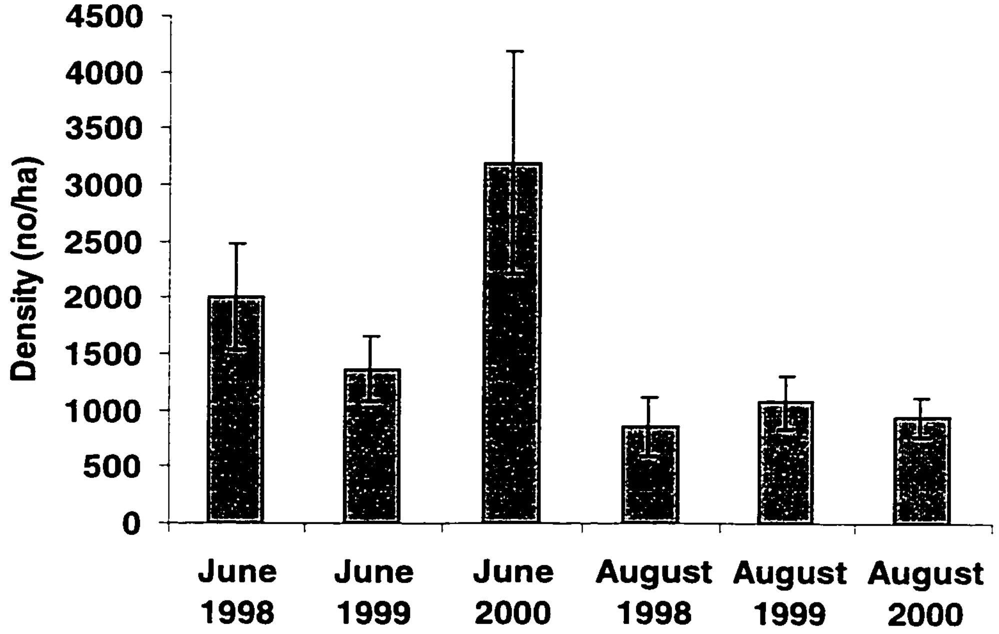

Figure 2.4. Average density of English sole (+/- SE) across all estuaries for each month during which trawl surveys were conducted in 1998-2000.

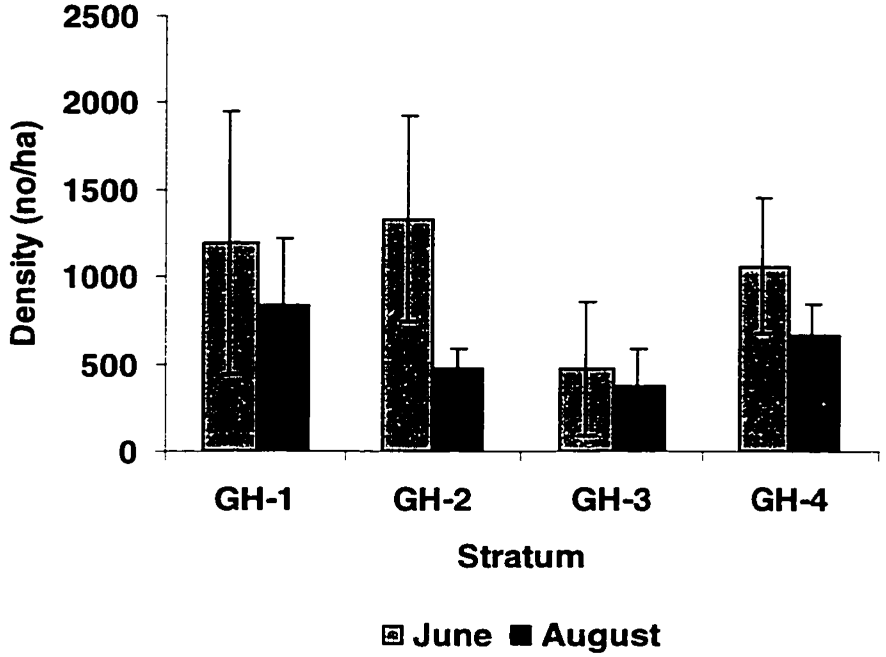

Figure 2.5. Average density (+/- SE) of juvenile English sole in Grays Harbor strata in June and August. Stratum designations are GH for Grays Harbor and stratum number 1-4. Averages are computed across all years of Grays Harbor data, 1983-1988 and 1998-2000.

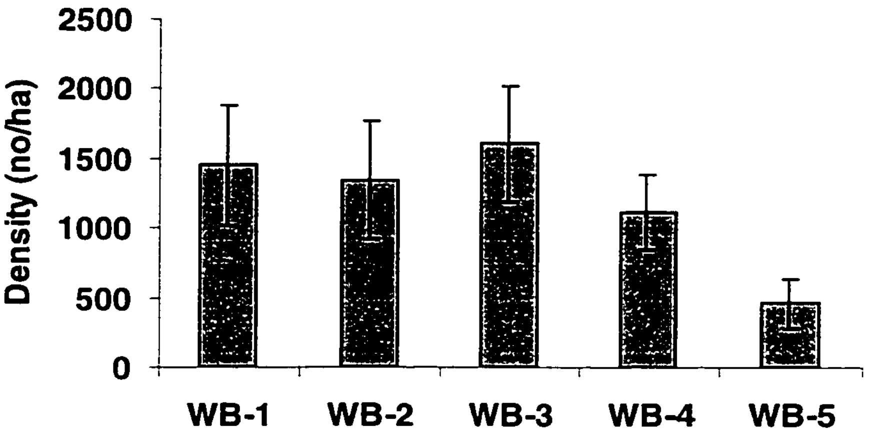

Figure 2.6. Average density (+/- SE) of juvenile English sole in Willapa Bay strata. Stratum designations are WB for Willapa Bay and stratum number 1-5. Averages are computed across all years and months of Willapa Bay data, 1985-1988 and 1998-2000.

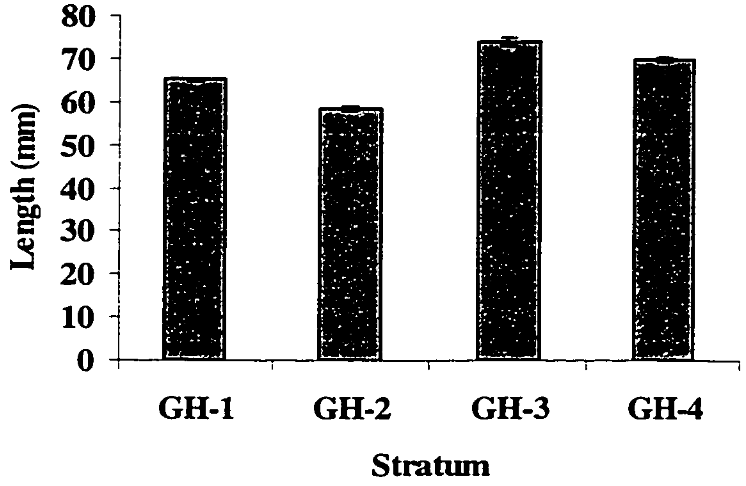

Figure 2.7. Average length (+/- SE) of juvenile English sole in Grays Harbor strata combined across both months of trawl surveys from 1983-1988 and 1998-2000.

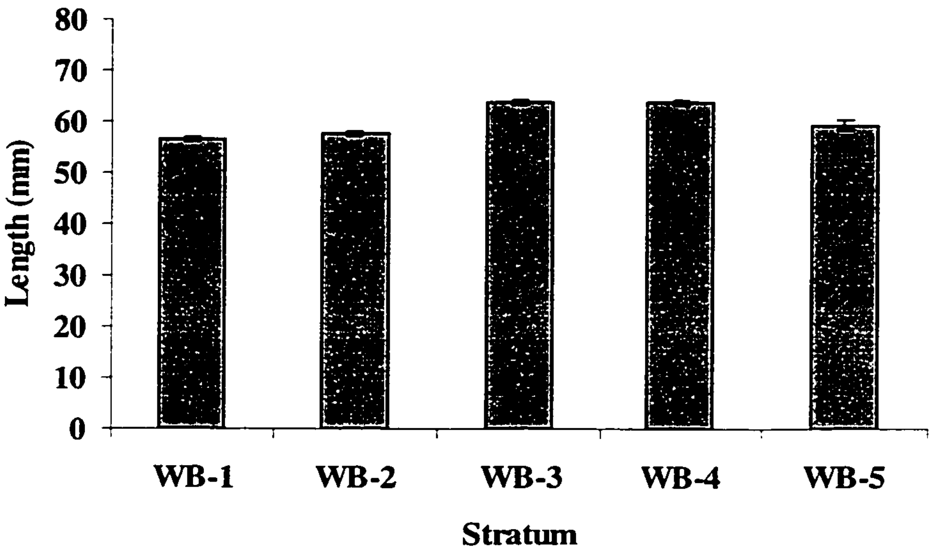

Figure 2.8. Average length (+/- SE) of juvenile English sole in Willapa Bay strata combined across both months of trawl surveys from 1985-1988 and 1998-2000.

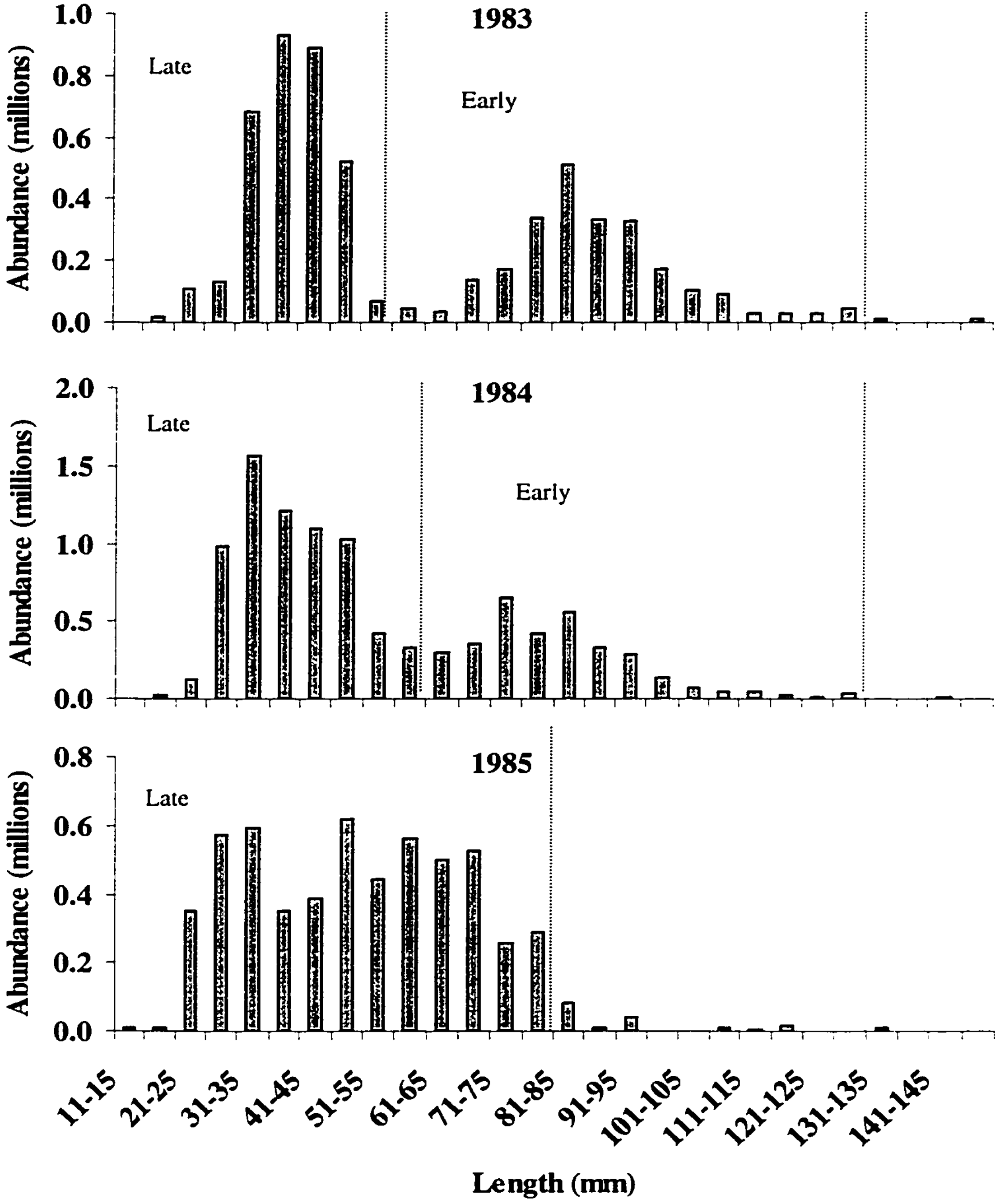

Figure 2.9. Length frequency of English sole captured in June trawl surveys of Grays Harbor in 1983-1988 and 1998-2000. Early and late settling fish are indicated by dashed lines.

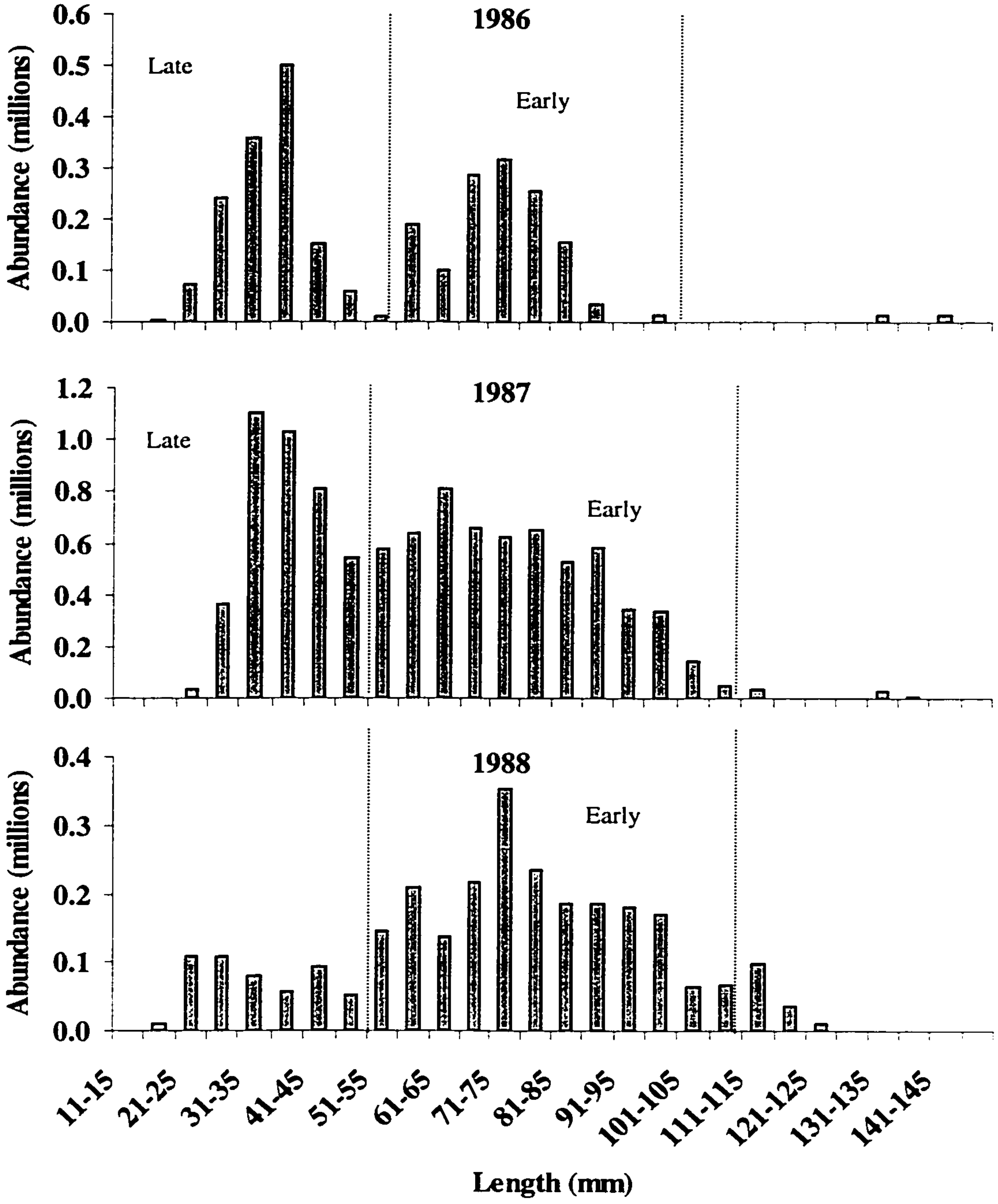

Figure 2.9 (continued). Length frequency of English sole captured in June trawl surveys of Grays Harbor in 1983-1988 and 1998-2000. Early and late settling fish are indicated by dashed lines.

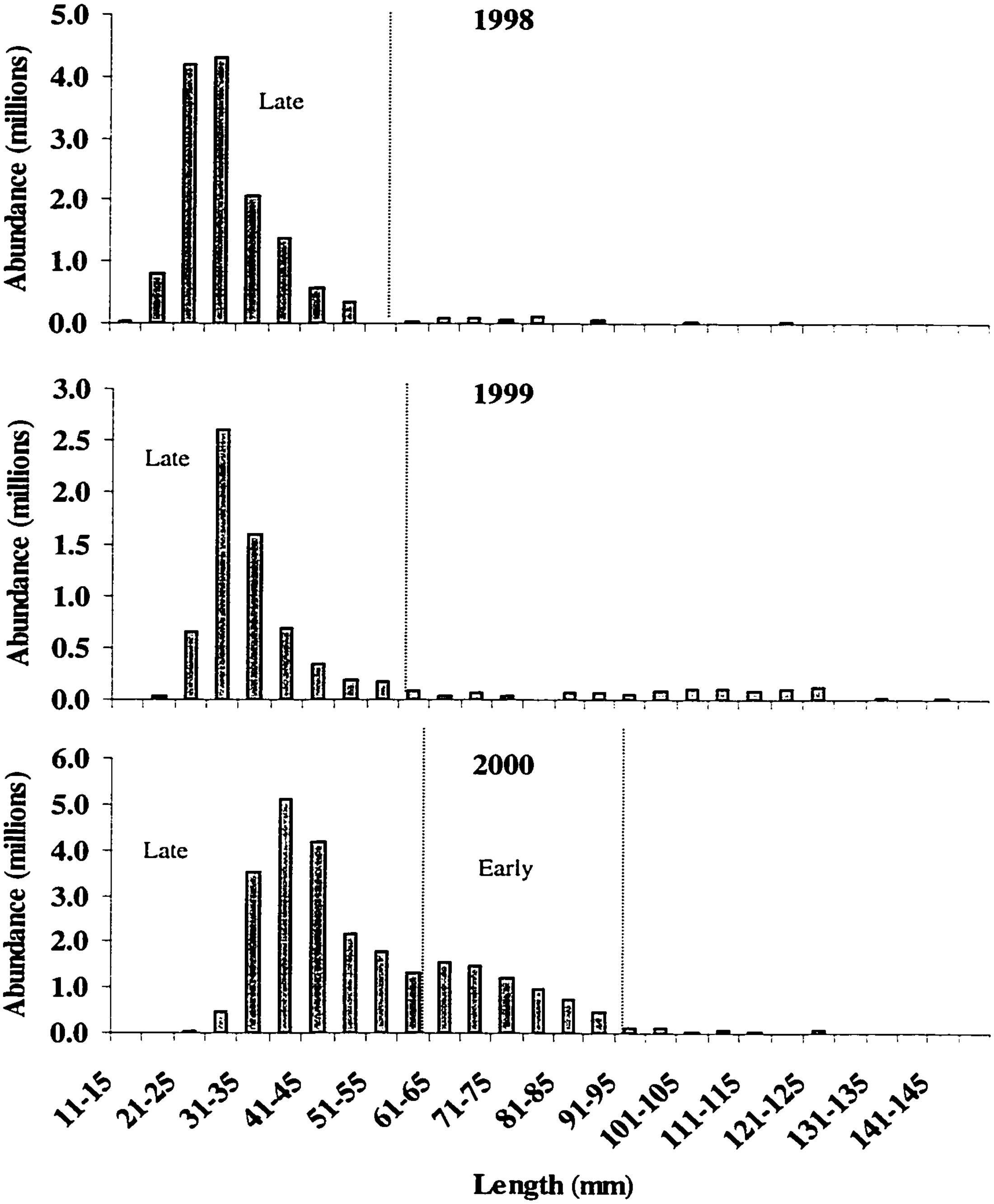

Figure 2.9 (continued). Length frequency of English sole captured in June trawl surveys of Grays Harbor in 1983-1988 and 1998-2000. Early and late settling fish are indicated by dashed lines.

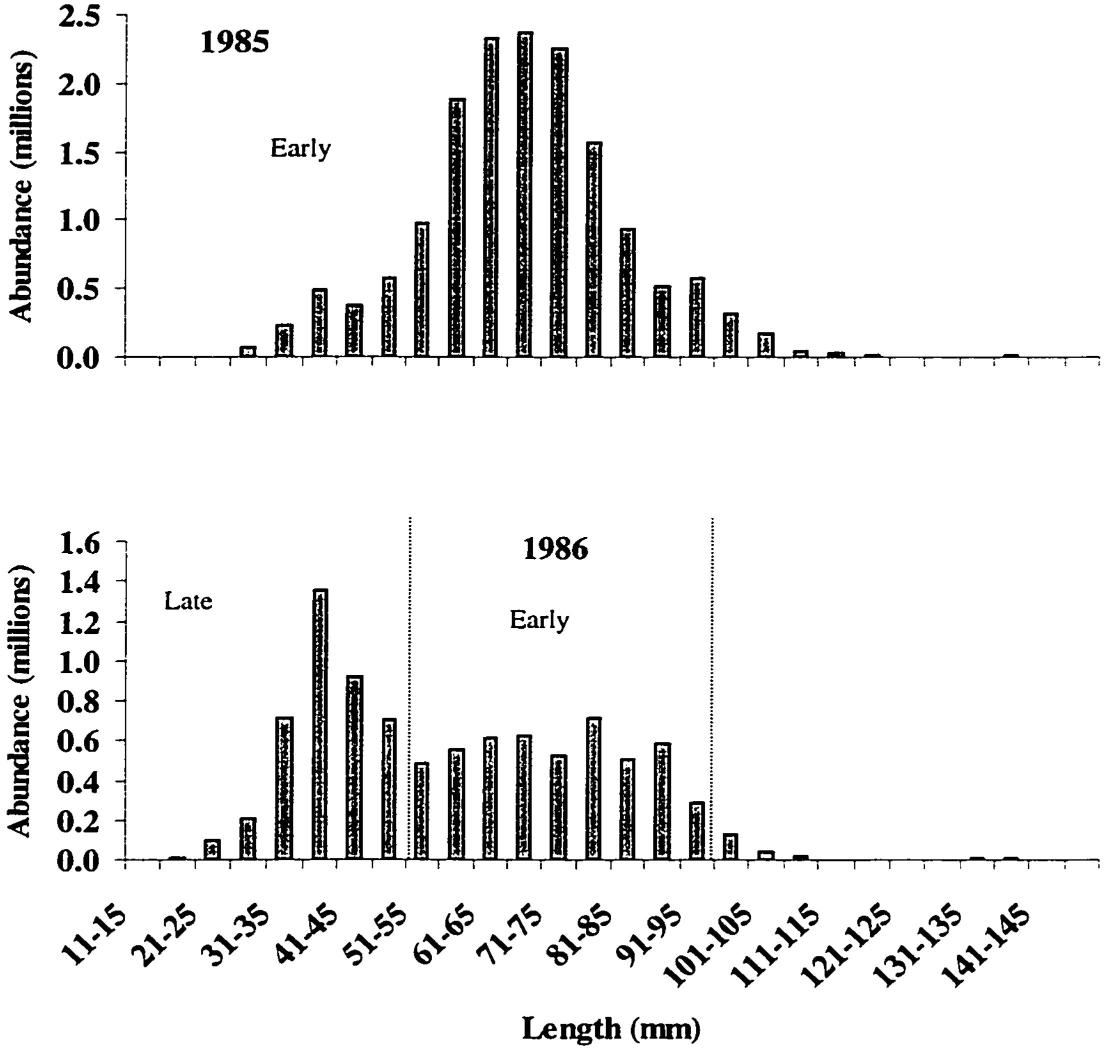

Figure 2.10. Length frequency of English sole captured in June trawl surveys of Willapa Bay in 1985-1988 and 1998-2000. Early and late settling fish are indicated by dashed lines.

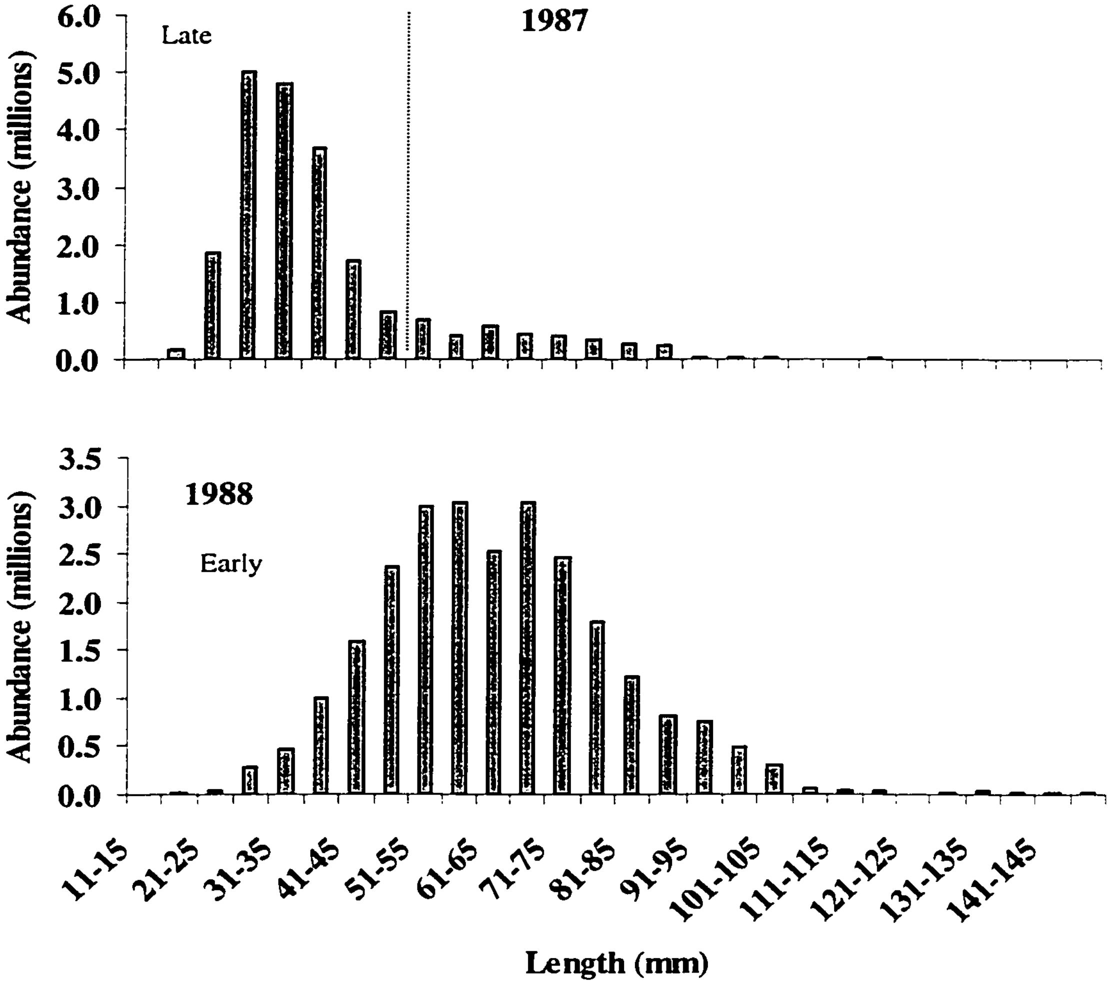

Figure 2.10 (continued). Length frequency of English sole captured in June trawl surveys of Willapa Bay in 1985-1988 and 1998-2000. Early and late settling fish are indicated by dashed lines.

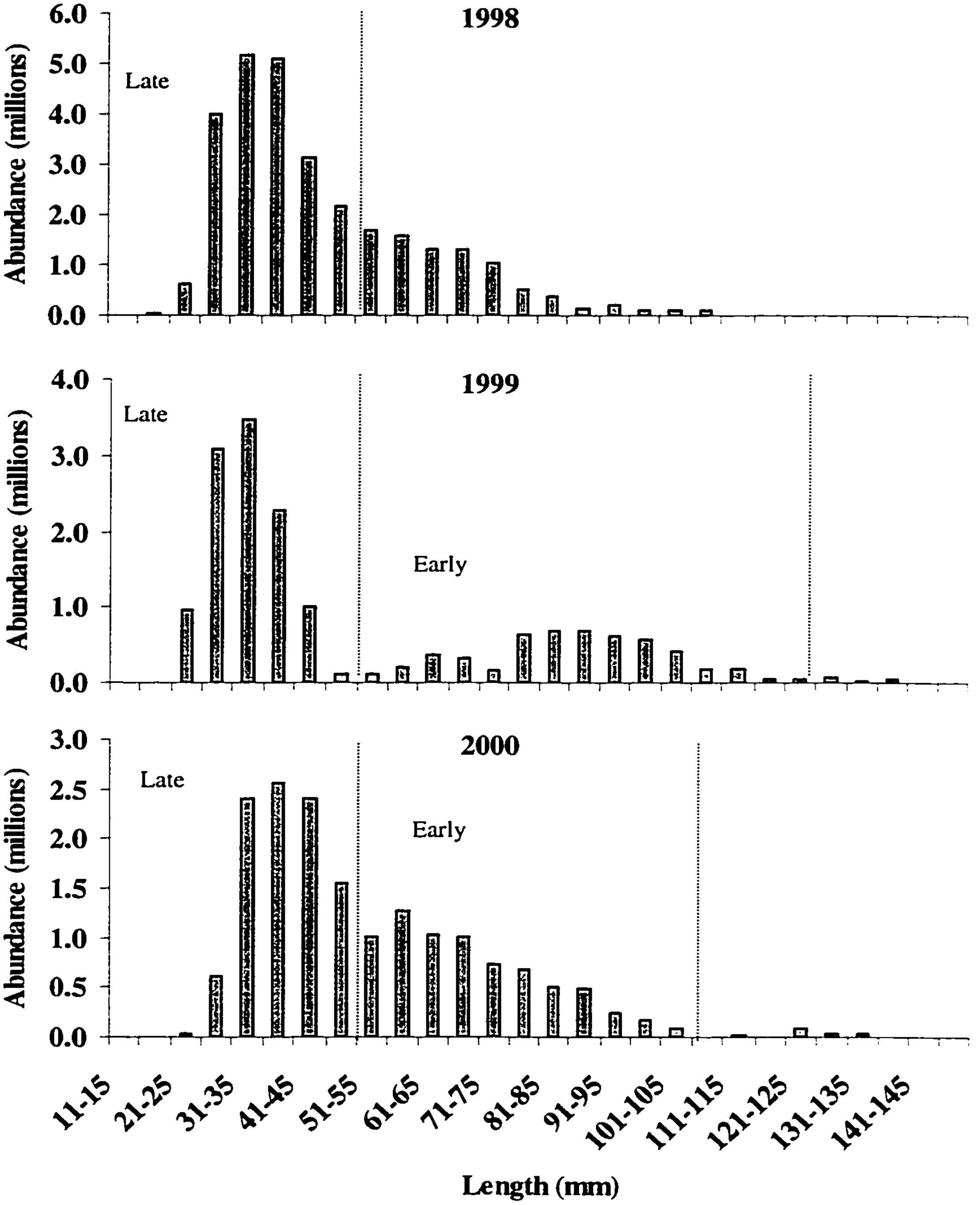

Figure 2.10 (continued). Length frequency of English sole captured in June trawl surveys of Willapa Bay in 1985-1988 and 1998-2000. Early and late settlers separated by lines.

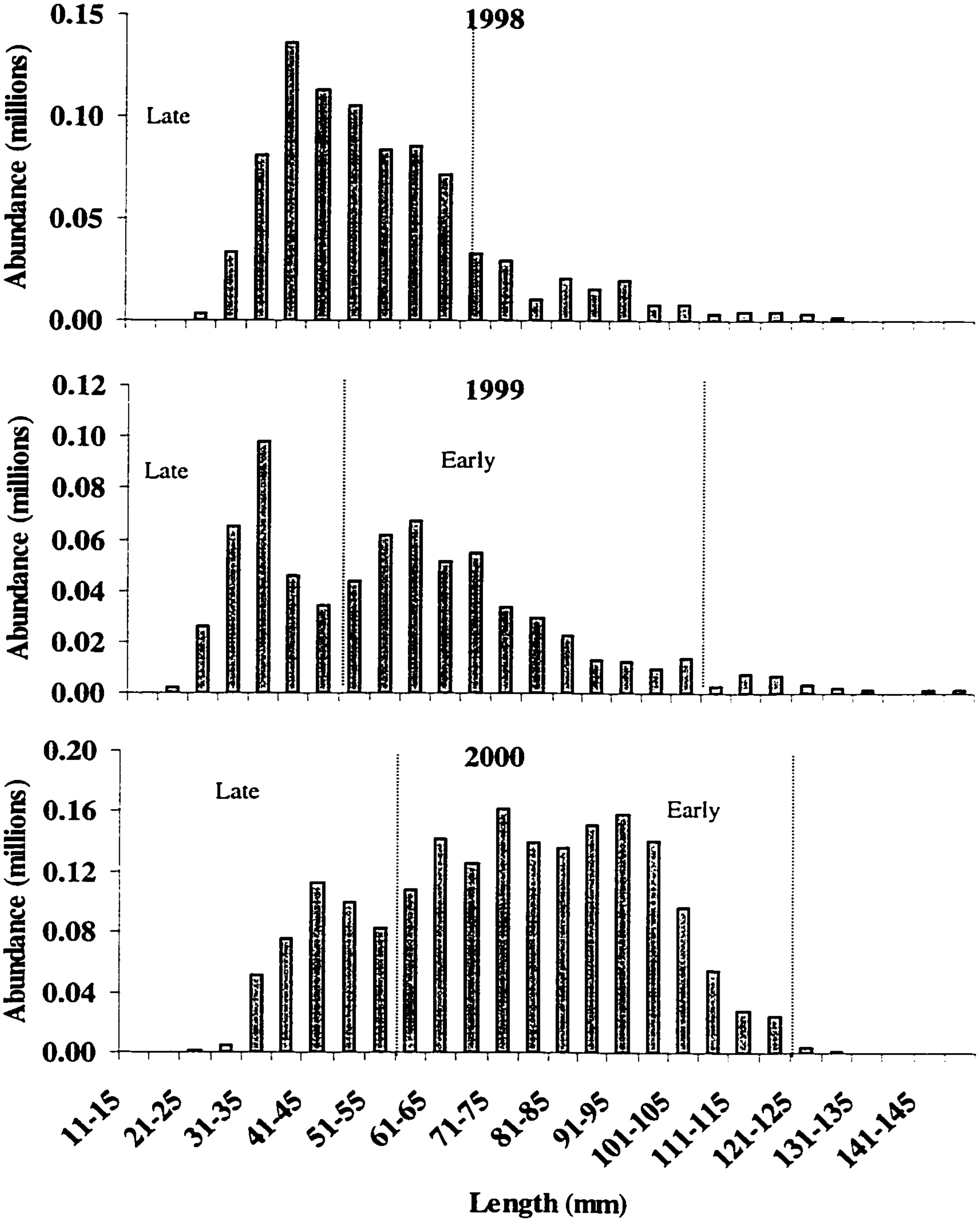

Figure 2.11. Length frequency of English sole captured in June trawl surveys of Yaquina Bay in 1998-2000. Early and late settling fish are indicated by dashed lines.

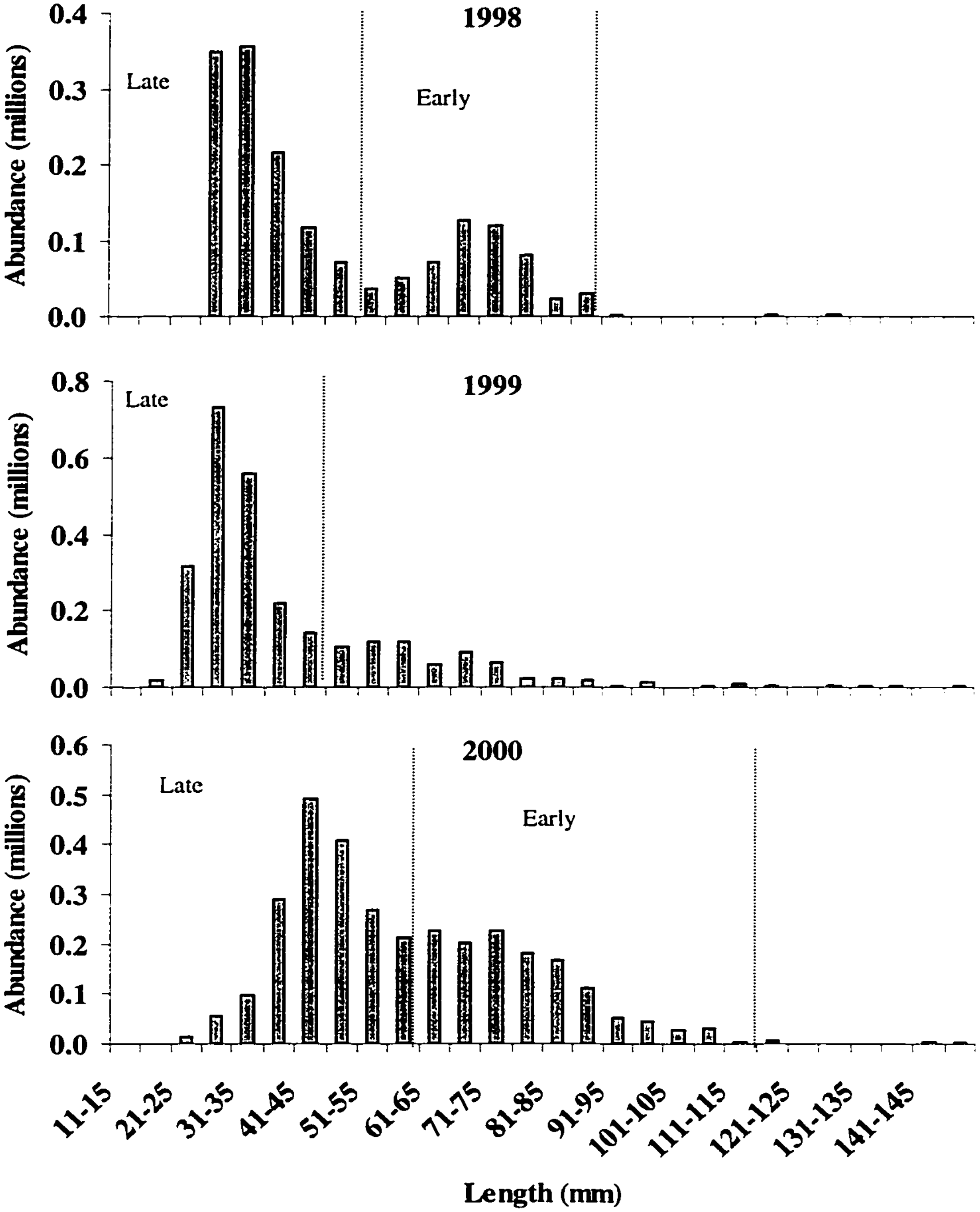

Figure 2.12. Length frequency of English sole captured in June trawl surveys of Coos Bay in 1998-2000. Early and late settling fish are indicated by dashed lines.

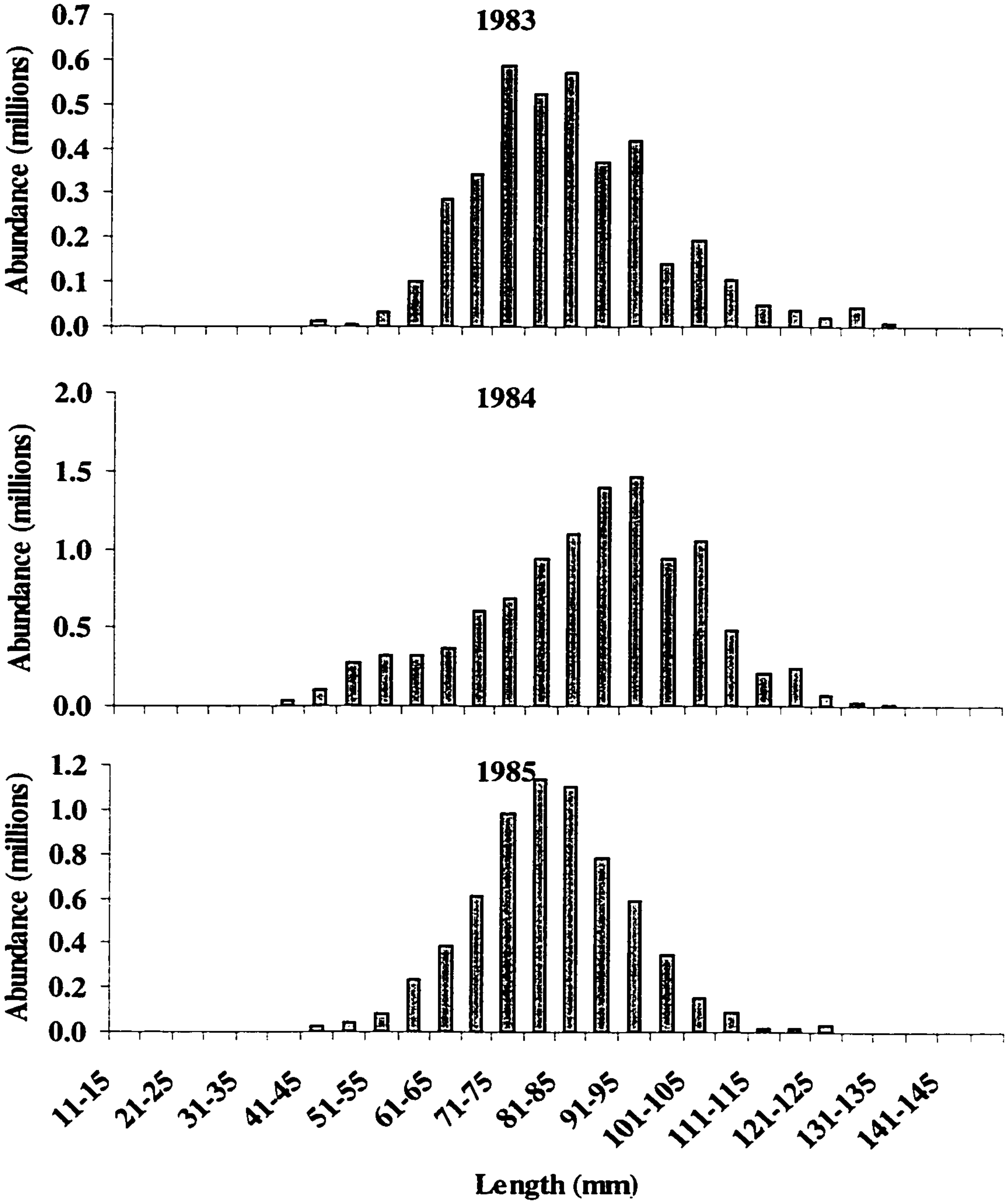

Figure 2.13. Length frequency of English sole captured in August trawl surveys of Grays Harbor in 1983-1988 and 1998-2000.

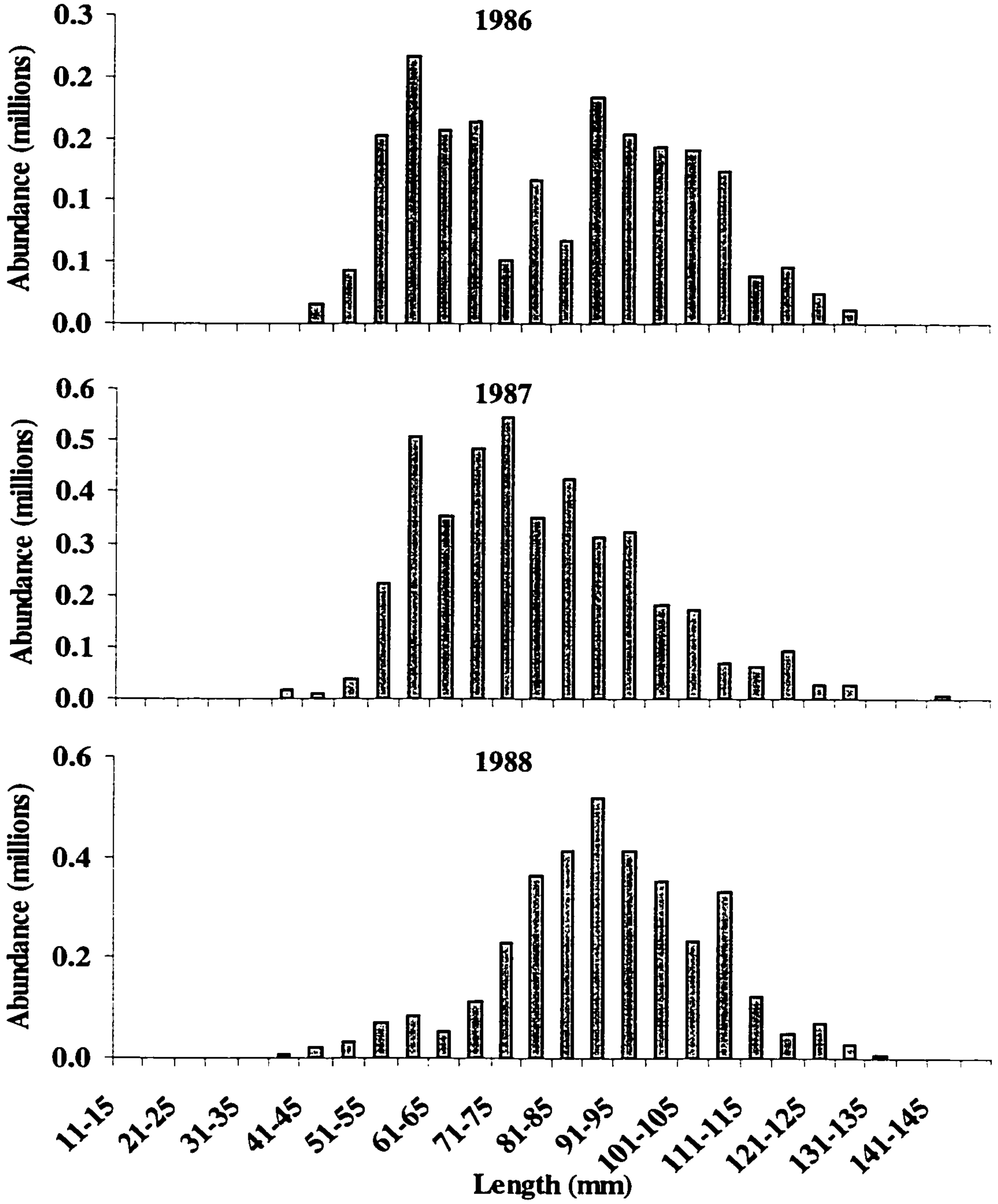

Figure 2.13 (continued). Length frequency of English sole captured in August trawl surveys of Grays Harbor in 1983-1988 and 1998-2000.

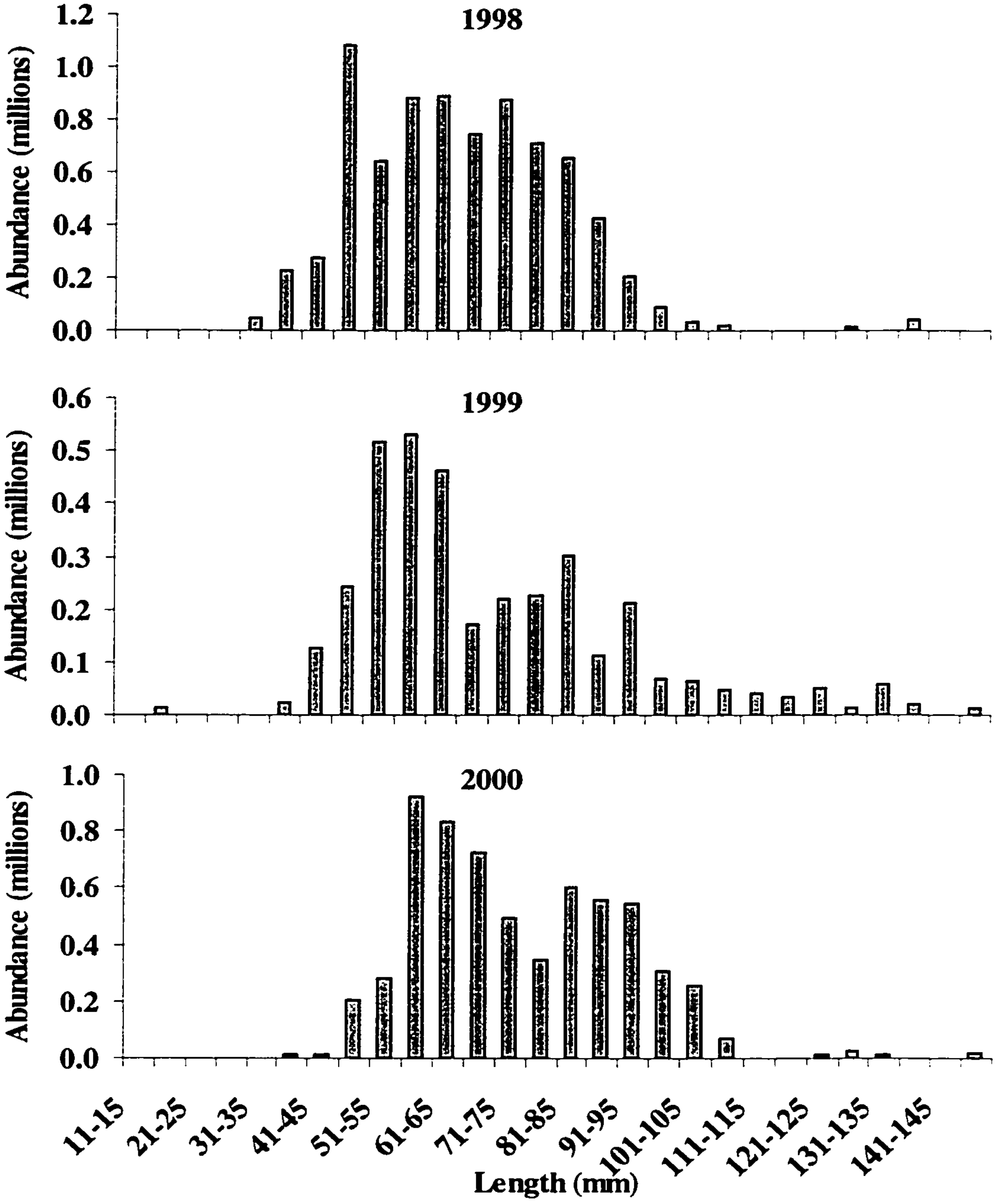

Figure 2.13 (continued). Length frequency of English sole captured in August trawl surveys of Grays Harbor in 1983-1988 and 1998-2000.

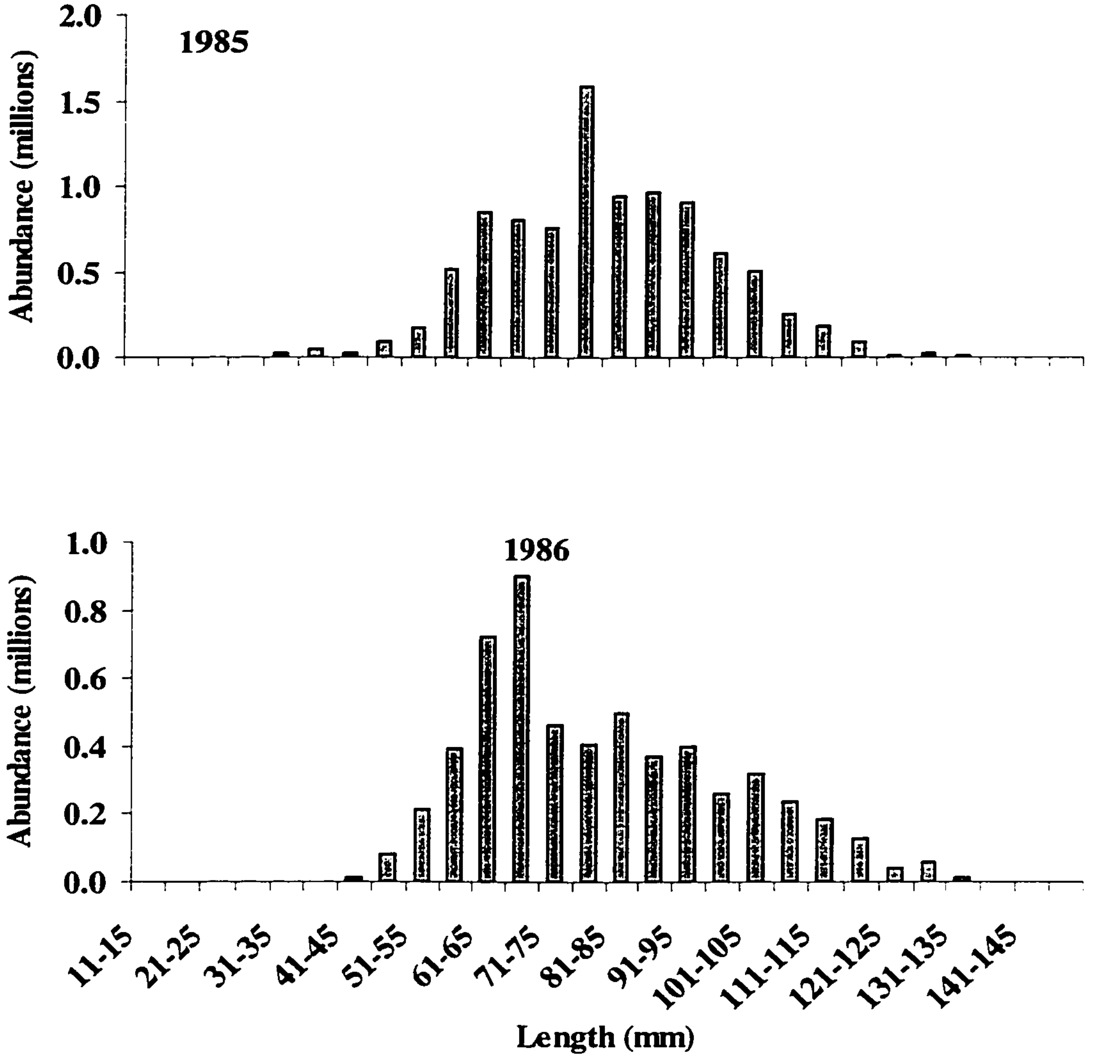

Figure 2.14. Length frequency of English sole captured in August trawl surveys of Willapa Bay in 1985-1988 and 1998-2000.

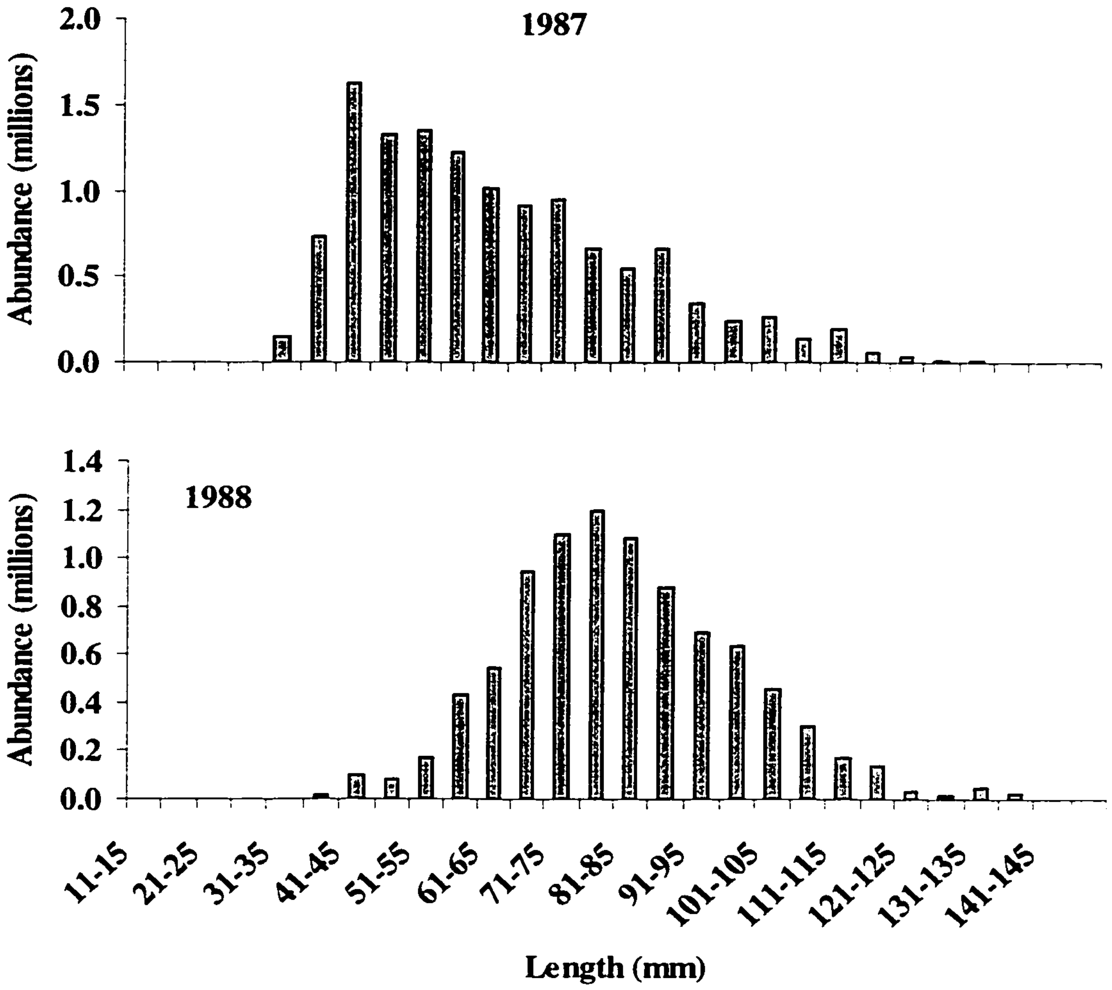

Figure 2.14 (continued). Length frequency of English sole captured in August trawl surveys of Willapa Bay in 1985-1988 and 1998-2000.

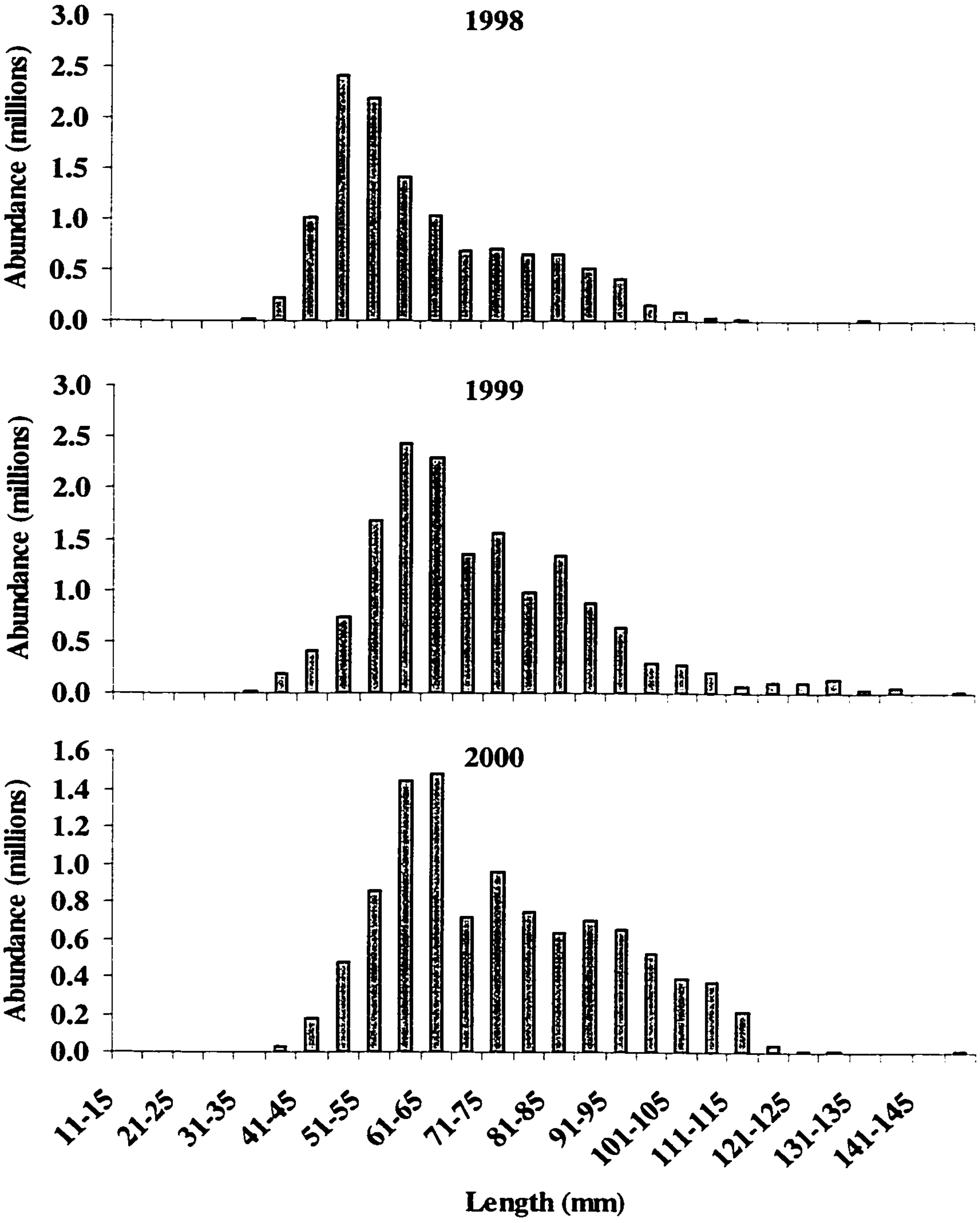

Figure 2.14 (continued). Length frequency of English sole captured in August trawl surveys of Willapa Bay in 1985-1988 and 1998-2000.

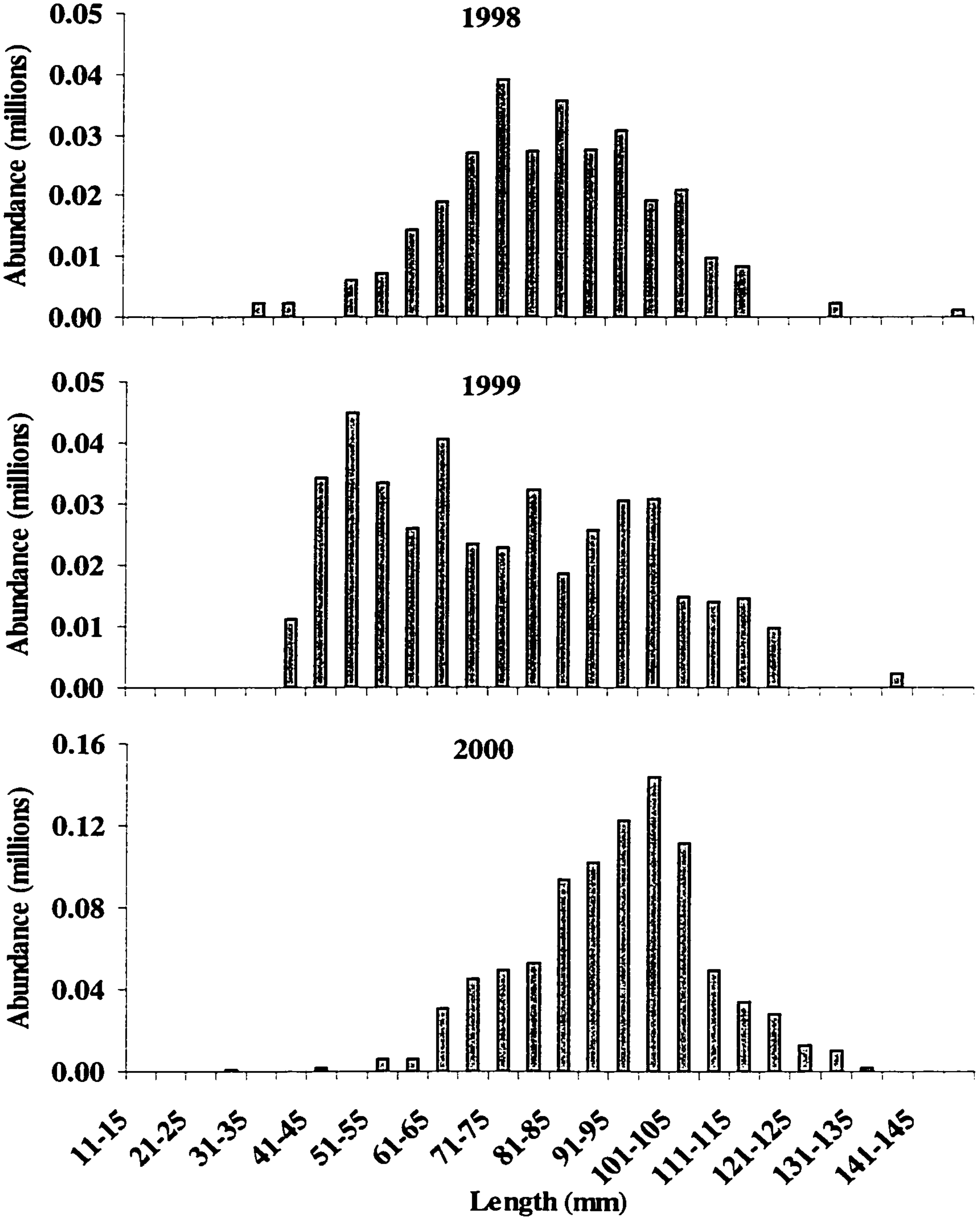

Figure 2.15. Length frequency of English sole captured in August trawl surveys of Yaquina Bay in 1998-2000.

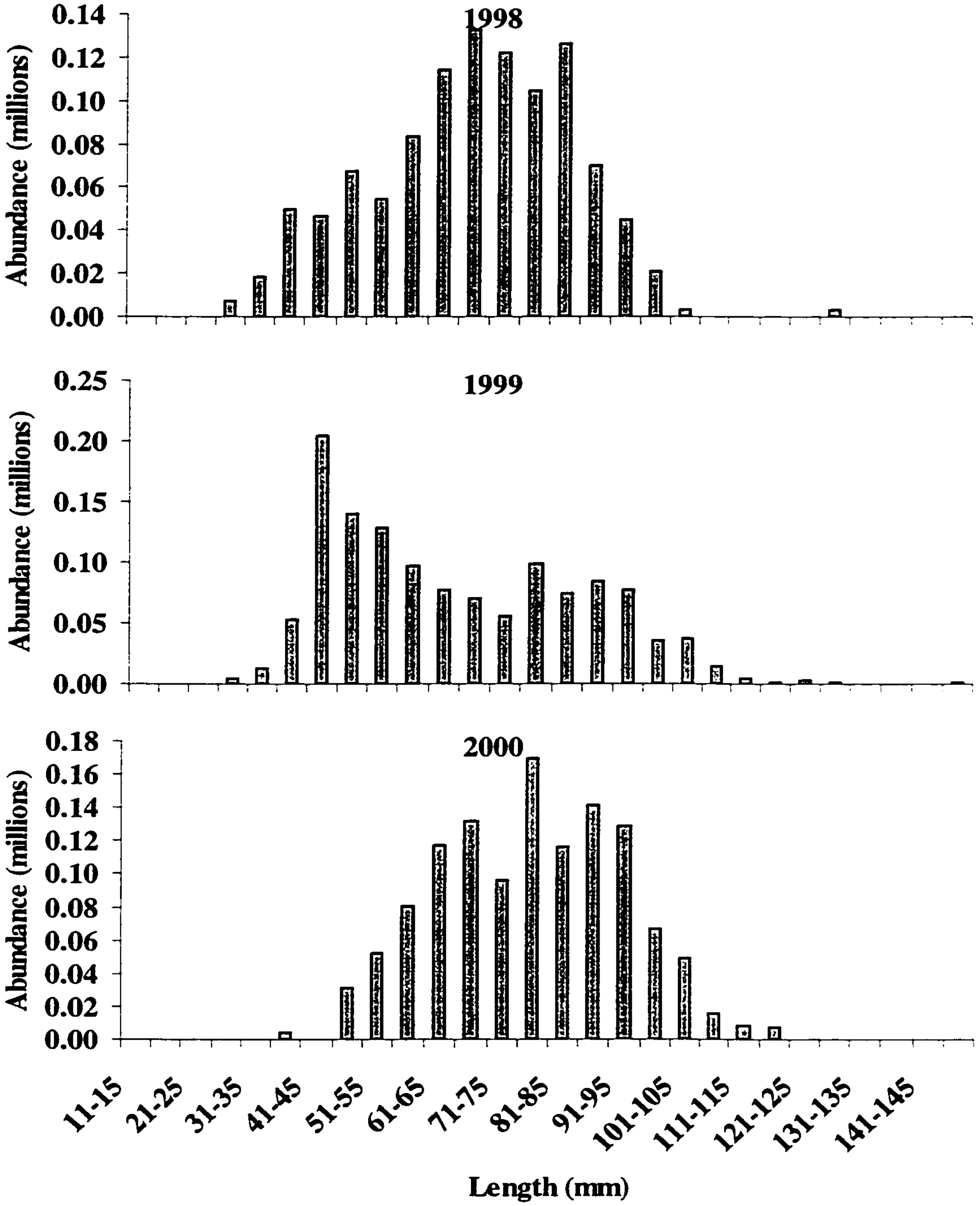

Figure 2.16. Length frequency of English sole captured in August trawl surveys of Coos Bay in 1998-2000.

Chapter 3. Transport of English sole larvae 1997-2000

3.1. Introduction

The retention of eggs and larvae in favorable areas has been hypothesized as an important determinant of marine fish year class strength (Iles and Sinclair 1982). For marine fish and invertebrate species with pelagic early life history stages, timing development so that larvae are able to settle when appropriate habitat is encountered is believed to be an important process affecting recruitment (Sale 1991, McConnaughy et al. 1994). Species that utilize nursery areas with specific characteristics, may have pelagic eggs and larvae that travel considerable distances to nurseries (Epifanio and Garvine 2001). It is therefore important that adults spawn at times and locations that maximize the likelihood that larvae will be ready to settle when they encounter appropriate nursery habitat.

The year class strength of species with pelagic life history stages has been commonly found to have strong correlations with environmental variables (Leggett et al. 1984, Botsford et al. 1989, Hollowed and Wooster 1992, McConnaughy et al. 1994, Quinn and Niebauer 1995, Schweigert 1995, Zebdi and Collie 1995). In the case of English sole (*Pleuronectes vetulus*), significant environmental correlates are found with events that occur during the pelagic early life history stages (Ketchen 1956, Hayman and Tyler 1980).

The eggs and larvae of English sole are at the mercy of oceanographic conditions for an extended period during the pelagic phase. Fertilized eggs typically float near the surface waters after release (Ketchen 1956, Orsi 1968), where the egg stage lasts 3.5 to 12 days dependent on water temperature (Ketchen 1956, English 1966, Alderdice and Forrester 1968). The total pelagic phase including both egg and larvae can last from 6-10 weeks (Ketchen 1956, Laroche et al. 1982). This extended pelagic phase provides ample time for variable environmental conditions to influence egg and larval abundance and transport.

The main stocks of English sole in Oregon and Washington spawn from 44 to 46^0 N. latitude (Hewitt 1980, Kruse and Tyler 1989, Shi 1994). The spawning season is highly protracted and spawning activity can occur from September to April (Kruse and Tyler 1983). Peak spawning usually occurs in January or February. Previous modeling indicates that water temperature and upwelling during the prior summer control development of eggs and subsequent spawning behavior (Kruse and Tyler 1983). Along the Oregon and Washington coast the suitable spawning habitat is located in a band from 0 to 30 km offshore, spanning depths of 35-90 m (Hewitt 1980, Kruse and Tyler 1989, Shi 1994).

At some point during the pelagic stages, onshore movement must occur, since metamorphosing larvae are found in shallow nearshore waters (Krygier and Pearcy 1986, Gunderson et al. 1990), offshore settlement has not been reported in the literature, although it could occur. The larvae are thought to utilize alongshore and cross-shelf current patterns associated with winter downwelling of the California Current system to move inshore. During or shortly after transformation and settlement, the juveniles move into estuaries to continue development. Metamorphosis begins at lengths of 18 to 21-mm (Ahlstrom and Moser 1975, Rosenberg and Laroche 1982), and is completed at lengths of 20 to 22-mm (Rosenberg and Laroche 1982).

The passively drifting egg and larval phases of English sole, the centralized spawning location and the dependence on current dispersal of the eggs and larvae make this species a good candidate for exploring the mechanisms by which oceanographic conditions control dispersal of this species. The estuarine dependence of the species provides an easily accessible population of juveniles for whom abundance may be estimated, and can be compared to events occurring during pelagic phases.

The purpose of this study is to examine the processes that influence transport of egg and larval stages from spawning grounds to estuaries. The objectives are to examine the correspondence of spawning to alongshore and onshore transport of English sole eggs and larvae. In Chapter 2 it was observed that multiple cohorts of English sole were found in some years in nursery areas. The modeling of transport and spawn timing was undertaken to elucidate mechanisms that were consistent with the multiple cohort phenomena for Oregon and Washington nursery estuaries.

3.2. Methods

The geographic area considered for modeling of English sole egg and larval transport was the coast of Oregon and Washington from 43^0 N latitude to 48.5^0 N latitude

(Figure 3.1). This encompasses the coastal shelf system from approximately Cape Blanco, Oregon to Neah Bay, Washington. Two aspects of the California current system were considered, alongshore (North-South) transport and cross-shelf (East-West) transport. These components of the system were treated separately. Alongshore currents were measured at three moorings along the shelf (Figure 3.1), while cross-shelf currents were simulated using Ekman theory (Pond and Pickard 1983).

Because of their protracted spawning season, English sole captured in estuaries during trawl surveys potentially originated from spawning events that occurred sometime in the previous September to April (Kruse and Tyler 1983). For example the juvenile English sole observed in estuaries in June 1999 originated from spawning events that occurred at some point between September 1, 1998 and April 30, 1999. California Current patterns were examined separately for three seasons, fall (September-December), winter (January-March) and spring (April-June).

A 300 kHz RDI Workhorse profiling current meter with a 20-degree beam angle was deployed on the mid-shelf region off Coos Bay, Oregon (position = 43.15 N latitude, 124.57 W longitude; Figure 3.1) from February 1998-June 2000 (Hickey 2000). A similar mooring was deployed offshore of Grays Harbor, Washington (position = 46.87 N latitude, 124.25 W longitude, Figure 3.1) from March 1998-May 2000 (Hickey 2000). The Coos Bay current meter was deployed in 96-m, and the Grays Harbor mooring was in 37 to 41-m of water. Data from both current meters were averaged into 1 or 2-m depth bins ranging from the surface to the bottom. All current meter data were low-low pass filtered prior to analysis and decimated to 6-hour intervals. The filter utilized was a symmetrical cosine filter spanning 121 hours with a half-power point of about 40 hours, so that 2.5 days of data are lost from the beginning and end of the record (Hickey 1981). Local topography is known to affect local currents, as water tends to travel parallel to isobaths (Smith et al. 1976, Kundu and Allen 1976). Based on the shape of the isobaths at the Coos Bay mooring location, the current meter data was rotated -15^0 to account for local turning, at the Grays Harbor mooring data was rotated 20^0 to account for local bathymetry.

Additional current meter data was obtained from a mooring off the coast of Newport, Oregon (position = 44.65 N latitude, 124.31 W longitude; Figure 3.1) from Dr. Michael Kosro (Oregon State University, Corvallis Oregon). This data was from 10-m depth and ranged from September 1997 to June 2000 with some gaps in the record. The data was rotated 21^0 to account for local bathymetry and low-low pass filtered.

Alongshore transport

Because of the availability of current meter data from three locations on the Oregon and Washington shelf, alongshore transport of English sole eggs and larvae were predicted from the current meter data themselves when possible. Alongshore currents are expected to be coherent during winter months (Hickey 1981), but may vary spatially during the spring and fall. Four transport regions were created to account for spatial variation in currents (Figure 3.1). In the region south of the Coos Bay mooring, the current meter data from the Coos Bay mooring was used to estimate the alongshore current speed and direction. In the region between the Coos Bay and Newport moorings, linear interpolation between current speeds measured at each location were used to estimate current speed and direction at a given latitude. In the region from the Newport mooring to the Columbia River, the Newport data alone determined current speed and direction. North of the Columbia River, river plume dynamics are important in determining current speed and direction (Hickey 1998, Berdeal et al. *in press*). Thus, in the region north of the Columbia River mouth, current meter data from Grays Harbor only were used to determine current speed and direction.

Some significant gaps existed in each of the mooring records. The majority of gaps were small, lasting a few hours to a few days when moorings were serviced or replaced. These small gaps were filled using relationships to other moorings that were in service at the same time. However, much larger gaps existed in the 1997-1998 record. During the fall of 1997 and early winter of 1998 there was no current meter data from the Coos Bay mooring (the record for this mooring began in February 1998). During the fall and winter of 1997-98 there was also no data for 10-m depth from the Grays Harbor moorings (the record for this mooring began in late March 1998). For the late fall of 1997 and entire winter of 1998 no records exist from the Newport mooring.

The substantial gaps in alongshore transport were filled utilizing the geostrophic assumption. In the California Current system off Oregon and Washington, winter predominantly northward wind push water onshore (in response to Ekman transport). This causes sea level height to increase at the shore, which drives a corresponding northward flow in response to the cross-shelf pressure gradient. Southward wind and offshore transport results in a decrease in sea level height nearshore and a corresponding southward flowing current. The equation for alongshore transport with the geostrophic assumption is

$$fv = \frac{1}{\rho}\frac{dp}{dx},$$

where v is the alongshore current, dp is the change in pressure acting over the distance x, f is the Coriolis force and ρ is the density of water (Pond and Pickard 1983). Because the offshore decrease in pressure gradient is unknown, it will be assumed to be constant across the shelf within seasons. Assuming that the pressure gradient is directly correlated to the sea level height, the geostrophic equation can be linearized to the form,

$$v = \alpha + \beta * ASL,$$

where the alpha and beta terms include information on dx, f, and ρ. The adjusted sea level height anomaly, ASL, is calculated by,

$$ASL = WL + (BP - 1000)$$

where WL is the sea level (in cm) and BP is the barometric pressure (in mb). The parameters alpha and beta can be determined by linear regression of adjusted sea level height against observed alongshore current velocities.

The alongshore transport on the Oregon-Washington shelf was modeled for the fall and winter of 1997-98 using adjusted sea level height anomalies at Charleston, Newport and Astoria, Oregon (Figure 3.1). Hourly sea level data was obtained from the National Oceanographic Data Center (NODC) for each station. Barometric pressure records were obtained from the nearby meteorological stations at Cape Arago (corresponding to Charleston), Newport (corresponding to Newport), Oregon and Neah Bay (corresponding to Astoria), Washington. The hourly sea level values were adjusted for barometric pressure, filtered and decimated to six-hour intervals. The adjusted sea level height (*ASL*) for each 6-hour data point was then standardized by subtracting the seasonal mean sea level from each data point and dividing by the seasonal standard deviation. Standardization allowed application of estimated regression parameters to *ASL* among all three stations where sea level was observed in order to calculate alongshore transport.

The alongshore current meter data for the Newport mooring was regressed against the *ASL* data from Newport to determine the relationship at 10-m depth for the fall of 1997. This relationship between sea level and alongshore current speed was then used to predict the current speed at the Coos Bay and Grays Harbor where no current meter data existed in the fall of 1997, and to fill small gaps in the Newport record in the fall of 1997.

Similarly, linear regressions to predict current meter data from *ASL* data were parameterized for the Coos Bay mooring in the winter of 1998. This relationship was then used to predict current speeds at Newport and at Grays Harbor during the winter of 1998 when data were not available at these moorings. This relationship was used to fill gaps in the Coos Bay mooring during early winter as well.

Cross-shelf transport

Cross shelf transport is not believed to be coherent along large sections of the coast (Brink et al. 1987). The relatively small scale of cross-shelf transport precludes the application of current meter data to the extensive coastline of Oregon and Washington. On the other hand, winds are coherent along the Oregon and Washington shelf (Hickey 1981), so frictional currents due to wind are expected to be coherent over large distances. Therefore, cross-shelf transport was calculated using Ekman formulae.

Cross-shelf transport calculations incorporated wind speed data from the National Centers for Environmental Protection (NCEP) reanalysis winds calculated based on observed atmospheric pressure fields. These winds were obtained from the National Oceanographic and Atmospheric Administration Cooperative Institute for Research in Environmental Sciences (NOAA-CIRES) Climate Diagnostics Center in Boulder Colorado. Wind records were taken for positions at 125^0 W longitude and latitudes from 42.5, 45 and 48.5^0 N latitude.

Ekman transport (U_E) was calculated using the assumptions (i.e. no boundaries, infinitely deep water, steady constant wind, etc.) and formulae derived in Pond and Pickard (1983):

$$u_E = V_0 \cos\left(\frac{\pi}{4} + \frac{\pi}{D_E} z\right) \exp\left(\frac{\pi}{D_E} z\right)$$

where

$$V_0 = 0.79 * 10^{-5} \frac{W^2}{D_E |f|},$$

W is the wind speed (m/s), f is the Coriolis force, and z is depth. The Ekman depth (D_E) was assumed constant within each season at 60-m for September to March, and 20-m for

April to June. These estimates were based on the long-term average mixed layer depth for the coastal shelf at 100-m depth over the Oregon continental shelf (Smith et al. 2001). The Ekman derived estimates of cross shelf flow were compared to observed cross shelf flow at 10-m depth from each of the three moorings for the fall, winter and spring of 1998-1999 to determine the accuracy of the predictions. Wind data from the closest location to the latitude of the egg or larvae was used to calculate cross-shelf transport.

English sole spawning activity

In this study two methods were available for estimating the spawn timing for English sole. English sole spawning activity was first estimated by back-calculating the spawn time from 19 juvenile cohorts observed in nursery estuaries from 1998-2000 (Table 3.1). The second method utilized an existing spawn timing model for English sole developed by Kruse and Tyler (1983).

The back calculation method required several assumptions regarding the development and growth of sole. Juvenile sole were assumed to settle at 20-mm total length based on literature estimates (Ahlstrom and Moser 1975, Rosenberg and Laroche 1982). The growth rate of juvenile English sole in Willapa Bay and Grays Harbor in 1985-1987 was estimated to average 0.42 mm/day, ranging from 0.21 to 0.50 mm/day (Shi 1994). Using these two pieces of information and the observed mean length for each cohort (Table 3.1), I back calculated the settlement date for each cohort of English sole observed in nursery estuaries.

Studies of egg development rates in the laboratory have indicated the time to hatch for English sole eggs can range from 4-8 days depending on the ambient temperatures (Ketchen 1956, English 1966, Alderdice and Forrester 1968). Based on these laboratory studies a development model was constructed for English sole eggs using temperature data (Figure 3.2). This model utilized an exponential equation, with slope = -0.1394 and intercept = 18.94.

Larval development rates are less well known. Larval stage duration has been estimated at between 42 and 70 days (Ketchen 1956, Laroche et al. 1982). At temperatures of 9-11^{0}C, larval development was found to last 56-70 days (Laroche et al. 1982). Because of the limited information on larval development, I assumed the same relationship to temperature as in the egg stage. Therefore, I fit the same slope as used for the egg stage (r = -0.1394) to the two larval data points, calculating a new intercept = 250 (Figure 3.3). The development models were driven using average water temperatures for the first 12 days after spawning and the first 42 days after hatching.

Water temperature data used to set the development rates for eggs and larvae was taken from three sources. The primary source of temperature data was the Newport buoy, but the presence of large gaps in the data series necessitated the use of auxiliary temperature data from the Columbia River buoy in 1998-1999 and 1999-2000. Regression relationships between temperature data at these two buoys were developed and the gaps in temperature data larger than 24 hours were filled using these relationships. For 1997-1998, gaps were filled using regression relationships between water temperature at the Newport buoy and the South Beach, Oregon monitoring station inside Yaquina Bay.

Using the back-calculated settlement date and the egg and larval stage lengths, the spawn time for each cohort of juvenile English sole observed in nursery estuaries was back calculated. The results of these back calculated spawn dates where then compared to the dates from the second method, a model of spawning activity derived by Kruse and Tyler (1983).

The Kruse and Tyler (1983) spawn timing model simulates English sole spawning based on an index of bottom temperature (Kruse and Huyer 1983) estimated from monthly sea level data at Neah Bay, Washington. The model calculates the average summer bottom temperature and computes a minimum date when peak spawning can occur after September 1 of each year. This date estimates the time when gonadal development is likely to have been completed for each year. Additionally, spawning does not occur below a temperature of 7.8^0C and spawning can be delayed by temperature increases of greater than 0.95^0C in any month. Peak spawning is also limited to two months or less and peak spawning must be completed by May of each year. Kruse and Tyler (1983) originally simulated spawning activity for the winters of 1947-51, 1969-75 and 1976-79. I programmed the Kruse and Tyler (1983) model into Visual Basic to estimate spawn time for the winters of 1997-2000, when spawning activity would produce English sole captured during trawl surveys in the following summers (1998-2000). Monthly sea level data for Neah Bay, Washington was obtained from NODC for

1997-2000. The dates of peak spawning were then calculated for 1997-2000 using this new data and the Kruse and Tyler (1983) model.

Simulation of English sole transport

The egg and larval transport model incorporated the alongshore and cross-shelf currents. The spawn dates back-calculated from juvenile cohorts observed in estuaries set the initial time when eggs were released into the water column. The egg and larval development models set the length of pelagic stages. The final piece of information necessary to predict egg and larval transport was the depth distribution of each life history stage. The egg stage is known to float near the surface when first spawned (Budd 1940, Orsi 1968), therefore currents for the 10-m depth were used to calculate the transport direction and distance during this stage. Larvae are thought to remain in surface waters in depths of less than 50-m (Kruse and Tyler 1989). The median depth distribution for larvae was also assumed to be 10-m and distance and direction traveled for this life history stage was calculated at the 10-m depth.

English sole spawning locations are known to occur in water of less than 90-m depth over soft bottom sediment (Kruse and Tyler 1989, Shi 1994). Potential spawning locations occur all the way along the Oregon and Washington shelf from Cape Blanco to Willapa Bay (Figure 3.1), but the majority of the spawning is believed to occur in a narrow band along the coast between 44 and 46^0 N latitude (Shi 1994). The most concentrated spawning locations are thought to occur just off the coast of Newport, Oregon. The transport model was run for larvae spawned at 44, 45 and 46^0 N latitude.

The cumulative pelagic transport for each cohort of juvenile English sole observed during trawl surveys of coastal estuaries was calculated by summing the total distance traveled over each day. Latitude was calculated daily for the Ekman formulae and to determine the region for alongshore transport. The daily larval trajectory and the cumulative transport were calculated and plotted to determine final destination of each cohort assuming passive transport by the coastal current.

3.3. Results

The alongshore current at 10-m depth was predominantly northward with periodic interruptions in the fall (September-December) of 1997 (Figure 3.4). In 1998 and 1999 September currents were predominantly southward, turning to northward in early November (Figures 3.5-3.6). Currents were strongest to the north during the winter from January to February in all years (Figures 3.7-3.9), and predominantly southward during the spring (April to June) in all years (Figures 3.10-3.12). There were substantial gaps (greater than 1 month) in the record for all three moorings in fall and winter 1997-1998, while only small gaps (5 to 24 days) in the current meter data existed in other years. The alongshore transport at the three moorings along the coast were generally well correlated ($r = 0.50$ to 0.91) during periods when the records overlapped, except during the spring of 1998 (Table 3.2).

Alongshore transport

Sea level anomalies at Charleston, Newport and Astoria, Oregon peaked during October and late November of 1997, and were consistent among the three stations (Figure 3.13). Sea level height at Newport were linearly related ($r = 0.63$) to alongshore transport measured at the Newport mooring (Figure 3.14). Predicted alongshore currents for the fall based on this linear relationship of sea level height and current meter data matched observed currents (Figure 3.15), although there was a tendency of predicted currents to have slightly lower magnitude peaks than observed currents. Where gaps in the current meter data occurred, this relationship was used to predict alongshore currents for the Coos Bay and Grays Harbor mooring in the fall of 1997 based on sea level height measured at Charleston and Astoria.

During the winter months (January-March) of 1998 sea level height at Charleston, Newport and Astoria were very coherent, with peak positive values occuring in January and February (Figure 3.16). The relationship between sea level height and alongshore transport was strong for the Coos Bay current meter ($r = 0.87$; Figure 3.17). The predicted currents using the linear parameters were very similar to the observed currents (Figure 3.18). Where gaps in the current meter record occurred, the relationship between current meter data in Coos Bay and Charleston sea level were utilized to estimate alongshore currents at Newport and Grays Harbor in the winter of 1998. The linear relationship for the Coos Bay mooring was also utilized to fill significant gaps in its own current meter record.

Cross-shelf transport model

During the fall of 1997-1999 winds were highly variable among sites along the Oregon and Washington shelf (Figures 3.19-3.21), but winds were predominantly northward during this period. Wind speeds were also northward with periodic interruptions during the winter of 1998-2000 (Figures 3.22-3.24) with greater coherence among stations. Northward winds drove predominantly onshore currents during the winter. In the spring of each year winds were predominantly southward (Figures 3.25-3.27), however there were frequent interruptions of the southward winds.

The calculated cross-shelf Ekman transport in the fall of 1998 was not similar ($r = -0.13$ to 0.43) to the observed transport at the moorings (Figure 3.28). In the winter correlations between observed currents and Ekman transport were worse ($r = -0.11$ to 0.28; Figure 3.29). In the spring the match between observed and predicted cross-shelf currents was better ($r = 0.36$ to 0.47; Figure 3.30). This is consistent with observations that cross-shelf currents are dominated by processes with short alongshelf scales (Brink et al. 1987).

English sole spawning activity

In 1998, the early settling cohort of juvenile English sole in Coos Bay was computed as derived from a spawning date of January 6, 1998 (Table 3.3). Late settling cohorts observed in June in all estuaries were spawned from February 24 to April 2, 1998 (Table 3.3). Some of these back-calculated spawn dates agreed well with periods of spawning predicted by the Kruse and Tyler (1983) model (Figure 3.31). The Kruse and

Tyler (1983) model predicted three spawning events, occurring in October, December and February-April. However, if spawning occurred in October, few of the larvae appear to have survived.

In 1999 there were early settling cohorts of sole in Willapa and Yaquina Bays derived from spawning that occurred on November 12 and December 27, 1998 (Table 3.3). Spawning from March 2-22 was predicted from back calculation of spawn dates for late settling cohorts in all estuaries (Table 3.3). The Kruse and Tyler (1983) model predicted spawning occurred in January, and during March to mid-April in 1999 (Figure 3.32). There was reasonable agreement in spawn dates for at least the late settling cohort of English sole observed in 1999 by both methods. The timing of spawning for the early settling cohorts was one week later for the Kruse and Tyler model than for back calculation. The settlement data indicate that some spawning occurred in November, although this was unexplained by the Kruse and Tyler model.

In 2000 early settling cohorts were observed in all four estuaries corresponding to spawning occurring from November 30 to December 9, 1999 (Table 3.3). Four late settling cohorts were also observed in the estuaries and were derived from spawning occurring in a fairly narrow window from February 13-23, 2000 (Table 3.3). According to the Kruse and Tyler (1983) model spawning occurred continuously in 2000 from about January 7-March 21 (Figure 3.33). As in the previous year, spawning predicted by back-calculation was consistent with the Kruse and Tyler (1983) model for the late settling cohorts, but back calculated spawn dates for the early settling cohorts were two weeks earlier than predicted by Kruse and Tyler (1983).

Simulation of English sole transport

Transport of the early cohort of English sole in 1997-98 was northward from the assumed spawning location and passively drifting larvae would have disappeared from the study area before settlement (Figure 3.34). The late settling cohorts from all estuaries would have moved southward (Figure 3.35), and exited the system to the south after 5-26 days assuming passive drift (Table 3.4).

In the winter of 1998-99, early settling cohorts again moved northward and onshore (Figure 3.36). The trajectory of the passively drifting larvae pushed them out of the system after 15 (Willapa Bay early cohort) and 34 (Yaquina Bay early cohort) days (Table 3.4). Late settling cohorts in 1998-1999 moved northward and onshore during the first half of pelagic life and then moved southward and offshore exiting the system after 20 to 43 days (Figure 3.37).

In 1999-2000 early settling cohorts would have moved onshore and northward (Figure 3.38), eventually settling out on the coast after 66-68 days assuming passive drift (Table 3.4). All late settling cohorts initially moved northward and onshore, eventually switching to southward and offshore (Figure 3.39). If they were drifting passively, larvae for these late settling cohorts would have exited the system after 25-45 days (Table 3.4).

In all but four of the cases examined, the cohorts of English sole would have been moved out of the system prior to settlement as juveniles. The assumption of passive transport of the larvae caused the larvae to move either south of Cape Blanco, Oregon or north of Cape Flattery, Washington usually after about 0.5 to 1.5 months. Based on the current patterns and assumed depth distribution of eggs and larvae only limited spawn dates would have allowed retention of passively drifting larvae within the boundaries of the Oregon and Washington coast (Figures 3.31-3.33). Based on back-calculation from settlement date, spawning was not predicted to occur during these times, except in 2000 (Figures 3.31-3.33).

3.4. Discussion

The measured and estimated currents utilized for this study were meant to predict the fate of eggs spawned on the coastal shelf of Oregon and Washington in 1997-2000. Adjusted sea level height anomalies were highly correlated to alongshore currents in the fall and winter of 1997-1998, as would be expected according to geostrophic assumptions. There was variation in northward transport on the order of 7-10 days throughout the fall and winter, with a strong transition towards southward transport usually occurring during late March. Coherence in alongshore currents was strong for the three moorings during the fall and winter, while currents were less coherent in the spring. These results were consistent with the present knowledge of the California current system and its characteristics during fall, winter and spring months (Hickey 1998).

A large proportion of the variance in observed cross-shelf transport was related to local effects (not explained by the Ekman simulation). It was expected that larvae would not experience such local effects throughout the entire region of interest. Therefore, Ekman formulae were considered more appropriate for modeling large-scale transport conditions. Use of the Ekman simulation eliminated local cross-shelf current variation (i.e. Brink et al. 1987). However when the observed cross-shelf current was used in the place of Ekman currents to predict larval trajectories, the difference was only slight (compare Figures 3.37 and 3.40 for example). This is because the cross-shelf transport is not large compared to the north-south transport. Therefore, the choice of cross-shelf current source has little effect on the results of the passive transport modeling, since in all cases eggs and larvae were lost from the system either to the north or south.

The results of the larval trajectories for English sole spawning in the winters of 1997-2000 demonstrate that passive larval drift in dominant alongshore currents cannot account for the distribution of sole in northwest estuaries. Total pelagic periods were long (46 to 73 days), allowing long distances of travel up and down the coast. Without exception the early cohorts of English sole moved north, while the late cohorts often moved north, then eventually south after the spring transition. Northward transport was generally associated with onshore transport, and while offshore transport accompanied southward transport. Ekman transport was onshore during the egg and early larval stage, except in 1997-98.

The predicted spawn timing from the back-calculation method and the Kruse and Tyler (1983) model were consistent with the late settling cohorts of English sole. However, while both methods predicted similar spawning times for late cohorts, the early cohort spawn times predicted by back-calculation were usually about one to two weeks earlier than those predicted by the spawning model. There are at least three potential errors that could account for the observed discrepancy; inaccuracy of the mechanisms used to predict spawn timing by the Kruse and Tyler (1983) model, error surrounding the growth rate estimation for juveniles in nursery areas used to calculate settlement dates, or erroneous assumptions about the egg and larval development rates.

Information is lacking on observed spawning activity for English sole in Oregon and Washington, but Kruse and Tyler (1983) formulated their model based on a number of sources of information including at sea and port sampling of various maturation stages of female English sole. Additionally, English sole eggs sampled during ichthyoplankton surveys from 1980-1987 indicated that peak spawning usually occurred in the late winter during those years (Doyle 1992), as was indicated by the Kruse and Tyler (1983) model.

The growth rate used in this model was an average estimated over five years for juveniles in Willapa Bay and Grays Harbor by Shi (1994). In that study, juvenile English sole growth rates were different for early settling and late settling cohorts. Growth of early settling cohorts averaged 0.39 mm per day, while late settling cohort growth rates averaged 0.46 mm per day. However, there was also significant interannual growth variation between the two cohorts so that growth rates for the early settling cohorts ranged from 0.33 to 0.45. The growth rates for late settling cohorts ranged from 0.43 to 0.49. Since sampling only occurred in June and August, there was no way to obtain reliable estimates of growth rates for the individual years (or estuaries) from my data. Shi's (1994) growth rate estimates ranged over almost the same values for both cohorts, so I chose to use an overall mean growth rate. In addition, the estimated settling times calculated by Shi (1994) were usually associated with a standard error of about a month.

One of the areas in which virtually no information exists for English sole is the larval development rate. Development rates have previously been related to temperature for larval fish (Blaxter 1992, Otterlei et al. 1999). Larval development rates have been seen to decrease with decreasing temperatures for a number of species of flatfish (Benoit and Pepin 1999, Weltzien et al. 1999, Shepard et al. 2000). Most studies have been conducted in a laboratory setting, rather than in the field. In this model, larval development rates were assumed to decrease with temperature based primarily on the observed relationships of egg development and temperature from laboratory studies. Feeding would also be expected to effect larval development, although there is no evidence either for support or contradiction from the English sole literature. Certainly larval feeding conditions have been found to influence growth and development in other species of larval fish and flatfish (e.g. Houde 1978). If English sole larval development rates are related to feeding conditions, or if the stage length-temperature relationship is erroneous, the model I have used may not be appropriate to determine larval stage length.

In some species of fish and invertebrates there may be some plasticity in settling time related to control of the larval duration by the larvae themselves (see review by Bradbury and Snelgrove 2001). If this is true for English sole, there may be some ability to settle out when appropriate habitat is encountered. Studies have found settlement ages of between 42 and 70 days for English sole based on timing of spawning and settlement (Ketchen 1956) and otolith aging (Laroche et al. 1982). In both 1998-99 and 1999-2000, retention times for the late cohorts were long, ranging to 45 days (Table 3.4). If larvae are able to control their timing of settlement they could potentially have settled to the bottom before leaving the system. However, this could not be true for all cohorts, especially those in 1997-98, which were predicted to exit the system after only five days.

The greatest weakness of the model appears to be in the prediction of larval development rates. The development rates reported here are within the bounds of reported values in the literature (Ketchen 1956, Laroche et al. 1982). The weakness in predicting larval development times is unfortunate, but nevertheless the spawning date calculations and modeling indicate that there are only very limited times when passively drifting larvae would be retained on the Oregon-Washington shelf for the duration of larval development.

Another key assumption of the modeling effort presented here is that the depth distribution of English sole larvae is constant at the 10-m depth. The depth distribution of larval English sole has not been well studied but it is estimated that over 95% of the larvae are located in the top 50-m of the water column, and 85% in the top 20-m of the water column (Kruse and Tyler 1989). Although the depth distribution used here may not be representative of the mean depth distribution, the current meter data indicates that the currents are very coherent from 8 to 50-m depth in the alongshore direction (Appendix 2). The current speeds decrease with depth, on average about 10-20 cm/s from 8 to 50-m. Thus, a poorly represented depth distribution in the model may slow or speed transport rates somewhat, but would not affect the direction of transport.

The primary effect of an inadequate depth distribution occurs in the spring months when the mixed layer depth was assumed to rise to 20-m. Thus, during the spring months if English sole larvae move below the mixed layer depth where Ekman dynamics do not apply, they could potentially maintain their longitudinal position. However, most studies of ichthyoplankton distribution have indicated that English sole tend to be found in the surface waters (Laroche and Richardson 1979). There is no indication of larval English sole moving to depth to escape Ekman transport offshore, and Laroche and Richardson (1979) actually found that larger larvae were more often found in the neuston.

A more important question with regards to the depth distribution of the English sole larvae is the effect of vertical migration. Use of selective tidal stream transport has been observed in flatfish, where they vertically migrate on a semi-diurnal cycle in order to promote retention in estuaries or other nursery grounds (Creutzberg et al. 1978, Rijnsdorp et al. 1985 Jager 1999). In this study I have filtered out subtidal frequencies, in order to examine mean transport during the pelagic period. Tidal velocities are weak (~5 cm/s) compared with alongshore currents along Oregon and Washington (Hickey 1998). It is possible that with limited vertical migration, larvae could maintain themselves near the shore using tidal cycles, by rising to the surface during flood tides to maximize inshore transport and moving deeper during ebb tides to minimize seaward transport.

The swimming speed of larval flatfish is very slow in comparison to the currents observed here. Typical escape response swimming speeds measured in the lab for larval flatfish are on the order of 5-15 body lengths per second (Miller et al. 1988, Williams and Brown 1992). Sustained swimming speeds typically average about 2 body lengths per second in larval fish (Blaxter 1986, Shepard et al. 2000). In the case of the largest English sole larvae this would only be 4 cm/s. The current speeds observed in this study were typically around 20-80 cm/s. English sole larvae would not be able to effectively swim against currents such as these and maintain themselves in the nearshore zone.

Some studies have suggested that alongshore currents may only be half as large in spring on the inner shelf at depths less than 50-m as on the mid-shelf (Huyer et al. 1978, Federiuk and Allen 1995, Allen and Newberger 1996). I performed sensitivity analyses to detect the reduction of currents within 10-km of shore that would affect my results. The model runs indicated that a 50% reduction in currents increased the amount of time eggs and larvae were retained in the system, but not enough to retain them for the duration of their development. A reduction of currents to 33% of the observed values resulted in the retention of the Willapa Bay early cohort in 1999, while a reduction to 25% of observed values resulted in the additional retention of the Yaquina Bay early cohort in 1999. However, both of these cohorts were present in the water column only during the winter season. Retention times for all other sole cohorts were unaffected.

Other studies have related English sole recruitment to a number of environmental variables. Hayman and Tyler (1980) related year class strength to pre-spawning conditions presumably associated with gonadal development rates. Average monthly offshore advection and unfavorable egg development temperatures during the pelagic stages, were found to be negatively correlated to year class strength (Kruse and Tyler 1989). In the Kruse and Tyler (1989) simulation model spawn timing was another important factor in determining cohort strength. For larval Dungeness crab (*Cancer magister*), another species in the Oregon-Washington coastal zone, alongshore (northward) transport has been correlated to year class strength (McConnaughy et al.

1994). Alongshore transport was not considered by the Kruse and Tyler (1989) simulation, but my results indicate that in most cases alongshore transport would transport passively drifting larvae out of the Oregon-Washington system before settlement.

In the previous correlations of English sole recruitment and environmental variables (i.e. Hayman and Tyler 1980, Kruse and Tyler 1989), the temporal scale (1-month or greater) on which the correlations were formed is inadequate for explaining the variation in cohort strength that occurs as a result of environmental effects. It is more likely that environmental variation on the order of the egg stage length (< 1 week) are important in determining the strength of the relationship between environmental correlates and year class strength in English sole.

The multiple cohorts could usually be explained by the multiple spawning events predicted by the Kruse and Tyler (1983) model. In the first two years, there were 2-3 spawning peaks predicted by the Kruse and Tyler model. In 2000, there was one prolonged period of predicted spawning, which may have been able to produce both early and late cohorts of English sole that were observed in the nursery estuaries. In fact, the distribution of lengths of juvenile sole captured in Yaquina Bay in June 2000 had very long tails around the mean length (Figure 2.11). This extended distribution of lengths for Yaquina Bay suggests a very prolonged settlement (and thus spawning) period.

The predicted spawn times based on back-calculation were consistent among estuaries. In general they were all grouped within a few weeks of each other, and in 1999-2000 they were all within ten days of each other. This probably indicates that even though the main spawning population is very narrowly distributed, their eggs and larvae disperse across a large area, north as far as Willapa Bay and south to Coos Bay.

Based on model trajectories for cohorts that settled successfully in estuaries, eggs were carried inshore before hatching in 13 of 19 cases. The three cases where transport of the egg stage was offshore occurred in 1997, when eggs were transported from 2.8-5.9 km eastward prior to hatch. For three cohorts in 1999, net offshore transport was less than 1-km during the egg stage and larvae were transported to shore within four days of hatch. In the cases where eggs were transported onshore, distances ranged from 8.3-15 km towards shore. This is consistent with ichthyoplankton studies in which pleuronectid eggs were found at shoreward stations during surveys of the Oregon coast (Doyle 1992).

The larvae of English sole have been found to be very narrowly distributed within 18-28 km of shore (Richardson and Pearcy 1977, Laroche and Richardson 1979, Doyle 1992). A number of authors have found that transforming larvae may concentrate in areas on the open coast, and move into a nearby estuaries after transformation is complete (Krygier and Pearcy 1986, Boehlert and Mundy 1987, Gunderson et al. 1990). By 30 mm most larvae that settled on the continental shelf have migrated into estuaries (Gunderson et al. 1990). Spawn timing may be coinciding with onshore currents so that eggs move inshore where they are retained in local hydrographic features such as eddies (Crawford et al. 1990). Other local features have also been implicated in retaining larvae in the coastal zone, such as upwelling fronts (Shanks et al. 2000), estuarine fronts (Kingsford and Suthers 1996) and surface slicks of internal waves (Shanks 1983, Kingsford and Choat 1986). A dominant feature of the Oregon-Washington shelf is the

Columbia River plume (Hickey 1998, Berdeal et al. *in press*) which may have eddy-like features that should retain larvae nearshore during periods of northward moving currents.

The question of why early settling cohorts occur only in specific estuary-year combinations remains unanswered by this study. For example, there were early settling cohorts of juvenile English sole observed in Coos Bay in 1998 and Yaquina Bay in 1999. The transport model predicts that these two cohorts moved toward the coastline in both years and then moved steadily northward. This should have exposed the cohort to opportunities to settle or use selective tidal stream transport to enter all estuaries along the coast as the larvae traveled north. It is possible that the larvae were captured by some local retention mechanism near the estuaries, such as an estuarine front or the Hecate Bank eddy. Once the eggs moved inshore from the original spawning location, they may have been trapped in the vicinity of Coos Bay and Yaquina Bay for the remainder of their development. Alternatively these two estuaries may have been supplied by larvae from spawning off northern California, as has been suggested for Dungeness crab in some years (McConnaughey et al 1994).

The infrequent appearance of early settling cohorts in some estuaries in certain years may imply that local features during the winter months may be especially important. These early settling cohorts occurred less frequently than their late settling counterparts, which seemed to occur almost every year. This would suggest that the late settling cohorts may be able to take advantage of fairly stable (with less interannual variability) oceanographic features, while the early settling cohorts may not have this advantage and thus occur more infrequently.

3.5. References

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Table 3.1. Cohorts of English sole observed in June trawl surveys of estuaries in 1998-2000. Total length, standard error (SE) and number measured for Coos Bay (CB), Yaquina Bay (YB), Willapa Bay (WB) and Grays Harbor (GH).

Cohort	Year	Mean total length (mm)	SE	n
CB-Early	1998	72	0.52	259
GH-Late	1998	31	0.29	590
WB-Late	1998	36	0.17	1479
YB-Late	1998	51	0.46	599
CB-Late	1998	37	0.33	327
WB-Early	1999	86	0.87	291
YB-Early	1999	67	0.63	617
GH-Late	1999	31	0.30	353
WB-Late	1999	33	0.26	464
YB-Late	1999	33	0.35	295
CB-Late	1999	33	0.27	726
GH-Early	2000	72	0.47	494
WB-Early	2000	70	0.70	361
YB-Early	2000	78	0.39	1513
CB-Early	2000	78	0.50	536
GH-Late	2000	41	0.21	955
WB-Late	2000	38	0.25	560
YB-Late	2000	46	0.30	465
CB-Late	2000	46	0.29	693

Table 3.2. Regression coefficients and R^2 values for the relationship between data from current meters at Coos Bay and Newport, Oregon, and Grays Harbor Washington. Data were from the 10-m depth.

Season	Regression data sources	Parameter	1997-1998	1998-1999	1999-2000
Fall	Coos Bay currents = f (Newport currents)	slope	-	0.862	0.635
		intercept	-	1.071	-0.125
		R^2	-	0.704	0.445
	Grays Harbor currents = f (Newport currents)	slope	-	0.747	0.934
		intercept	-	16.705	13.858
		R^2	-	0.604	0.484
Winter	Coos Bay currents = f (Newport currents)	slope	-	0.739	1.01
		intercept	-	4.422	-3.076
		R^2	-	0.552	0.641
	Grays Harbor currents = f (Newport currents)	slope	-	1.168	0.455
		intercept	-	14.768	8.085
		R^2	-	0.629	0.325
Spring	Coos Bay currents = f (Newport currents)	slope	0.167	0.783	2.202
		intercept	-3.221	-7.699	68.43
		R^2	0.016	0.311	0.826
	Grays Harbor currents = f (Newport currents)	slope	0.226	0.809	0.370
		intercept	-0.346	21.13	8.085
		R^2	0.029	0.325	0.248

Table 3.3. Summary of data for cohorts of juvenile English sole in coastal estuaries, Coos Bay (CB), Yaquina Bay (YB), Willapa Bay (WB) and Grays Harbor (GH). The mean length of each cohort was used to back-calculate the settlement date, and the oceanographic model was used to calculate the development times, spawn dates and total transport during pelagic stages for each cohort. Negative transport values indicate transport offshore or southward, positive values indicate onshore or northward transport.

Cohort	Year	Settlement date	Larval stage (days)	Egg stage (days)	Spawn date	Net cross-shelf transport (km)	Net alongshore transport (km)
CB-Early	1998	2/23/98	44	4	1/6/98	15	1494
GH-Late	1998	5/15/98	42	4	3/30/98	-40	-952
WB-Late	1998	5/7/98	42	4	3/22/98	-7	-1000
YB-Late	1998	4/11/98	42	4	2/24/98	10	-464
CB-Late	1998	5/18/98	42	4	4/2/98	-36	-748
WB-Early	1999	1/7/99	52	4	11/12/98	13	281
YB-Early	1999	3/9/99	67	5	12/27/98	15	278
GH-Late	1999	5/15/99	67	6	3/3/99	-85	-1279
WB-Late	1999	5/14/99	67	6	3/2/99	-84	-1229
YB-Late	1999	5/29/99	62	5	3/22/99	-121	-1691
CB-Late	1999	5/26/99	63	5	3/19/99	-107	-1646
GH-Early	2000	2/9/00	62	5	12/4/99	15	284
WB-Early	2000	2/15/00	63	5	12/9/99	12	286
YB-Early	2000	2/6/00	61	5	12/2/99	13	288
CB-Early	2000	2/4/00	61	5	11/30/99	13	285
GH-Late	2000	4/23/00	63	5	2/15/00	-5	279
WB-Late	2000	5/2/00	64	5	2/23/00	-17	-44
YB-Late	2000	4/23/00	63	5	2/15/00	-5	279
CB-Late	2000	4/21/00	63	5	2/13/00	-6	283

Table 3.4. Calculated retention times for English sole eggs and larvae on the Oregon and Washington shelf. Larvae were retained while between Cape Blanco, Oregon and Cape Flattery, Washington within 60-km of shore. Retention times are calculated assuming all spawning occurred offshore of Newport Oregon at a latitude of 45^0 N for Coos Bay (CB), Yaquina Bay (YB), Willapa Bay (WB) and Grays Harbor (GH) early and late cohorts.

Cohort	Year	Spawn date	Retention time in coastal Oregon and Washington (days)
CB-Early	1998	1/6/98	12
GH-Late	1998	3/30/98	5
WB-Late	1998	3/22/98	12
YB-Late	1998	2/24/98	26
CB-Late	1998	4/2/98	6
WB-Early	1999	11/12/98	15
YB-Early	1999	12/27/98	34
GH-Late	1999	3/3/99	40
WB-Late	1999	3/2/99	43
YB-Late	1999	3/22/99	20
CB-Late	1999	3/19/99	24
GH-Early	2000	12/4/99	67
WB-Early	2000	12/9/99	68
YB-Early	2000	12/2/99	66
CB-Early	2000	11/30/99	66
GH-Late	2000	2/15/00	42
WB-Late	2000	2/23/00	25
YB-Late	2000	2/15/00	42
CB-Late	2000	2/13/00	45

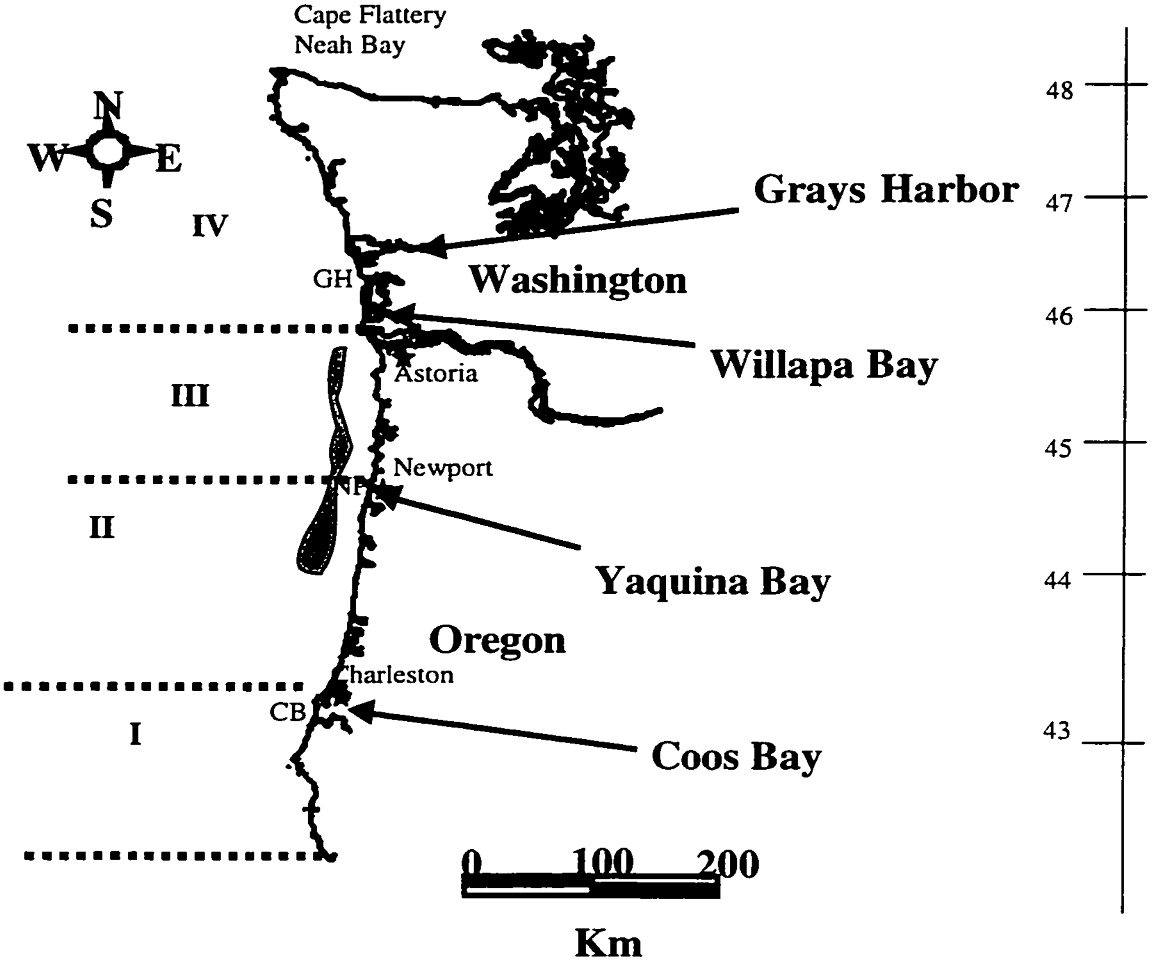

Figure 3.1. Map of the coast of Oregon and Washington showing PNCERS study estuaries and the boundaries of the system modeled to predict English sole transport. The shaded area indicates presumed English sole spawning areas (Shi 1994), CB, NP and GH indicate mooring location at Coos Bay, Newport and Grays Harbor respectively. The dashed lines delineate the regions where the Grays Harbor (IV), Newport (III) and Coos Bay (I) current meter data was applied, in region II linear interpolation between NP and CB data was used. Latitude is indicated in the bar on the right side of the diagram.

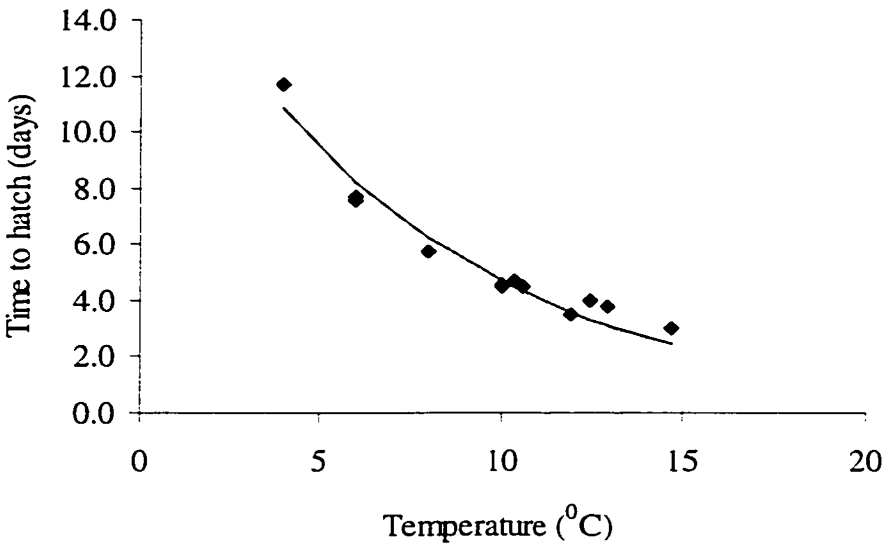

Figure 3.2. Relationship of egg stage length and temperature from laboratory studies (Ketchen 1956, English 1966, Alderdice and Forrester 1968). The line represents the fit of an exponential equation with intercept = 18.94 and slope –0.1394.

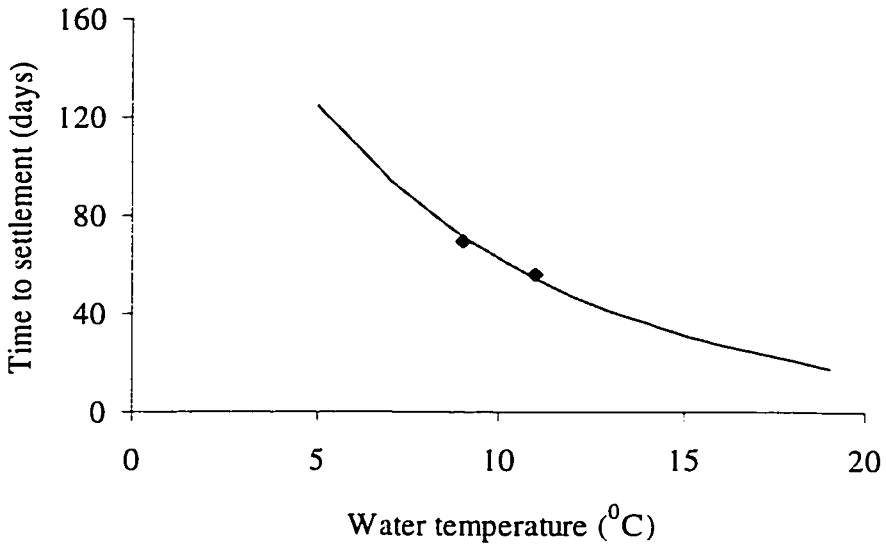

Figure 3.3. Assumed relationship of larval stage length and temperature based on data from Laroche et al (1982). The slope =-0.1394 was taken from the egg relationship (Figure 3.2), and the intercept was fit to the two points shown in the graph. For the assumed relationship, the intercept = 250.

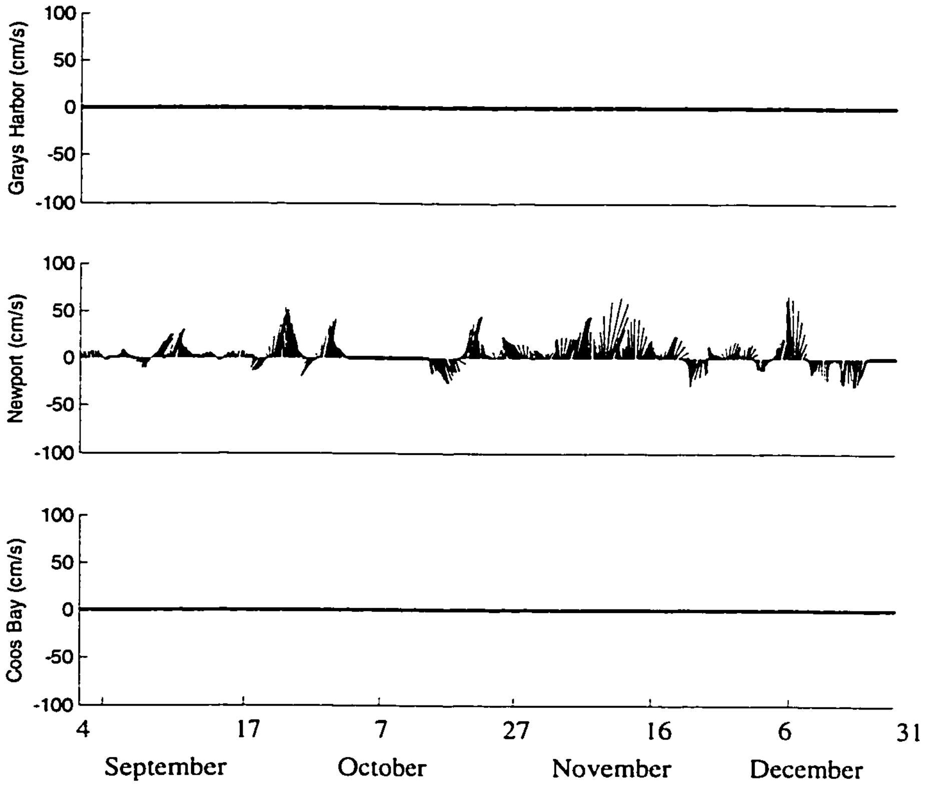

Figure 3.4. Recorded currents at 10-m depth from September 3 to December 31, 1997 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport. Missing data are indicated by zero values.

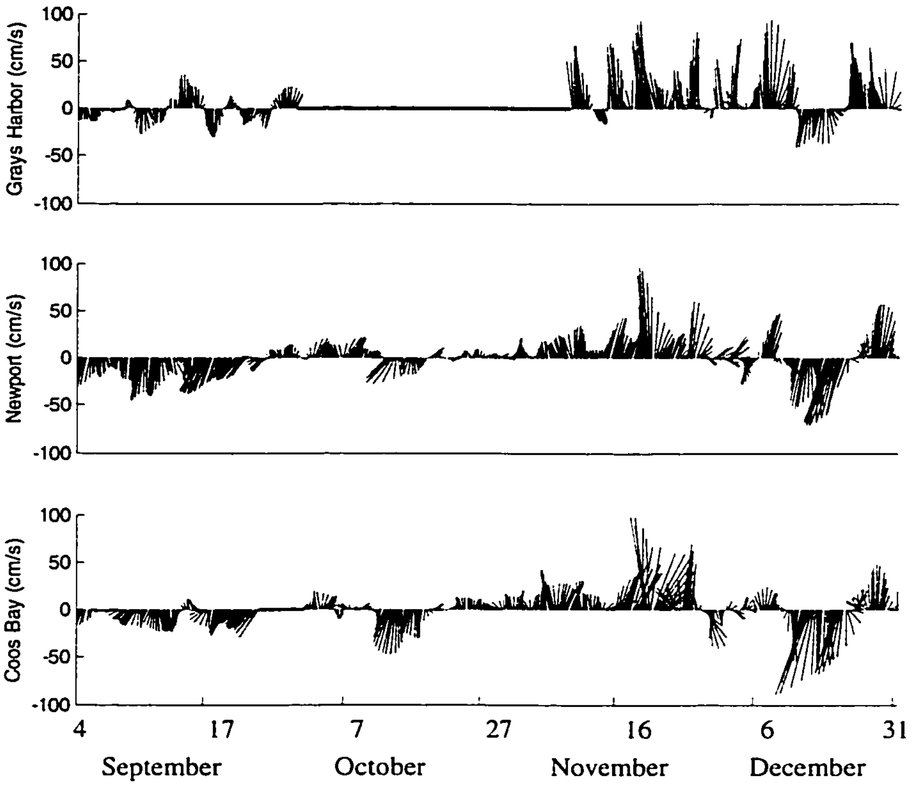

Figure 3.5. Recorded currents at 10-m depth from September 3 to December 31, 1998 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport.

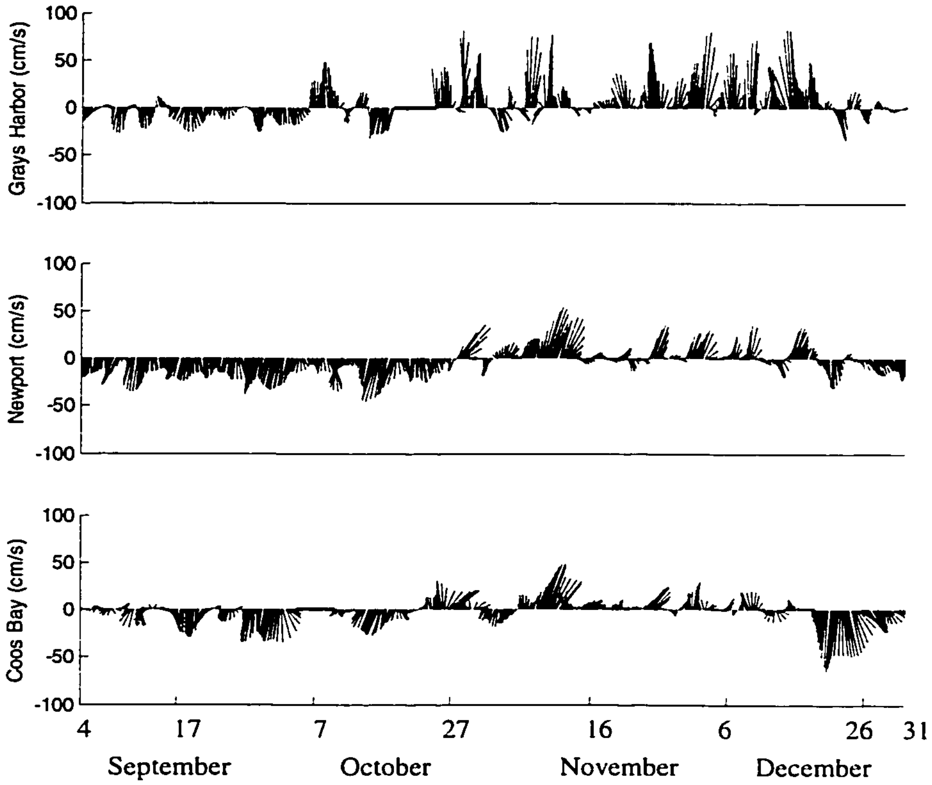

Figure 3.6. Recorded currents at 10-m depth from September 3 to December 31, 1999 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport.

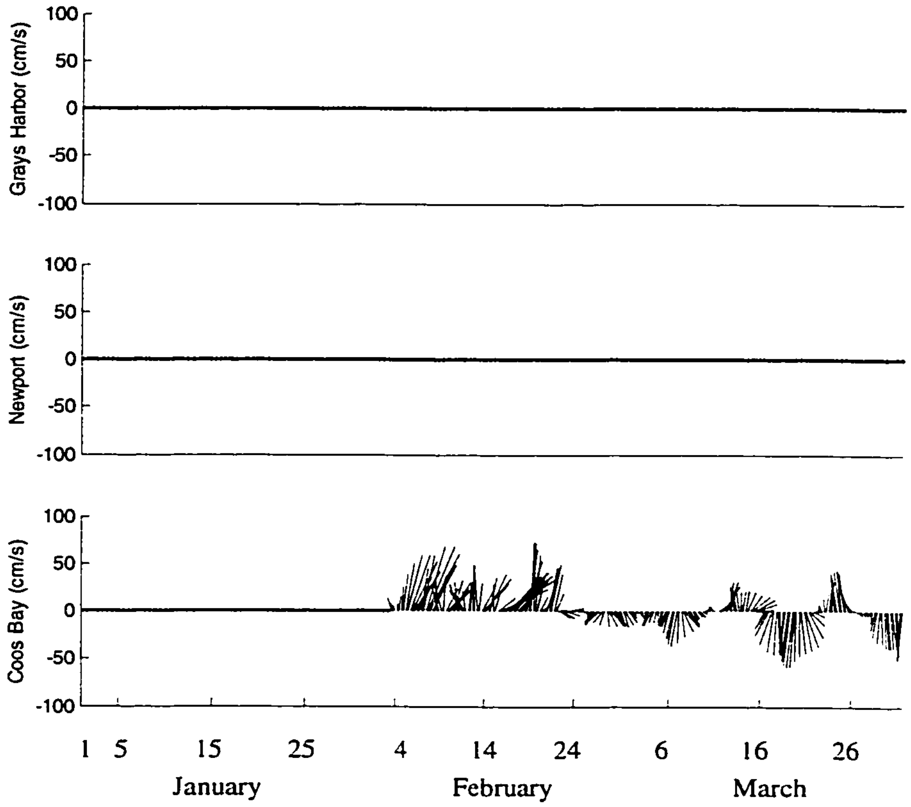

Figure 3.7. Recorded currents at 10-m depth from January 1 to March 31, 1998 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport.

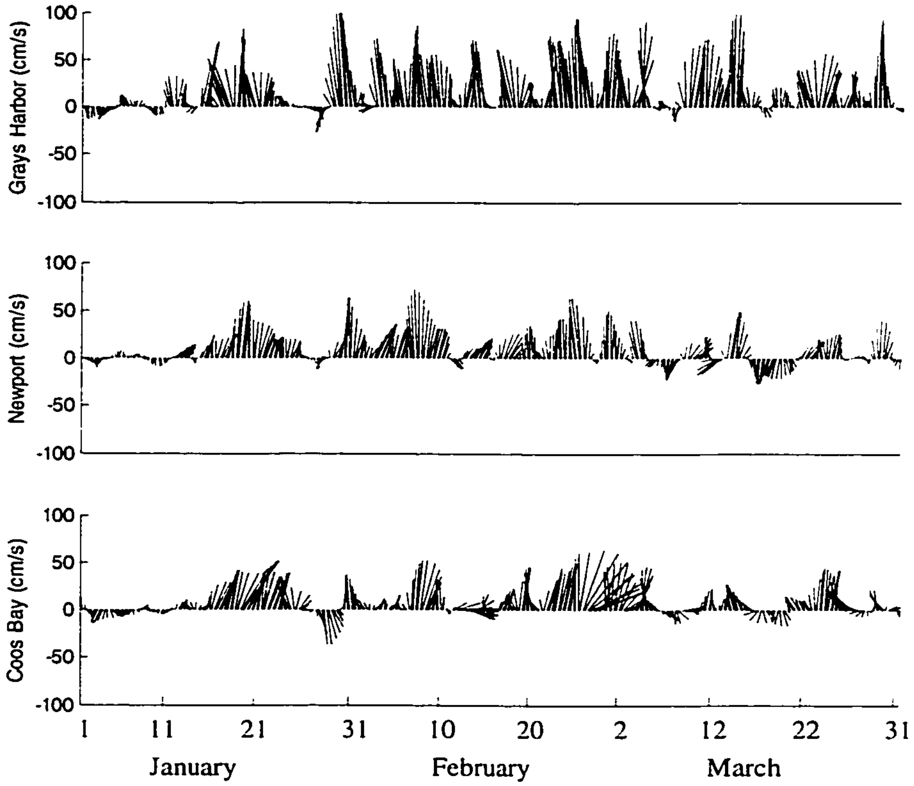

Figure 3.8. Recorded currents at 10-m depth from January 1 to March 31, 1999 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport.

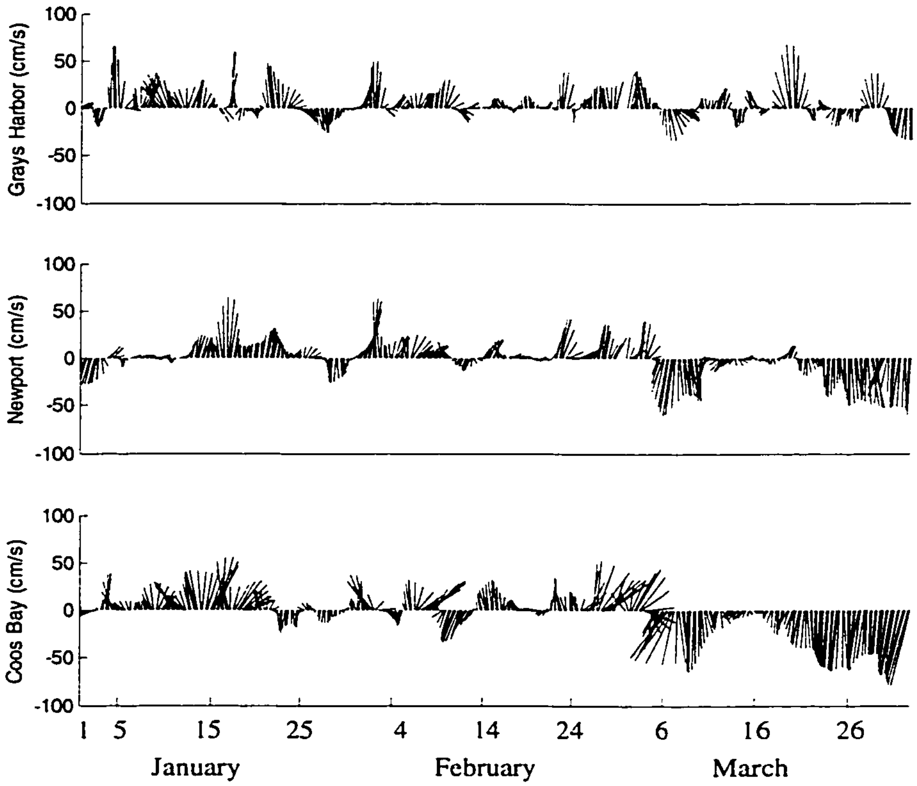

Figure 3.9. Recorded currents at 10-m depth from January 1 to March 31, 2000 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport.

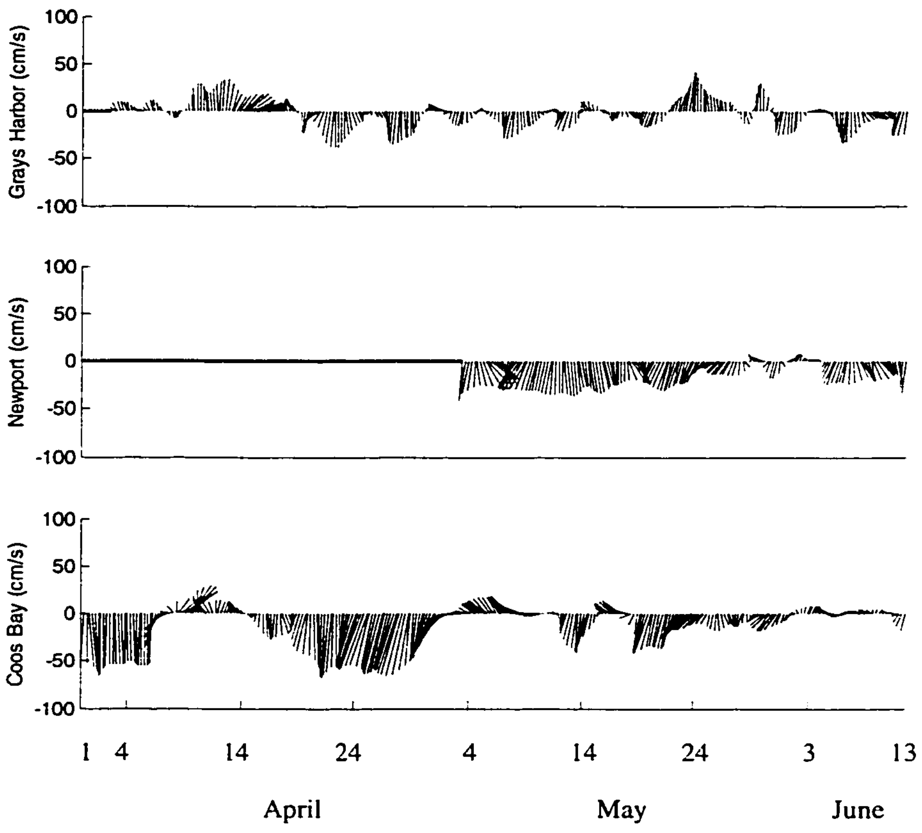

Figure 3.10. Recorded currents at 10-m depth from April 1 to June 12, 1998 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport.

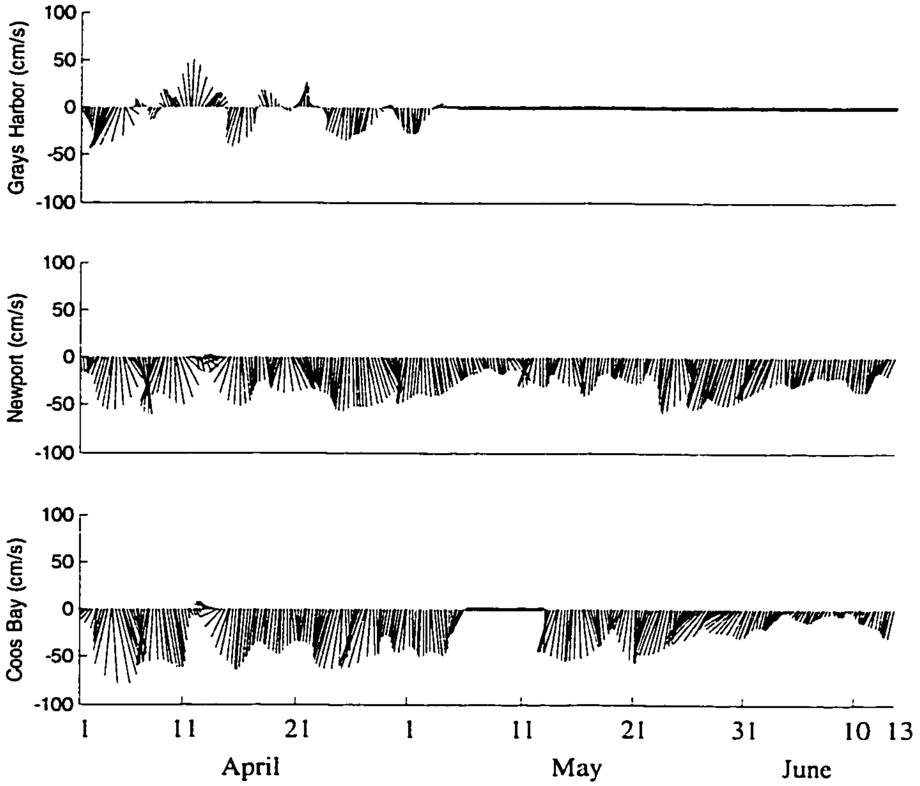

Figure 3.11. Recorded currents at 10-m depth from April 1 to June 12, 1999 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport, zero values indicate missing data.

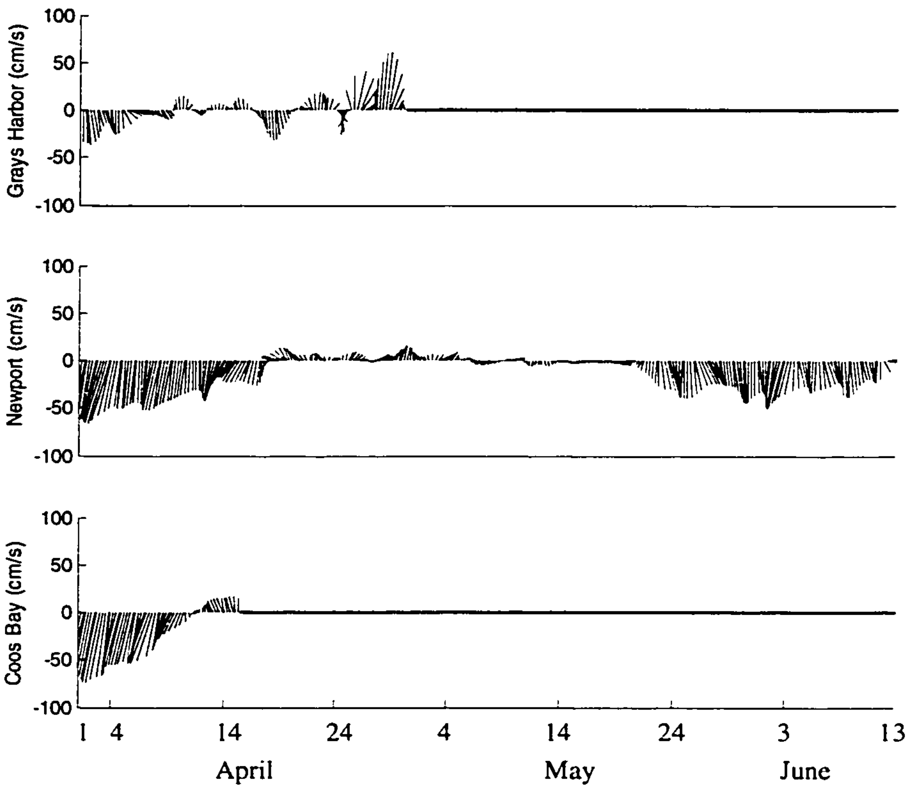

Figure 3.12. Recorded currents at 10-m depth from April 1 to June 12, 2000 at moorings near Grays Harbor, Washington, and Newport and Coos Bay, Oregon. Positive values indicate northward transport, while negative values indicate southward transport, zero values indicate missing data.

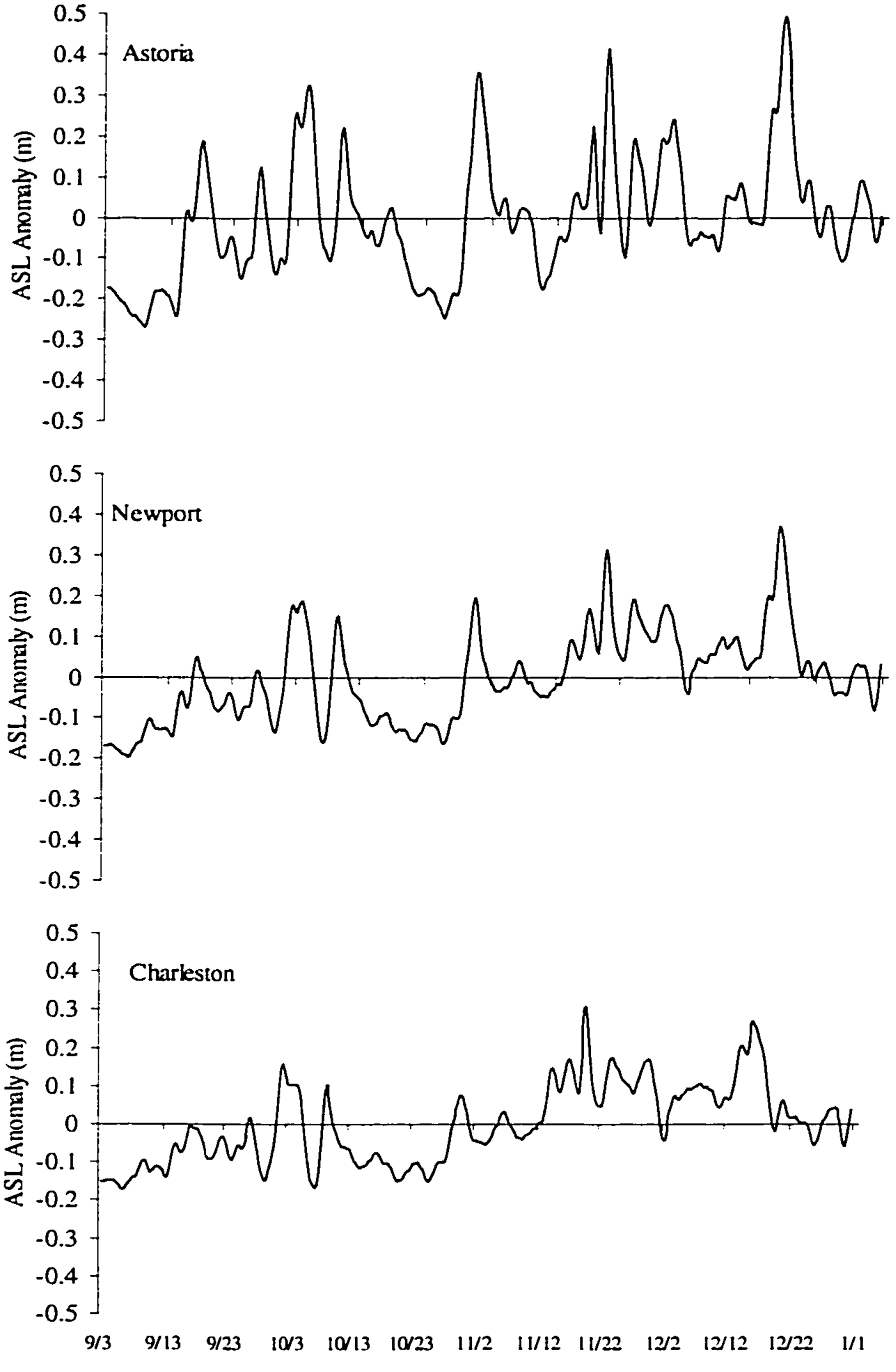

Figure 3.13. Adjusted sea level height anomaly for Charleston, Newport and Astoria Oregon in the fall of 1997. Sea level height anomalies were calculated seasonally.

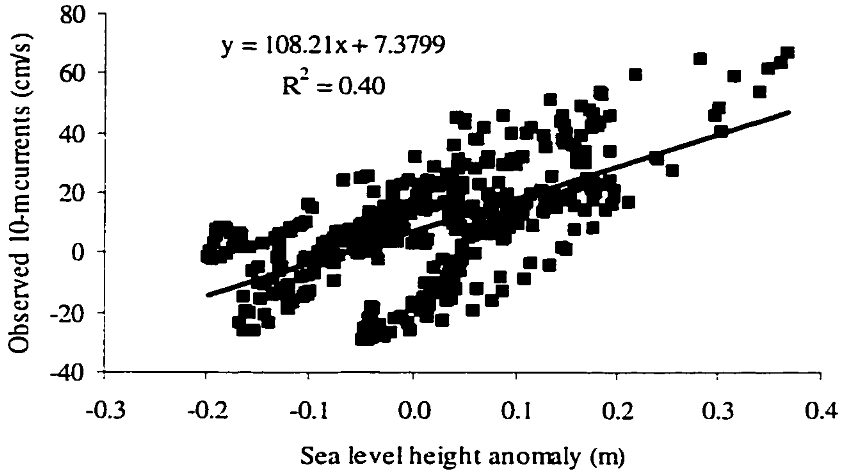

Figure 3.14. Observed alongshore currents for the fall of 1997 at 10-m depth from the Newport mooring and sea level height anomalies for Newport. Positive values indicate northward currents, negative values indicate southward currents.

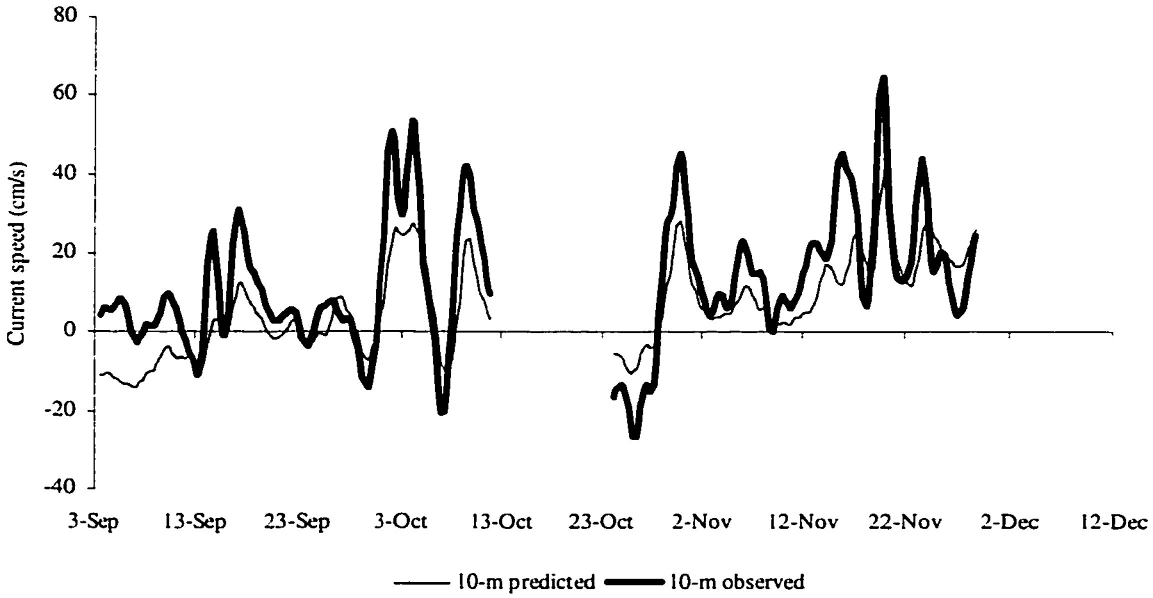

Figure 3.15. Observed and predicted alongshore currents for the fall of 1997 at Newport, Oregon from the 10-m depth. Positive values indicate northward transport and negative values indicate southward transport.

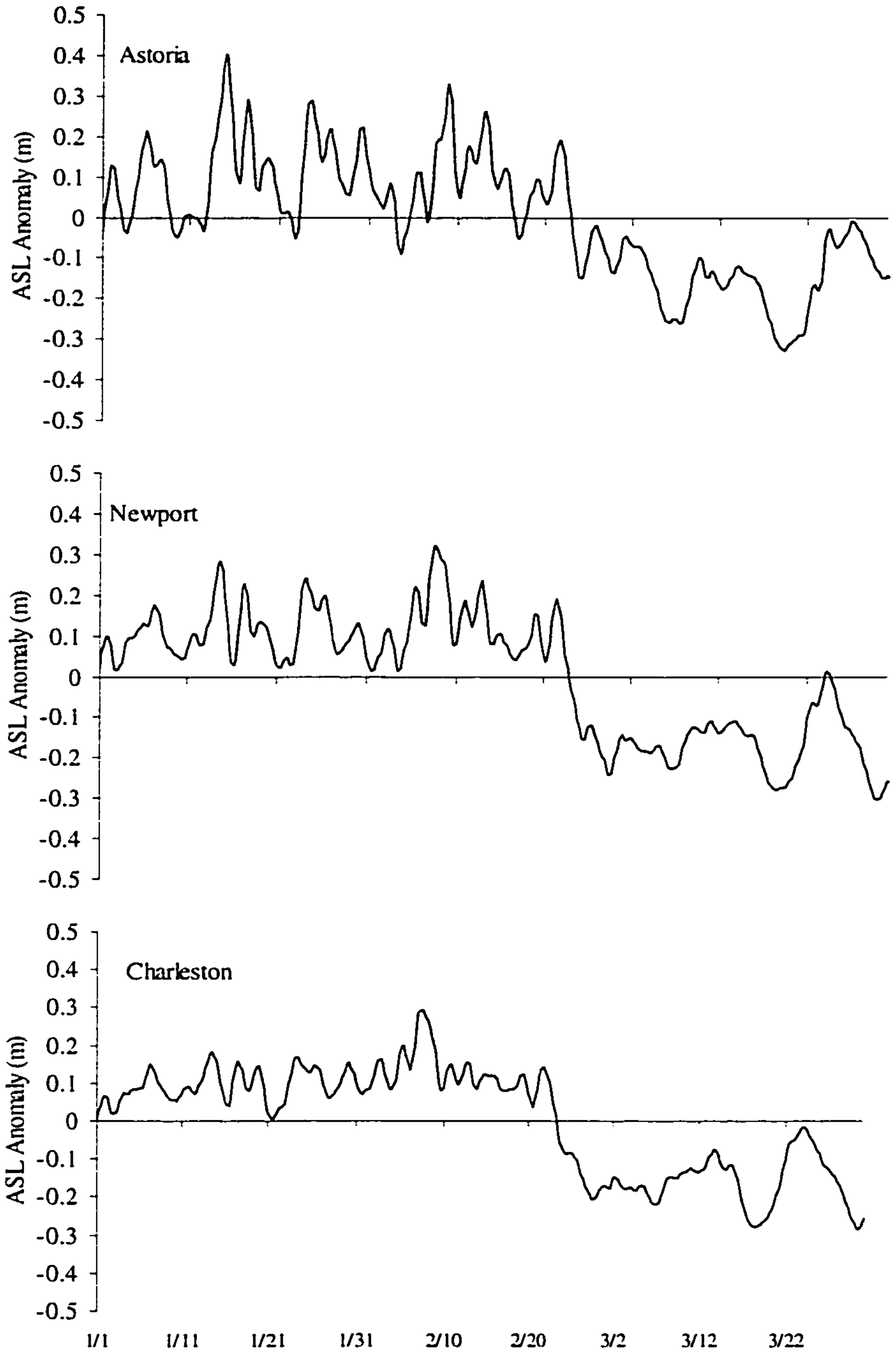

Figure 3.16. Adjusted sea level height anomaly for Charleston, Newport and Astoria Oregon in the winter of 1998. Sea level height anomalies were calculated seasonally.

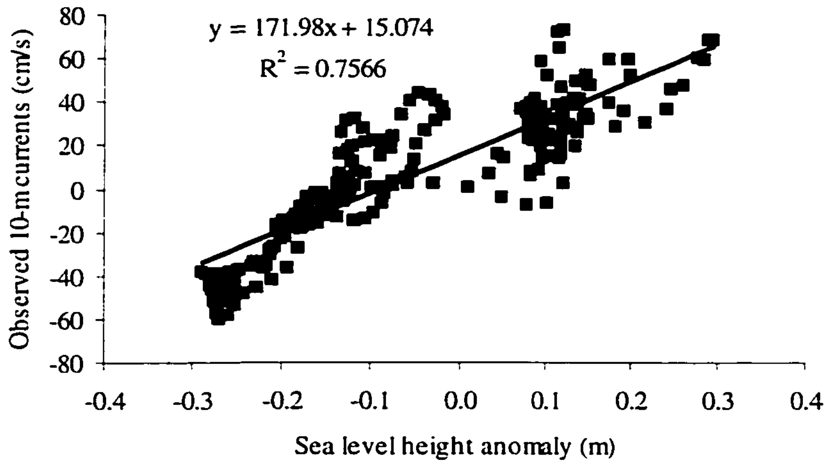

Figure 3.17. Observed alongshore currents for the winter of 1998 at 10-m depth from the Coos Bay mooring and sea level height anomalies for Charleston. Positive values indicate northward currents, negative values indicate southward currents.

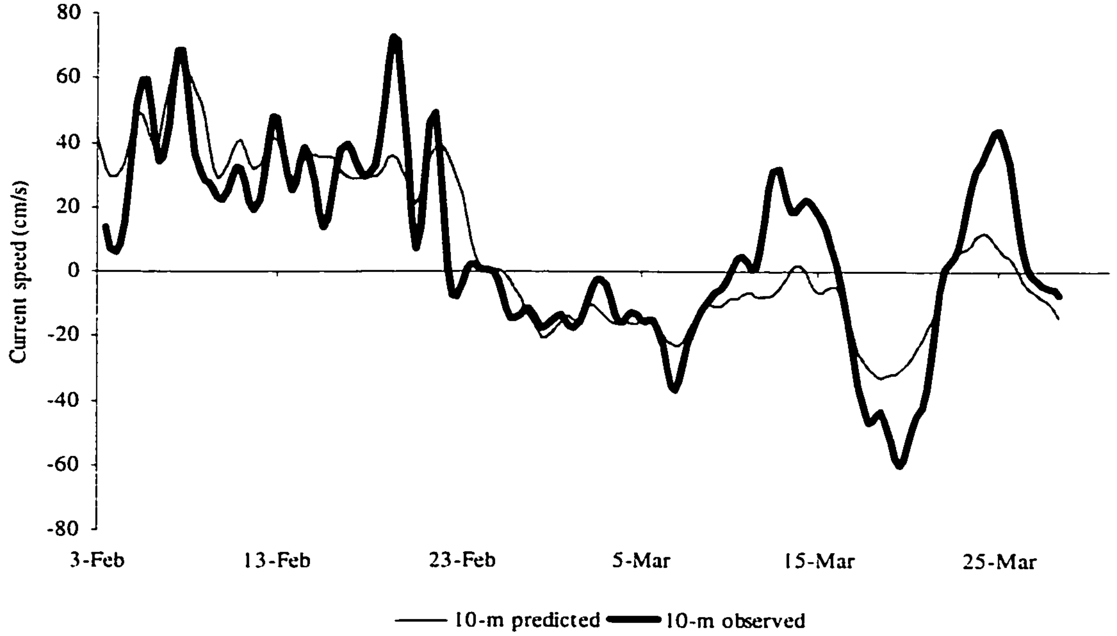

Figure 3.18. Observed alongshore currents in the winter of 1998 at Coos Bay, and predicted currents using Charleston ASL anomalies and the regression parameters. Positive values indicate northward transport, negative values indicate southward transport.

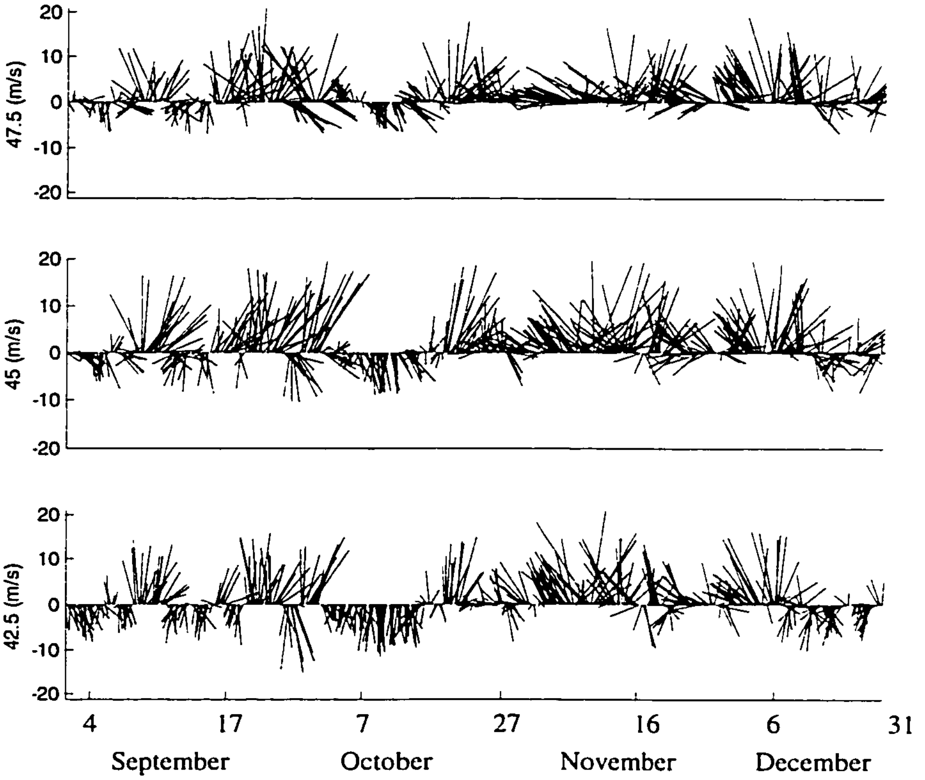

Figure 3.19. Time series of reanalysis wind speed (m/s) and direction for the fall of 1997 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

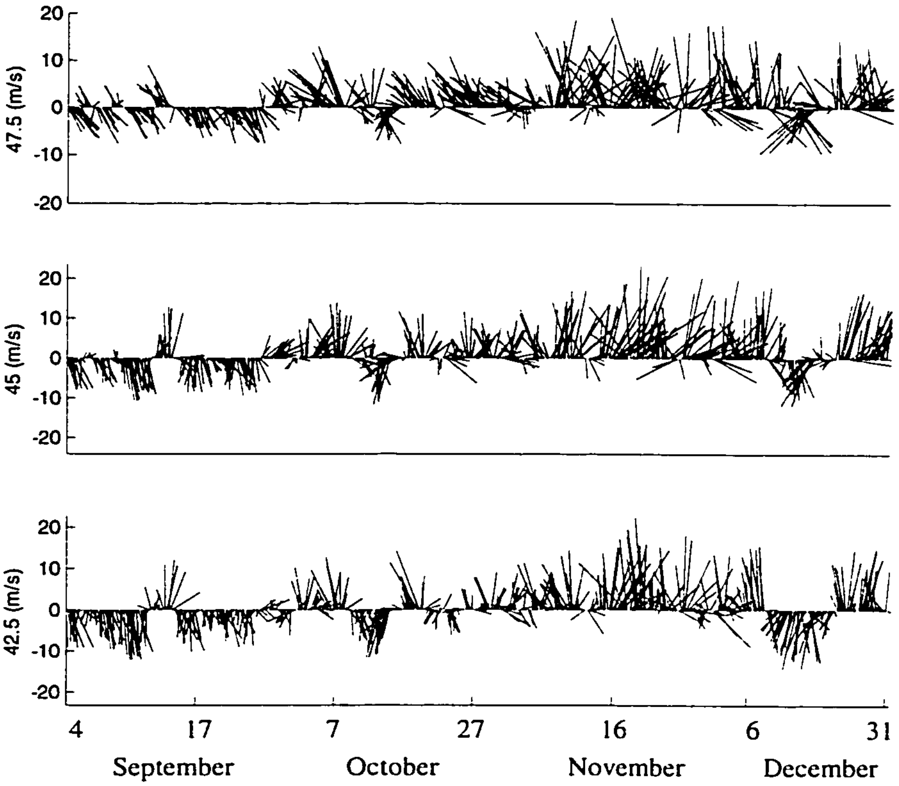

Figure 3.20. Time series of reanalysis wind speed (m/s) and direction for the fall of 1998 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

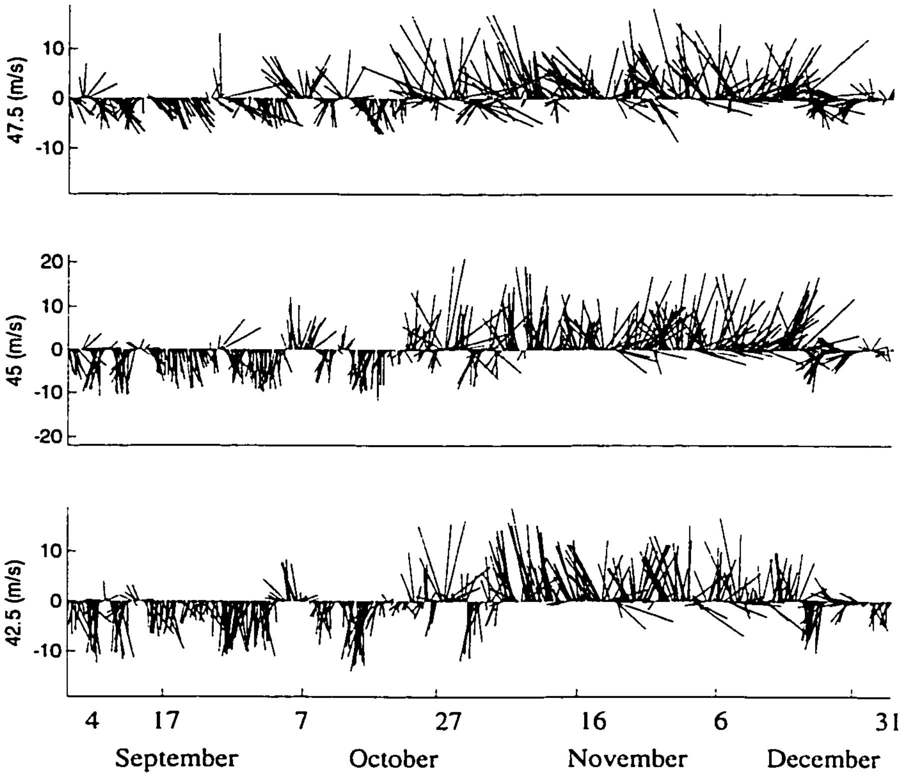

Figure 3.21. Time series of reanalysis wind speed (m/s) and direction for the fall of 1999 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

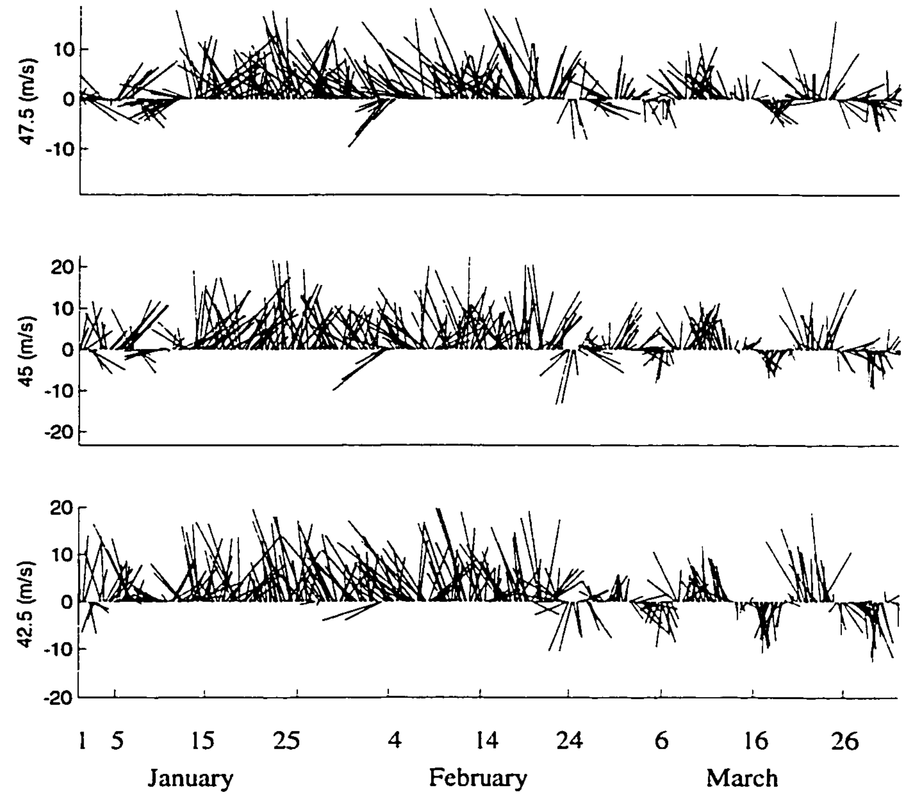

Figure 3.22. Time series of reanalysis wind speed (m/s) and direction for the winter of 1998 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

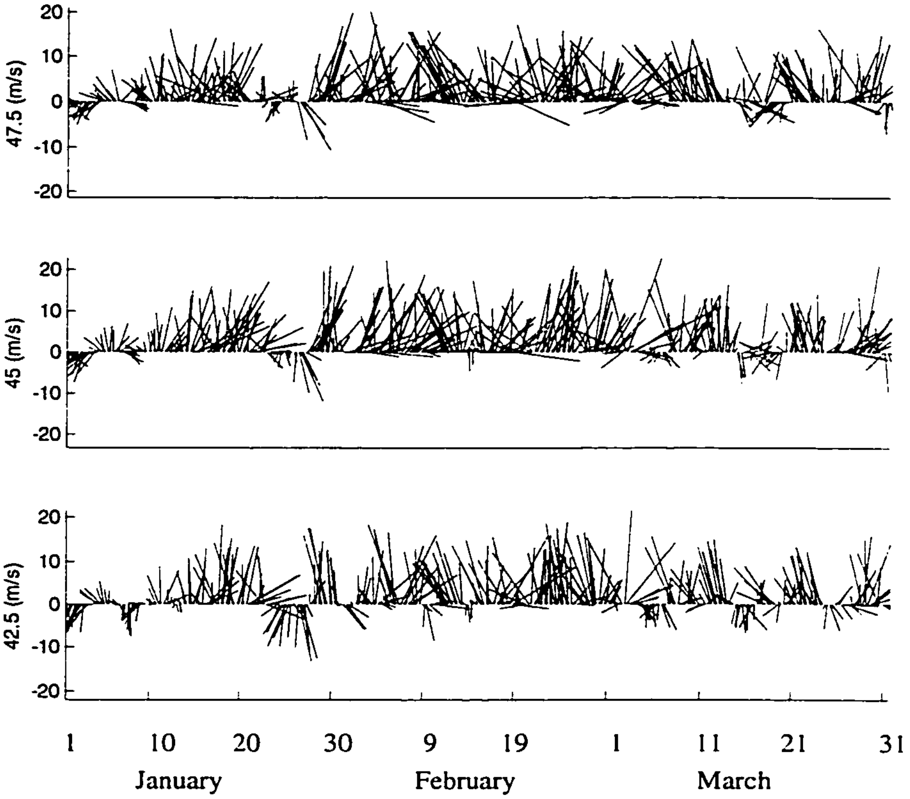

Figure 3.23. Time series of reanalysis wind speed (m/s) and direction for the winter of 1999 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

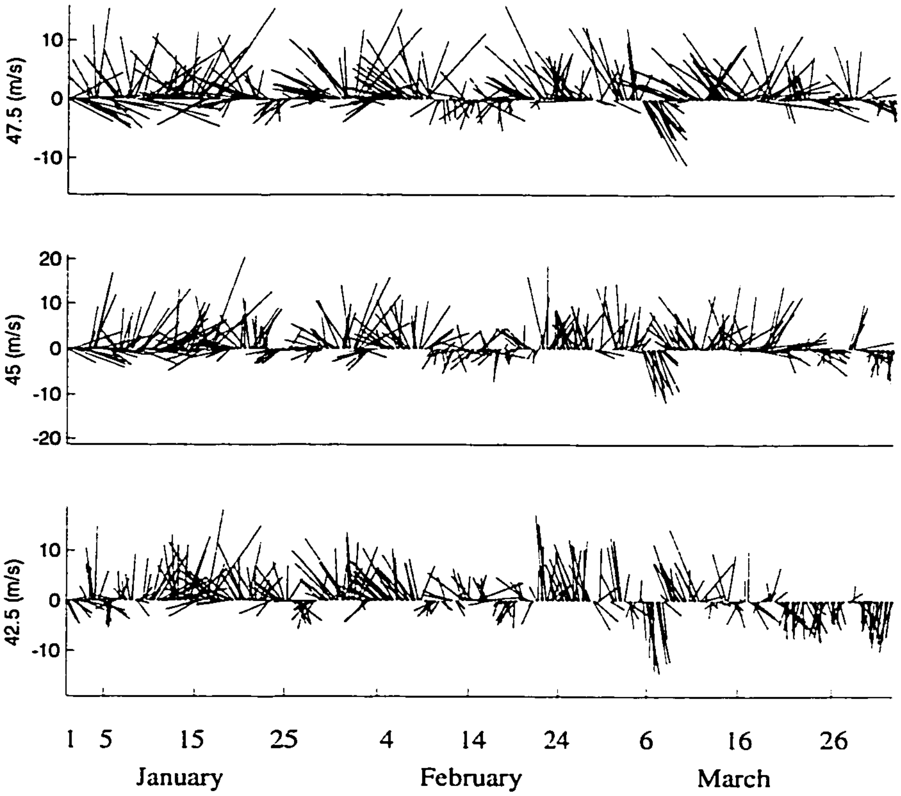

Figure 3.24. Time series of reanalysis wind speed (m/s) and direction for the winter of 2000 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

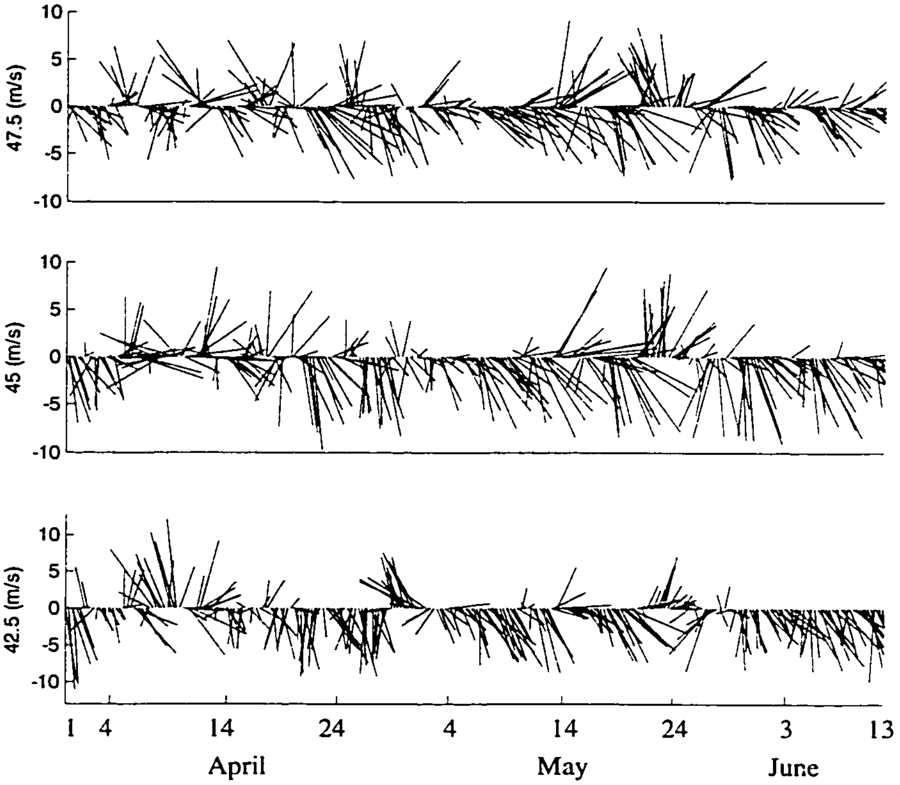

Figure 3.25. Time series of reanalysis wind speed (m/s) and direction for the spring of 1998 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

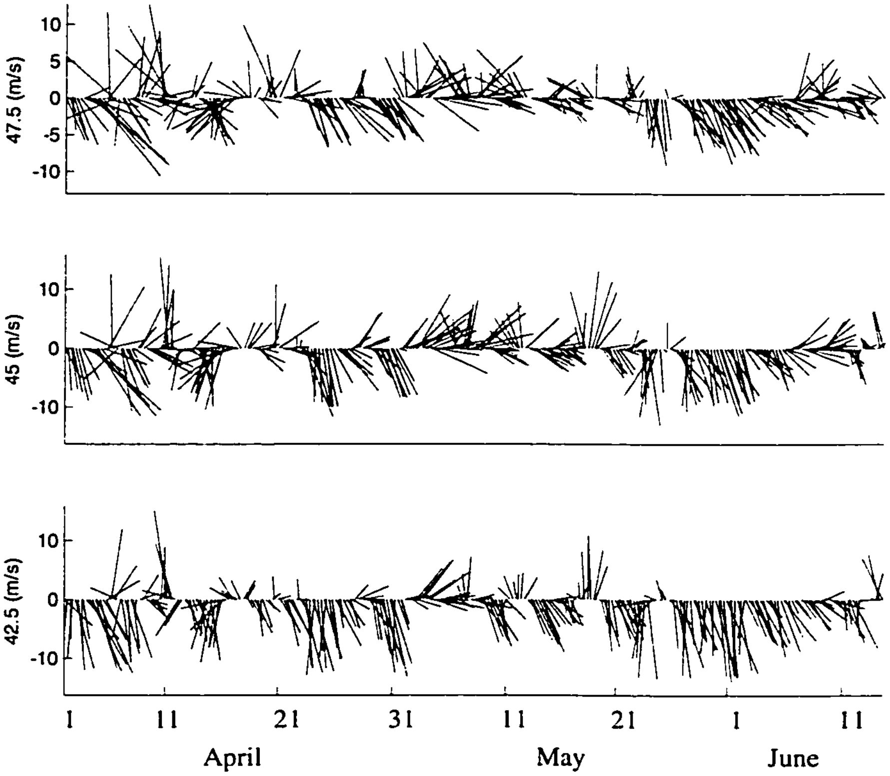

Figure 3.26. Time series of reanalysis wind speed (m/s) and direction for the spring of 1999 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

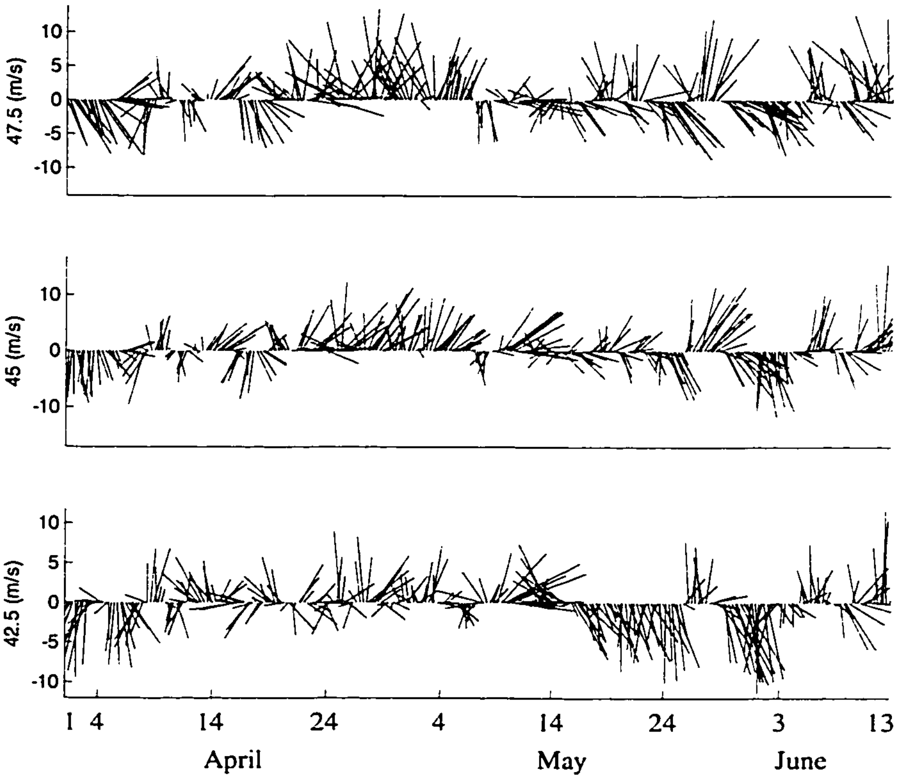

Figure 3.27. Time series of reanalysis wind speed (m/s) and direction for the spring of 2000 at three locations (47.5, 45 and 42.5 degrees N latitude) along the Oregon and Washington coasts.

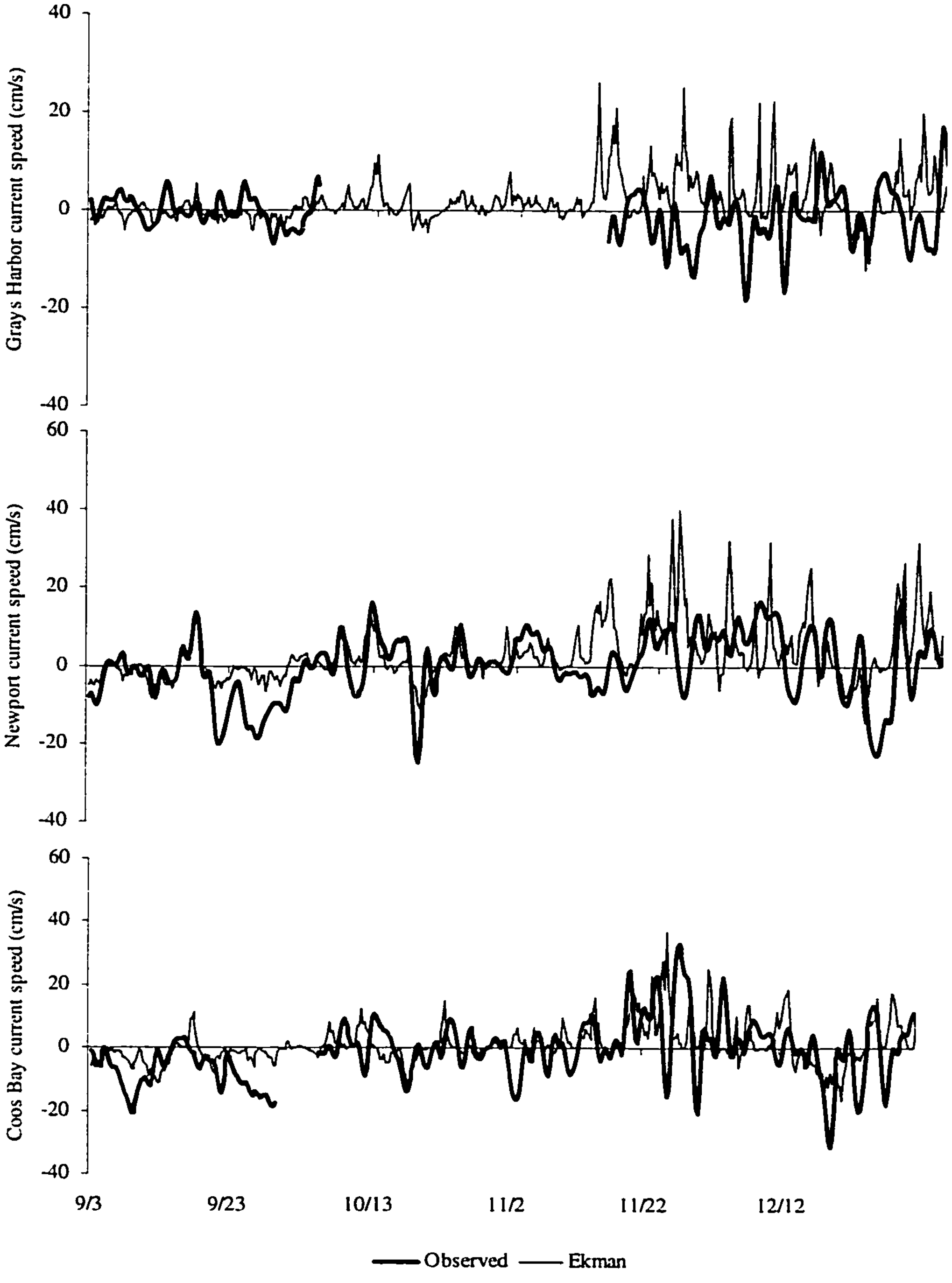

Figure 3.28. Calculated Ekman transport and observed cross-shelf currents from moorings for the fall of 1998 at 10-m depth. Positive values indicate onshore transport, negative values indicate offshore transport.

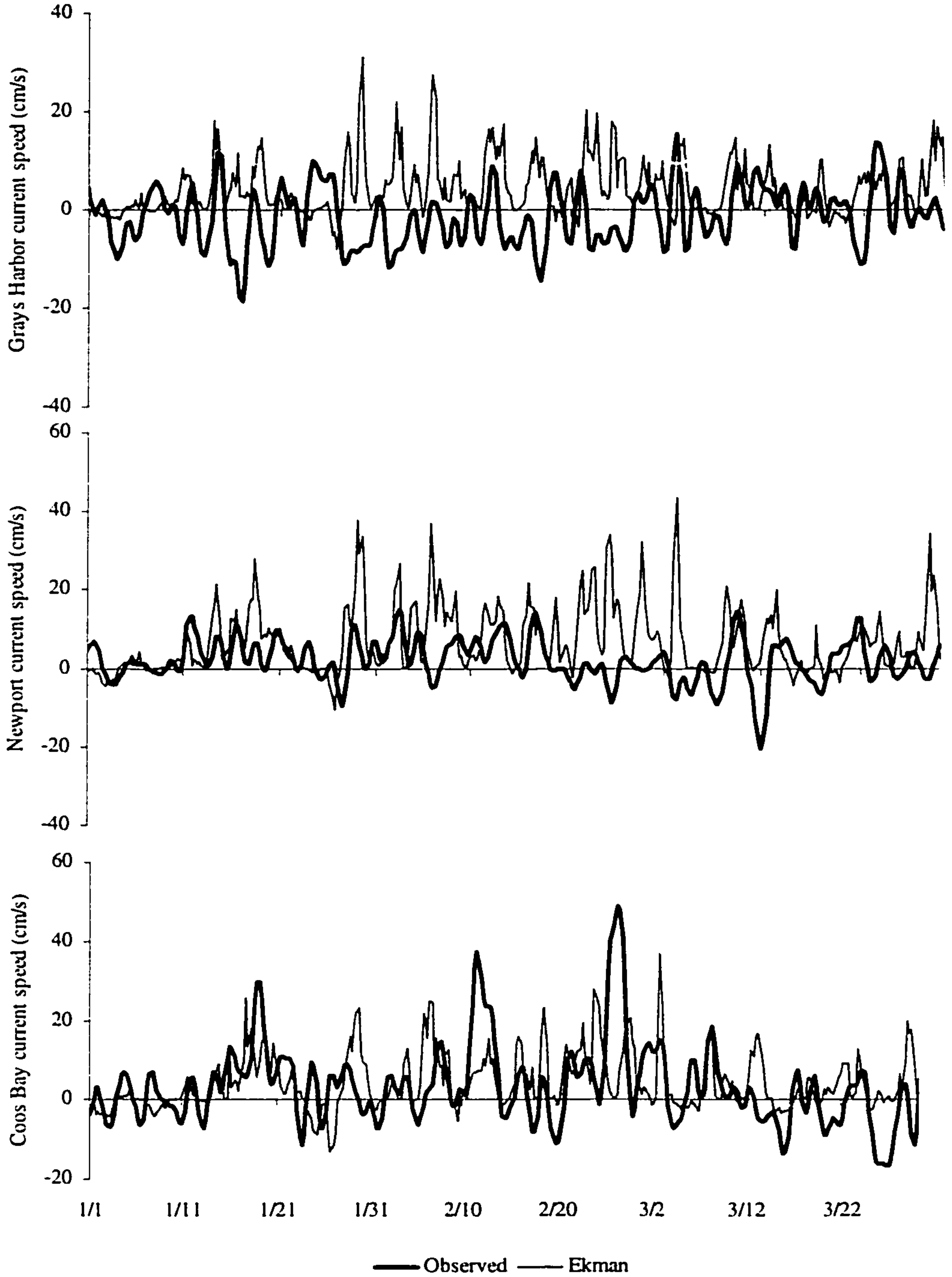

Figure 3.29. Calculated Ekman transport and observed cross-shelf currents from moorings for the winter of 1999 at 10-m depth. Positive values indicate onshore transport, negative values indicate offshore transport.

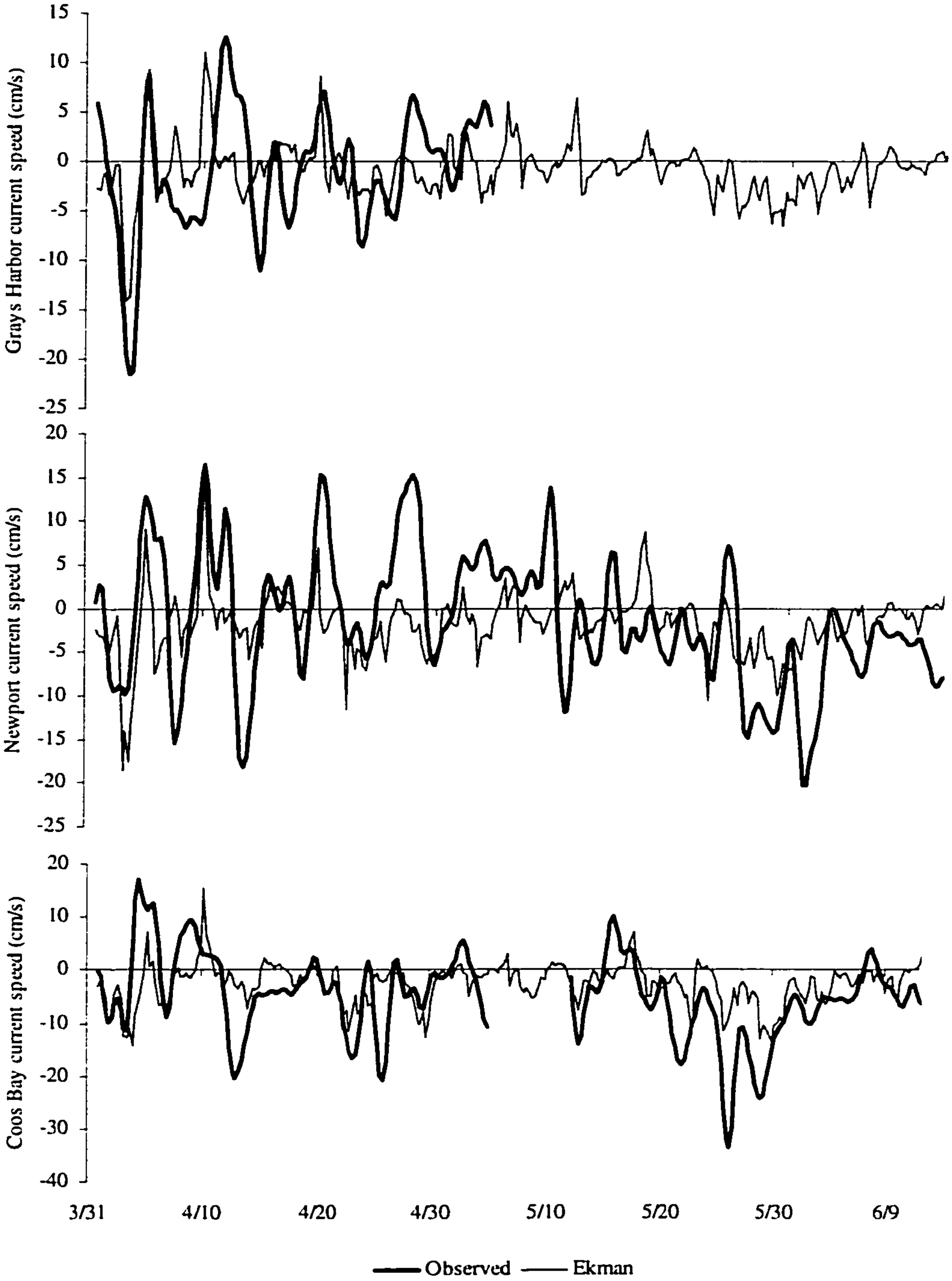

Figure 3.30. Calculated Ekman transport and observed cross-shelf currents from moorings for the spring of 1999 at 10-m depth. Positive values indicate onshore transport, negative values indicate offshore transport.

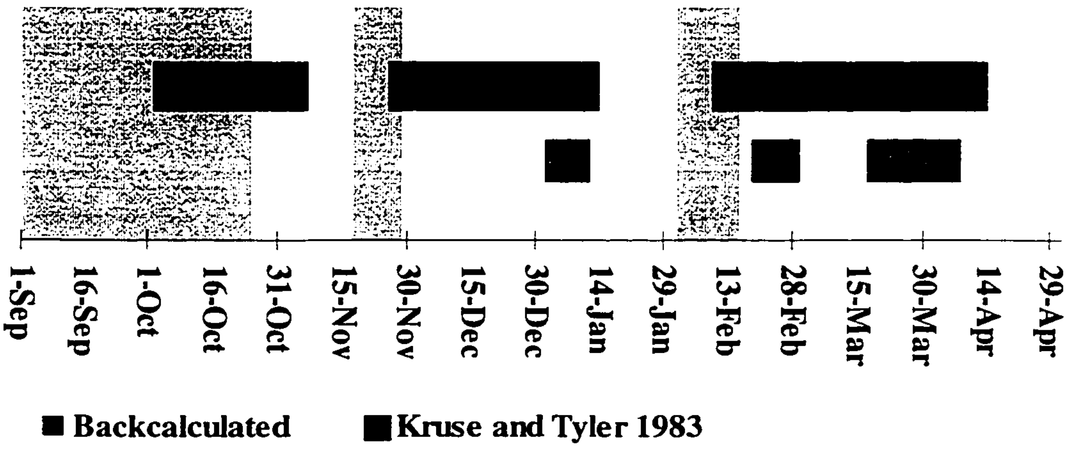

Figure 3.31. Times of English sole spawning for the winter of 1997-98. The spawning times were predicted by the model of Kruse and Tyler (1983), and also from backcalculation based on lengths of juveniles captured during June trawl surveys of coastal nursery estuaries. Gray areas indicate the dates for which larvae spawned from 44 to 46^0 N latitude would be retained in an area from Cape Blanco to Cape Flattery based on passive transport.

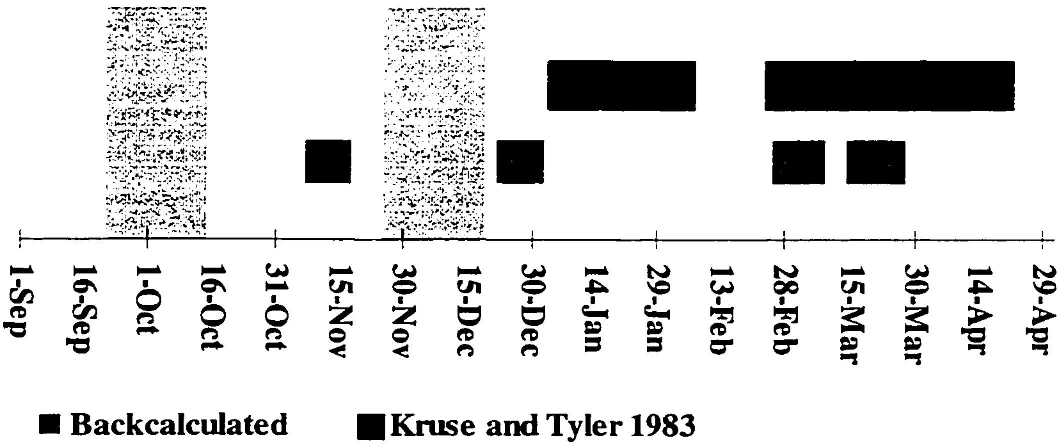

Figure 3.32. Times of English sole spawning for the winter of 1998-99. The spawning times were predicted by the model of Kruse and Tyler (1983), and also from backcalculation based on lengths of juveniles captured during June trawl surveys of coastal nursery estuaries. Gray areas indicate the dates for which larvae spawned from 44 to 46^0 N latitude would be retained in an area from Cape Blanco to Cape Flattery based on passive transport.

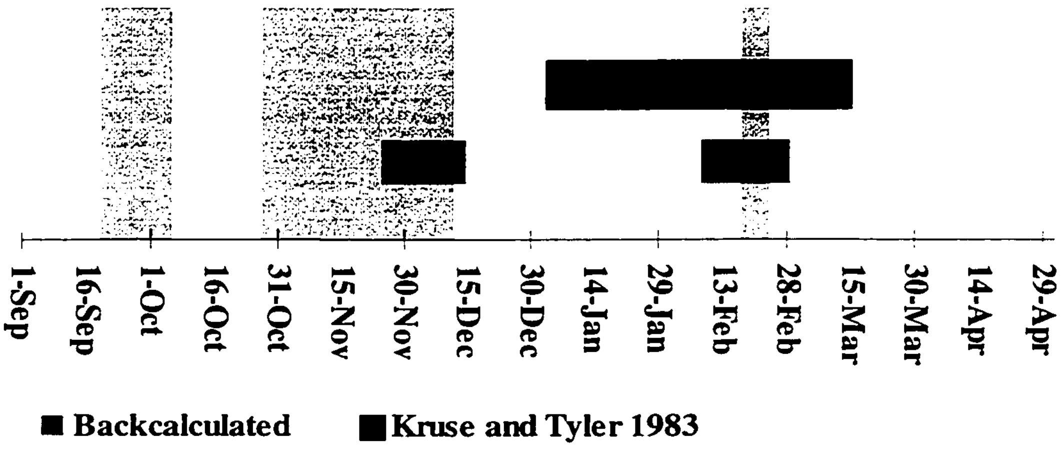

Figure 3.33. Times of English sole spawning for the winter of 1999-2000. The spawning times were predicted by the model of Kruse and Tyler (1983), and also from backcalculation based on lengths of juveniles captured during June trawl surveys of coastal nursery estuaries. Gray areas indicate the dates for which larvae spawned from 44 to 46^0 N latitude would be retained in an area from Cape Blanco to Cape Flattery based on passive transport.

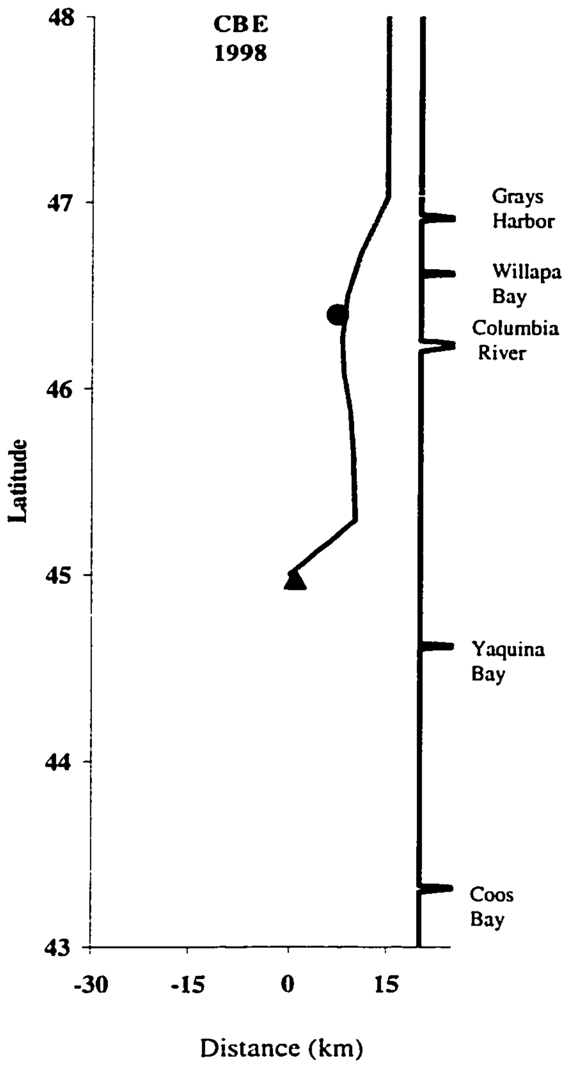

Figure 3.34. Trajectory of English sole early cohort eggs and larvae spawned in the winter of 1997-98. Spawn dates, development rates and current patterns are computed from a cohort of English sole observed in Coos Bay (CBE) in June of 1998. Triangle represents assumed spawning location, circle represents hatching location.

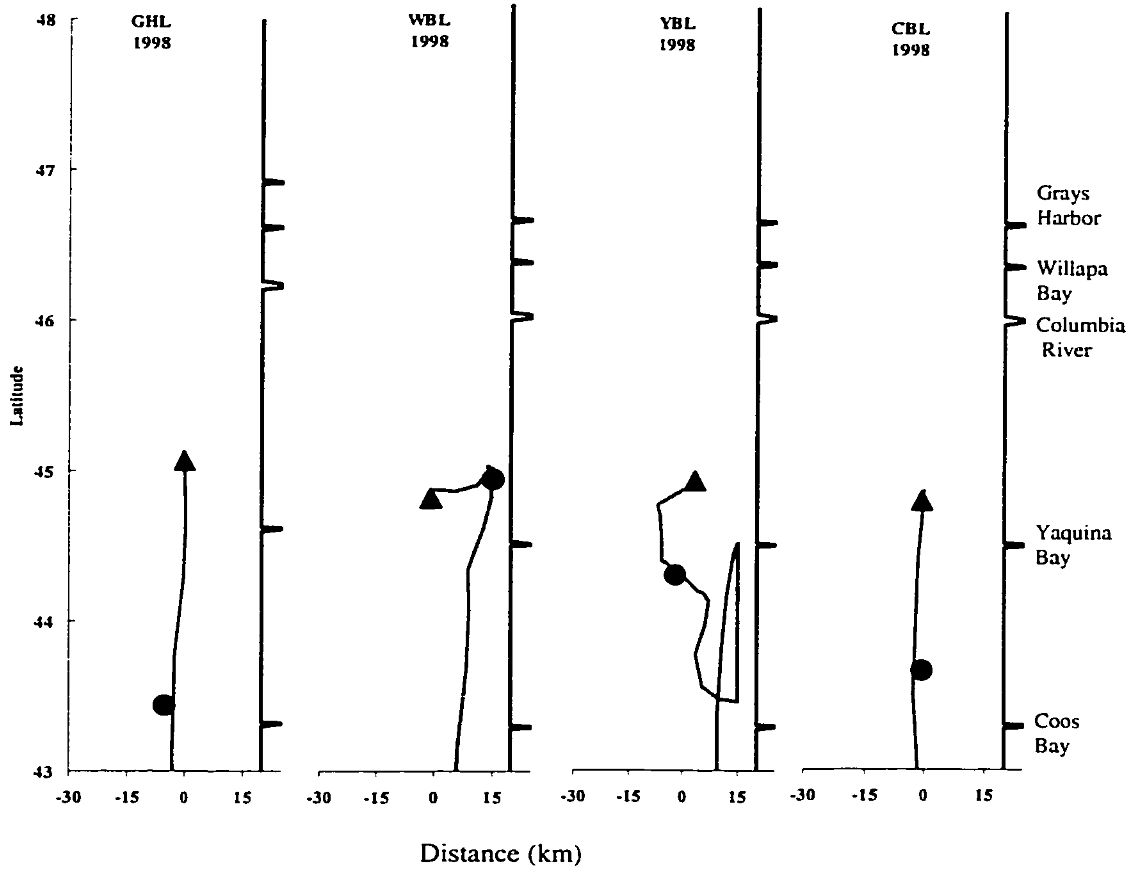

Figure 3.35. Trajectories of late cohort English sole eggs and larvae spawned in the winter of 1997-98. Spawn dates, development rates and current patterns are computed from four cohorts of English sole observed in trawl surveys of PNCERS estuaries in June of 1998. The cohorts depicted are Coos Bay (CBL), Yaquina Bay (YBL), Willapa Bay (WBL) and Grays Harbor (GHL) late settling sole. Triangle represents assumed spawning location, circle represents hatching location.

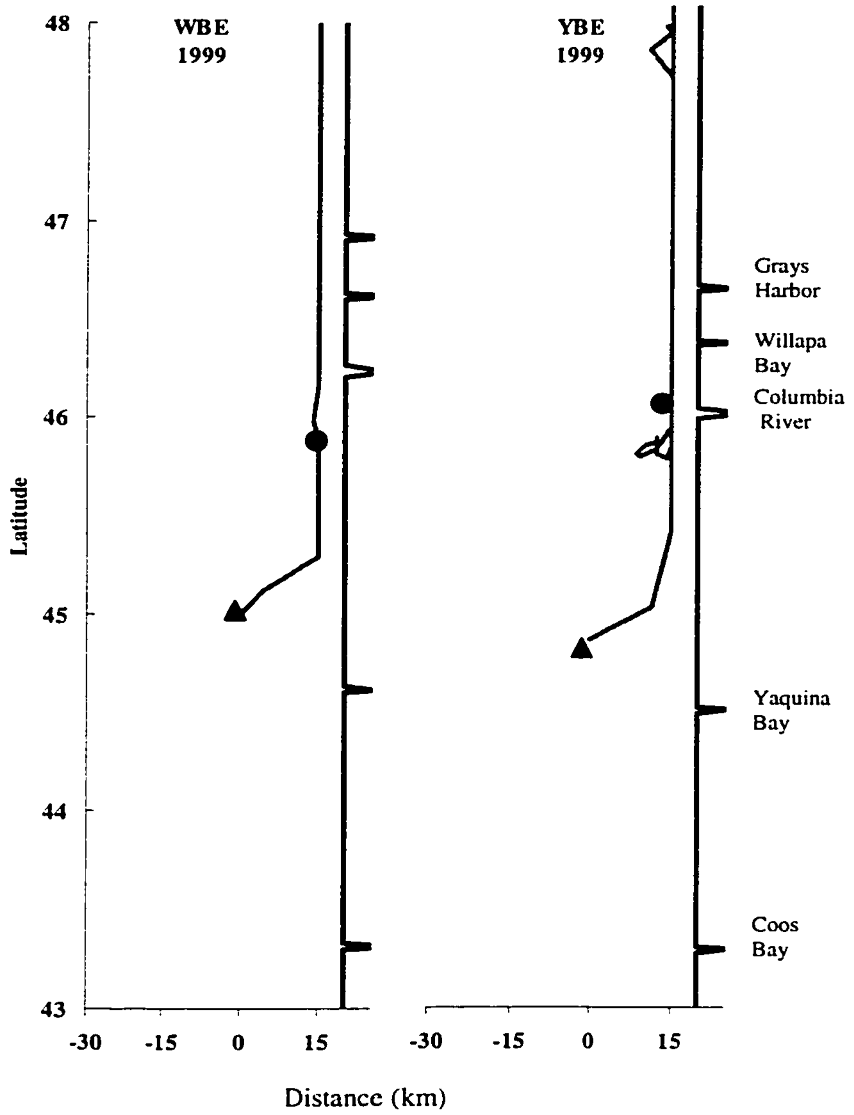

Figure 3.36. Trajectories of early cohort English sole eggs and larvae spawned in the winter of 1998-99. Spawn dates, development rates and current patterns are computed from two cohorts of English sole observed in estuarine trawl surveys in June of 1998. The cohorts depicted are Yaquina Bay (YBE) and Willapa Bay (WBE) early settling sole. Triangle represents assumed spawning location, circle represents hatching location.

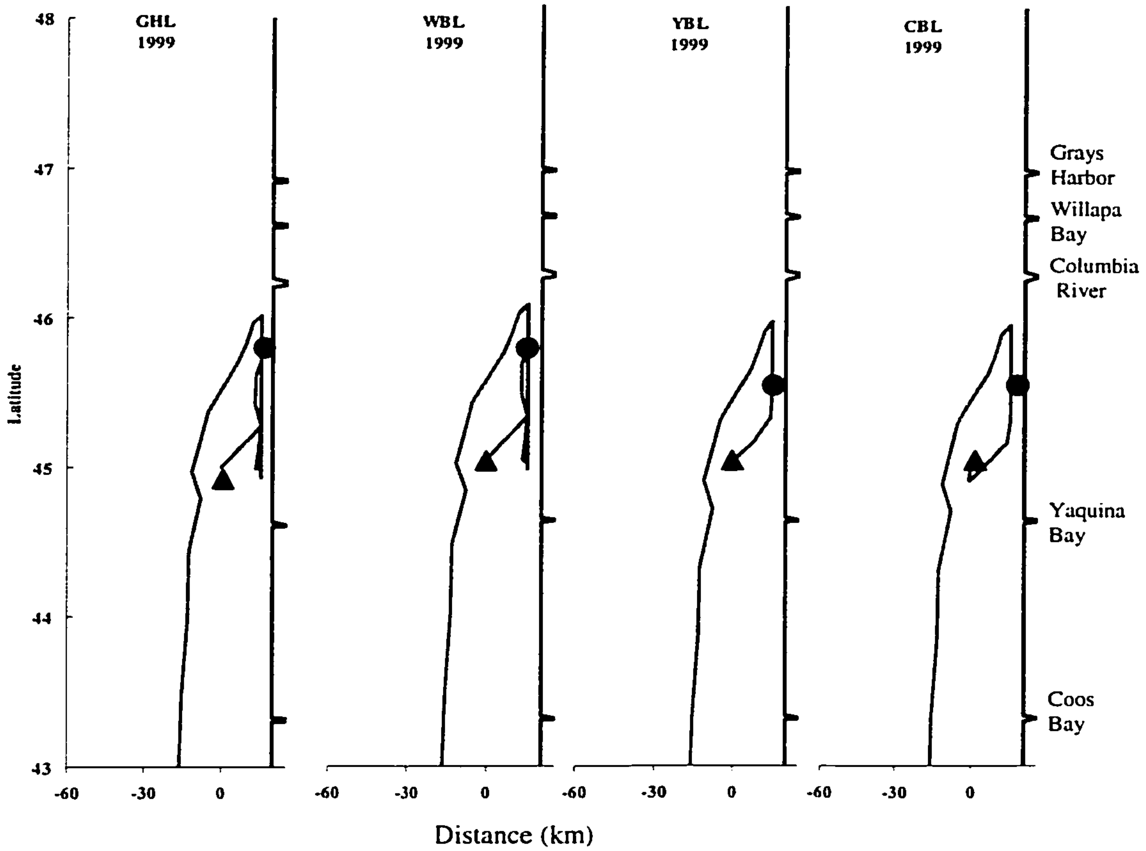

Figure 3.37. Trajectories of late cohort English sole eggs and larvae spawned in the winter of 1998-99. Spawn dates, development rates and current patterns are computed from two cohorts of English sole observed in estuarine trawl surveys in June of 1998. The cohorts depicted are Coos Bay (CBL), Yaquina Bay (YBL), Willapa Bay (WBL) and Grays Harbor (GHL) late settlers. Triangle represents assumed spawning location, circle represents hatching location.

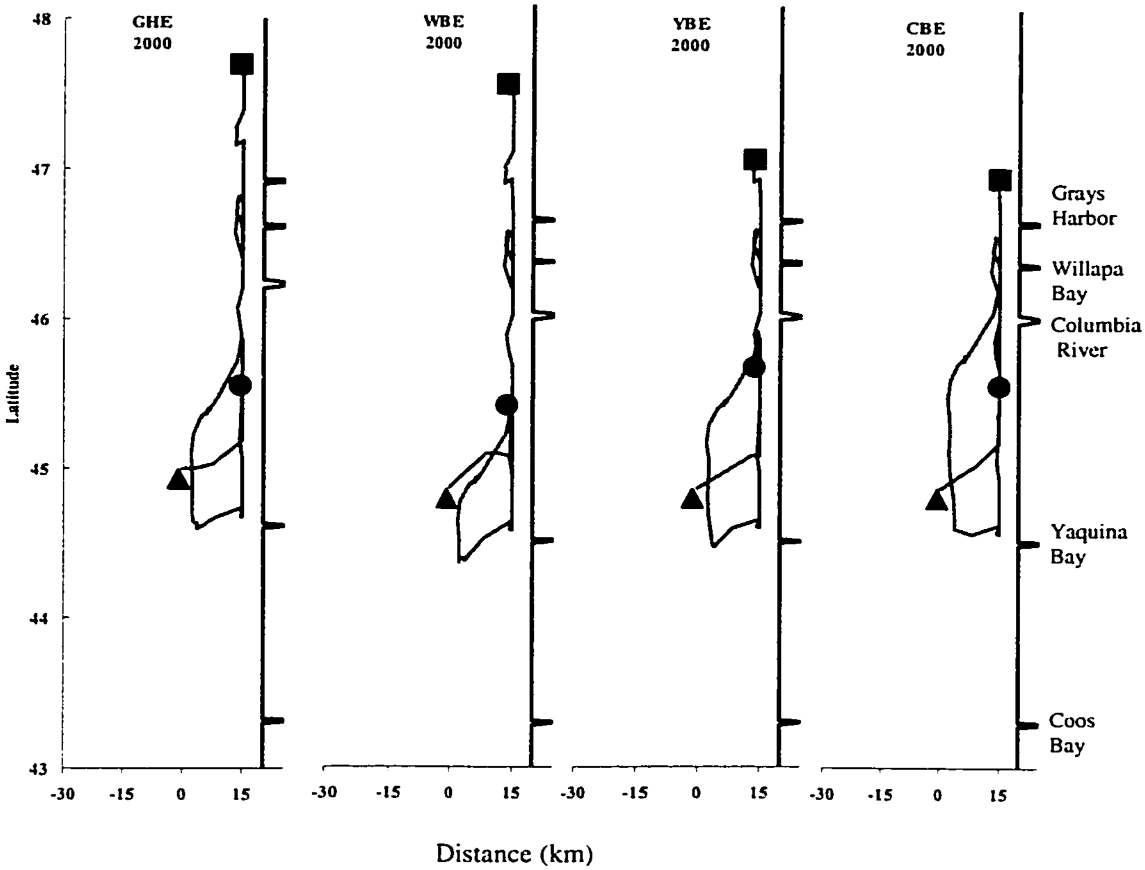

Figure 3.38. Trajectories of early cohort English sole eggs and larvae spawned in the winter of 1999-2000. Spawn dates, development rates and current patterns are computed from four cohorts of English sole observed in June 2000 trawl surveys of PNCERS estuaries. The cohorts depicted are Coos Bay (CBE), Yaquina Bay (YBE), Willapa Bay (WBE) and Grays Harbor (GHE) late settling sole. Triangles represent assumed spawning locations, circles represent hatching locations, squares are settlement locations.

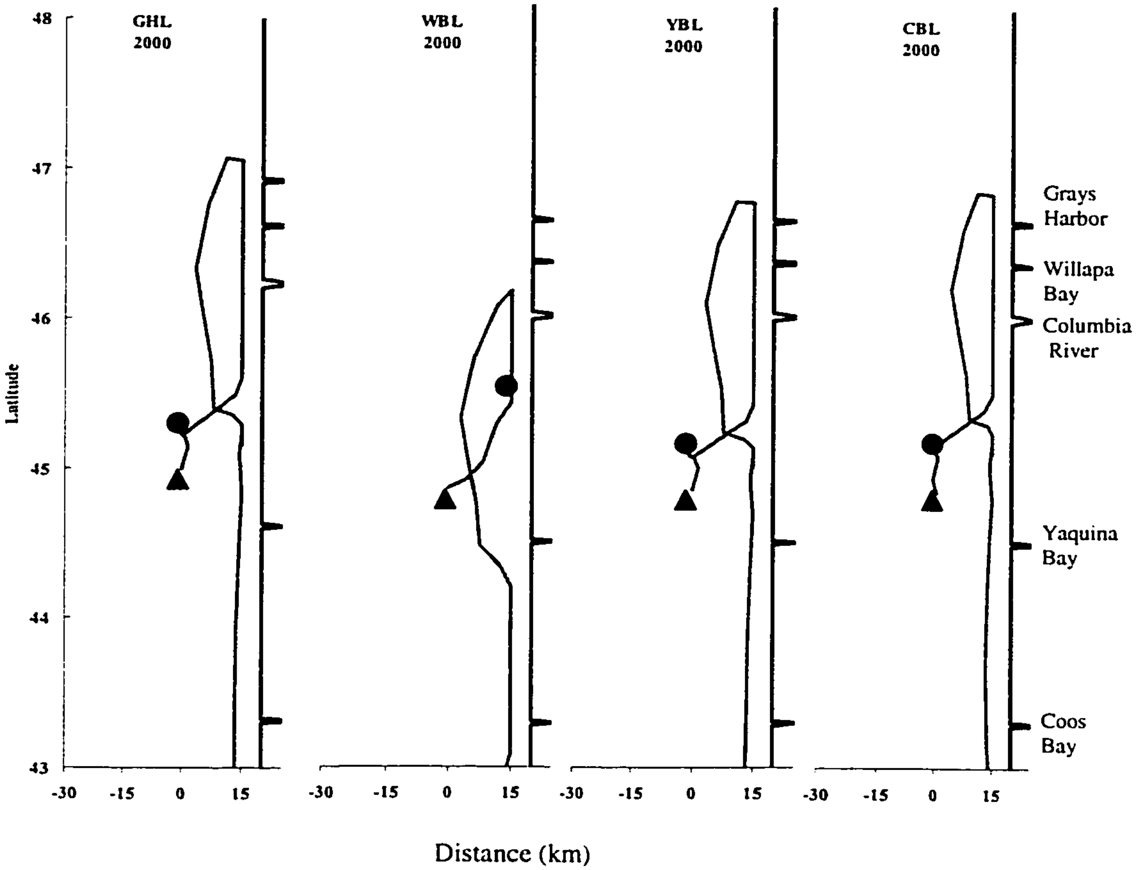

Figure 3.39. Trajectories of late cohort English sole eggs and larvae spawned in the winter of 1999-2000. Spawn dates, development rates and current patterns are computed from four cohorts of English sole observed in trawl surveys of PNCERS estuaries in June of 2000. The cohorts depicted are Coos Bay (CBL), Yaquina Bay (YBL), Willapa Bay (WBL) and Grays Harbor (GHL) late settling sole. Triangle represents assumed spawning location, circle represents hatching location.

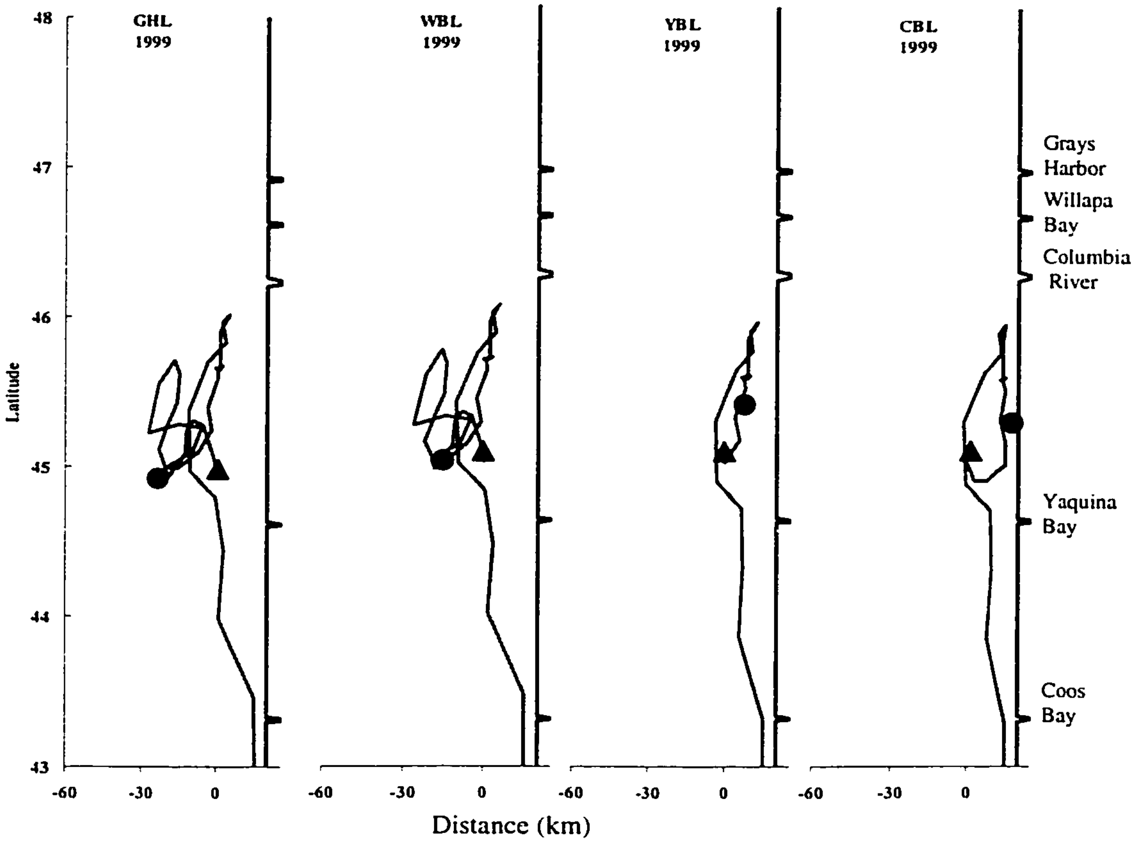

Figure 3.40. Trajectories of late cohort English sole eggs and larvae spawned in the winter of 1998-99 using observed cross-shelf currents from current meter measurements. The cohorts depicted are Coos Bay (CBL), Yaquina Bay (YBL), Willapa Bay (WBL) and Grays Harbor (GHL) late settlers. Triangle represents assumed spawning location, circle represents hatching location.

Chapter 4. Use of estuarine habitat by juvenile English sole

4.1. Introduction

For many species of marine fishes and invertebrates, the habitat used as juveniles is believed to be important to survival through these stages. The amount and type of habitat available can influence predation rates (Fernandez et al. 1993, Lipcius et al. 1997), growth rates (Berghahn et al. 1995, Tupper and Boutilier 1995, Phelan et al. 2000) and distribution (Norcross et al. 1997, Howell et al. 1999, Abookire et al. 2000) of juveniles. The early juvenile stage is a time where recruitment patterns can be set or modified in marine fish species (Bailey and Spring 1992, Bradford 1992, Iles and Beverton 2000). Thus, the type and quality of habitat available to the juvenile stage of marine fishes may be especially important to the future contribution of a year class to the adult population.

For species of flatfish the concentration of juveniles in nursery areas is believed to be especially important in stabilizing recruitment variation (Iles and Beverton 2000). For species that have egg and/or larval stages exhibiting strong correlation to environmental variables, wide fluctuations in larval supply can result in high variability in year class strength. When fish concentrate at some point during the early life history stages, wide fluctuations in larval supply may be ameliorated by density dependent affects. In flatfish species that concentrate in nursery areas, the amount and type of suitable habitat for survival is critical to determining the total number of flatfish that can be produced in any given year.

Numerous field and laboratory studies exploring juvenile flatfish habitat associations have been conducted. These studies have documented flatfish association with depth, sediment type, overlying litter, presence of predators, salinity, temperature or combinations of multiple factors (Dorel et al. 1991, Kerstan 1991, Marchand 1991, Nash et al. 1991, Burke et al. 1991, Neuman and Able 1998, Wennhage and Gibson 1998, Howell et al. 1999, Steves et al. 1999, Walsh et al. 1999, Phelan et al. 2001, Stoner et al. 2001). In a number of studies, the habitat associations of juvenile flatfish have been found to change both seasonally (Abookire, and Norcross 1998, Marshall and Elliot, 1998, Stoner et al. 2001), and with changes in fish size (Walsh et al. 1999, Phelan et al. 2001, Stoner et al. 2001). Many of these studies have focused on only one nursery area, or on only a limited selection of habitat variables.

The English sole (*Pleuronectes vetulus*) is one of few commercially important species on the West coast of North America that is heavily dependent on estuarine nursery areas for juvenile rearing (Olson and Pratt 1973, Krygier and Pearcy 1986, Gunderson et al. 1990). Adult English sole are distributed from Baja California to southwestern Alaska along the shallow continental shelf at depths from the surface to 130-m (Hart 1973). The Oregon/Washington English sole stock is believed to spawn off the central Oregon coast (Hewitt 1980, Kruse and Tyler 1989), and the spawning season is very protracted with peak spawning occurring from September to April, often with multiple peaks (Kruse and Tyler 1983, see Chapter 3). The combination of multiple spawnings and variable ocean currents can produce multiple cohorts of English sole settling and residing in nursery estuaries in the summer (see Chapter 2). Juvenile English sole inhabit nursery estuaries on the outer Pacific coast from Elkhorn slough in California (Yoklavich 1982), to the tip of Washington state. Estuarine residence is usually limited to age 0+ juveniles for English sole during summer months, when fish size is typically between 20 and 100-mm in total length (Gunderson et al. 1990).

This study was focused on habitat associations of age 0+ English sole within four nursery estuaries extending over 400 km of the Oregon and Washington coast. The data on English sole were collected over nine years of subtidal trawl surveys across four estuaries. The objectives were two-fold; to identify common habitat types which could be used to categorize all four estuaries, and to determine if there were consistent patterns in spatial use of these habitats by age 0+ English sole. The analysis was conducted using a wide assortment of habitat variables designed to address important aspects of estuarine systems, and density observations for two size cohorts of age 0+ English sole that commonly occurred in each estuary.

4.2. Methods

This study was carried out at four estuaries on the Oregon and Washington coasts, Grays Harbor, Willapa Bay, Coos Bay, and Yaquina Bay (Figure 4.1). All four estuaries were originally divided into 4-5 strata based on degree of oceanic influence (i.e. distance from estuary mouth). Trawl stations were chosen by random sampling within each strata with the caveat that no two stations were adjacent (Figure 4.2). Stations were allocated based on abundance of English sole and Dungeness crab within the stratum, with strata of higher abundance receiving more stations (Shi et al. 1994). From 17 to 20 sites were chosen in each estuary. A constant location for each of the trawl survey sites was maintained throughout all years of the study. During the initial years of surveying (1983-1988) in Willapa Bay and Grays Harbor, sites were located using recognizable landmarks. During the final three years of the study (1998-2000), sites were located using a combination of these landmarks and global positioning system (GPS) readings. Thus, the exact site location varied somewhat from sampling period to sampling period roughly on a scale of 50 m.

Survey data collection

Trawl surveys of all four estuaries were conducted in both June and August from 1998-2000. During 1983-1988 trawl surveys were conducted at least monthly from May to September in Grays Harbor. For comparative purposes only trawls from the June and August surveys from 1983-1988 data were used in the analysis with the 1998-2000 data. Benthic organisms including English sole were collected during daylight using a 3-m beam trawl described in Gunderson and Ellis (1986). The beam trawl had an effective opening width of 2.3-m and a height of 0.6-m. The net was towed at a speed of 0.8 to 0.9 $m*s^{-1}$ behind a 6.4-m research vessel with a minimum 5:1 scope of line out to depth. The distance towed averaged 139-m in 1998-2000, and 260-m in 1983-1988. Trawls were made against the prevailing current, and efforts were made to conduct trawling near the time of daylight low tides. Sampling was not conducted at high current velocities during maximum ebb and flood to allow the greatest adherence of the beam trawl to the substrate. All fish and invertebrates captured were identified, and English sole caught during the surveys were measured for total length to the closest mm.

Transitions in life history of English sole occur as the fish grow in nursery estuaries. In estuaries English sole undergo a feeding transition from feeding mainly on epibenthic prey (primarily harpactacoid copepods) to feeding on benthic prey (primarily polychaetes and juvenile bivalves) at lengths of 50-65 mm (Toole 1980). Predation pressure should also decrease with increased size of sole. In North Sea plaice (*Pleuronectes platessa*) an escape from predation by crangonid shrimp is usually attained at about 30-mm (Van der Veer et al. 1990). It was expected that the feeding transition, as well as the potential reduction of predation pressure as size increased would lead to different habitat requirements for different size classes of juvenile sole. Therefore, at each site densities of age 0+ English sole in the small (10-50 mm) and large (50-150 mm) size classes were calculated by dividing the catch in each size class by the area swept. The area swept was calculated using the net mouth opening width and the distance towed. Distance for each tow was measured from differential GPS readings in 1998-2000 (Appendix 1), and using a rangefinder and marker buoys from 1983-1988 (Shi et al. 1994).

It has been previously observed that significant variation in density of juvenile English sole occurs among estuaries, as well as on a seasonal and interannual basis (see Chapter 2). To standardize for this variation, I used the anomaly of English sole densities in each size class as the dependent variable in the analyses. The mean density for each estuary in each of the years and months where sampling occurred was calculated and removed from each individual density estimate. The values were then normalized by dividing by the standard deviation of the densities in each period so that

$$a_i = \frac{x_i - \overline{x}_{emy}}{sd_{emy}}.$$

In this equation the subscript *i* refers to an individual density estimate from a trawl survey site within an estuary-month-year combination. Thus, *emy* refers to the estuary-month-year combination where a trawl survey occurred, and *x* and *sd* are the mean and standard deviation of all trawl surveys occurring in that estuary-month-year combination. By using the anomaly of the densities for each cohort I attempted to reduce the large scale variation in the dataset that was attributed to interannual, estuarine and seasonal sources in order to concentrate solely on the component of variation related to within estuarine habitat types.

Habitat characteristics

In addition to documenting the fish and invertebrates captured during trawl surveys, additional samples and data were collected to further characterize each trawl site (Table 4.1). The substrate material (i.e. macroalgae, shell, woody debris etc.) caught during each tow was weighed and/or its volume estimated. Additionally, the depth, bottom temperature and bottom salinity were measured at the time of each trawl. In some cases this information was not recorded due to oversight or equipment failure. For missing depth values, the average depth calculated from other survey periods was used to fill gaps. For salinity and temperature, small gaps of missing stations were filled by the closest adjacent station sampled during the same time period. During the June 2000 surveys, a large number of stations had no temperature or salinity data due to equipment failure. The average temperature and salinity for each of these stations during the previous years June trawl surveys were utilized.

A variety of known and suspected predators of juvenile sole that may influence the distribution of their prey inhabit estuaries, including crangonid shrimp (Van der Veer et al. 1990, Wennhage and Gibson 1998), and age 1+ Dungeness crab, *Cancer magister*, (Gotshall 1977, Stevens et al. 1982). Both of these predators were commonly captured during trawl surveys. The total density of age 1+ crab and the total biomass of crangonid shrimp were calculated for each trawl, and utilized in an index of predation pressure.

In 1998 a benthic grab was used to collect a sediment sample at most sites. In the laboratory grainsize analysis was undertaken according to the methods in Rooper et al. (in press). The analysis gave the amount of sediment standard size classes according to the modified Wentworth scale (Cummins 1962). The average grain size at each site was determined based on the proportions of sediment in each size category and the midpoint of the grain size within each category. For example, the proportion of sediment sorted into a 1-mm sieve was assigned a grain size of 1.5-mm, as the grains were smaller than 2-mm yet larger than 1-mm. Sediment samples were not collected for five of the 73 trawl survey sites, so these sites were assigned the average grain size for the closest neighboring trawl survey site.

A number of other variables used to characterize each trawl survey site were taken from NOAA nautical charts. To assess the prevalence of intertidal area adjacent to each trawl survey site, the percentage of a 3.6 km^2 (one nautical mile) area around each trawl site that was composed of tide flat was estimated from nautical charts. The depth of each site relative to mean low water was also identified for each site. Finally, the distance of each site from the estuary mouth calculated as a percentage of the farthest up-estuary point sampled (in order to account for the large size difference among the four study estuaries) was calculated for each trawl survey location.

Data Analysis

Habitat characteristics for each site at which trawl surveys were conducted were classified as either ephemeral or static (Table 4.1). Ephemeral habitat characteristics were those that were likely to change between sampling dates, and thus needed to be treated separately from survey to survey. For example, the depth at which a trawl was conducted was considered to be ephemeral, since it varied with the tide stage and exact station location between sampling trips. Static habitat characteristics were either stable or assumed to be fairly stable over the time of the study. The static variables included; depth of the site relative to mean low water, the average sediment grain size, the proportion of surrounding tidal flats and the relative distance from the mouth of the estuary to each site. Additionally, the weight per ha of woody debris and average weight per ha of shell debris averaged across all trawls at each site from 1998-2000 were classified as static variables, since these weights did not appear to vary substantially among years or seasons.

The static habitat variables were used to group sites across the estuaries in terms of a shared set of characters. Because of the correlation among the static variables (for example the amount of woody debris generally increased with distance from the mouth of the estuary), this was accomplished through principle component analysis. Prior to analysis the static variable data for the 73 trawl survey sites was standardized, and the resulting covariance matrix was used in a principle component analysis to identify patterns in the data (SAS 1987). A classification scheme was developed based on these results in order to group trawl survey sites into categories that would apply across estuaries. The resulting classification scheme was used as a categorical variable in subsequent analyses of English sole density anomalies.

The ephemeral variables were also explored using principle components analysis to determine which of the habitat characters exhibited the most variation over the estuaries. Principle components analysis was conducted on the six ephemeral variables over the 431 trawls that were conducted from 1998-2000. This analysis revealed variables that were both uncorrelated to each other, and varied substantially within the estuaries. These components were then used to guide the further analyses of English sole densities, where it was hoped that this variability would help explain the variability in English sole density anomalies.

A final variable was added to the analysis to account for the overall density of English sole in each size class in each estuary-year-month combination. This variable classified the density of each size class of sole within each estuary-year-month combination into one of three categories; high, average or low. The categorization was accomplished by calculating the overall average density of each size class of English sole over all 800 trawls conducted in the nine years of the study. Then the estuary-year-month combinations that fell within two standard errors of the mean were categorized as average, two SE's above the mean as high and two SE's below the mean as low. The purpose of this relative density variable was to determine if there was an expansion of the range of English sole during years of high densities.

Factorial analyses of variance was used to determine important variables affecting English sole density in the two size classes. Factorial analysis of density anomalies of the small size class of English sole were conducted only for the June survey data. In August surveys, there were very few English sole that were less than 50-mm total length, since settlement generally occurred in May of each year (Chapter 3).

In all of the factorial analyses, an initial model was formulated including all main effects, as well as interaction terms. Insignificant ($p < 0.05$) terms in the analysis were removed sequentially until only significant terms remained. Pairwise comparisons for significant class variables were conducted using the least squares means approach (SAS 1987), with a Tukey adjustment for multiple comparisons (Zar 1974).

4.3. Results

Densities of small English sole at sites in June of 1998-2000 were between 0 and 11,300 per ha in Grays Harbor, 0 to 6,800 per ha in Willapa Bay, 0 to 6,000 in Yaquina Bay and 0 to 5,400 per ha in Coos Bay. Densities of large cohort English sole in June and August 1998-2000 were observed over a wider range of values. During June and August trawl surveys, the density of large cohort ($50 < TL < 150$) English sole in Grays Harbor ranged from 0 to 5,200 per ha, in Willapa Bay densities ranged from 0 to 7,900, in Yaquina Bay densities were between 0 and 33,000 per ha, and in Coos Bay densities ranged from 0 to 3,900 per ha. Thus, there was considerable variability in density of both English sole size classes among sites in the estuaries.

In 3 of 12 sampling trips from 1998-2000 (see Chapter 2) there were significant cohorts of early settling (large size class) fish observed in the June surveys. This resulted in a bimodal length frequency distribution in June (Figure 4.3). The more typical length frequency histogram from June showed a smattering of large fish in the estuary, with a large number of late settling small fish (Figure 4.3). In August, the late settling fish had grown to a larger size, and the early settling fish may have moved out of the study area, resulting in a single mode of large fish (Figure 4.3).

Static variable analyses

The principle components analysis of static habitat variables resulted in each trawl survey site being classified into one of three categories; lower side channel, lower main channel or upper estuary. The first three principle components explained over 70% of the variation in the static habitat variables (Table 4.2). The first principle component was weighted heavily on the average amount of woody debris found at each site, and the depth relative to mean low water. The second component was highly correlated with the percentage of surrounding tide flats in an area around each site, and the third component was most highly correlated with the distance from the mouth of the estuary. A scatterplot of PC1 against PC2 clearly separates the lower main channel sites from those in the rest of the estuary (Figure 4.4). The lower main channel sites fall primarily within the area of negative values for both PC1 and PC2. The scatterplot of PC1 against PC3 separates out the lower side channel sites, with negative PC3 values, from the upper estuary sites, with predominantly positive PC3 values (Figure 4.4).

Lower side channel sites were typically shallower, had a slightly smaller average grainsize, and had larger areas of tide flats surrounding them than main channel sites (Table 4.3). Upper estuary sites were typically shallow with slightly less surrounding tide flats, exhibited higher amounts of both woody and shell debris and were farther from the mouth of the estuary (Table 4.3).

Ephemeral variable analyses

Of the six ephemeral variables assumed to change on a seasonal and interannual basis, three accounted for the majority of the variance in the habitat data set. Three principle components explained 67% of the variance in the ephemeral habitat variables (Table 4.4). The first principle component was highly correlated to bottom temperature and salinity measured at the time of trawling. These two variables were correlated to each other (r = -0.52), but because of its importance to growth rates in fishes and the consistency with which this data was collected, bottom temperature was chosen as the variable to be used in further analysis of English sole density anomalies. The second principle component was most strongly correlated to the depth at the time of trawling, and the third component was highly correlated to the two measures of predation, crangonid shrimp biomass and Dungeness crab density. Information on Crangon biomass was not adequately collected during the early period (1983-1988) of trawling, therefore age 1+ crab density was the only predation variable available over all years of the study. Because of their importance in the PCA, age 1+ crab density and bottom temperature were chosen as a covariates for analysis of small English sole density anomalies. For factorial analysis of large English sole density anomalies and bottom temperature were utilized as covariates. In both of these analyses depth was combined into 2-m bins in order to account for the variations in bottom depth that occurred over each trawl site. Thus, depth was used as a class variable in the analysis of both large and small English sole density anomalies.

Factorial Analyses

For analyses of the small size class of English sole density anomalies the factors used were estuary location and three ephemeral variables, bottom temperature, depth and an index of predation (age 1+ crab density). The relative density of small fish in each estuary-year-month combination was also used in the analyses.

Factorial analysis of small (TL < 50-mm) English sole June density anomalies resulted in one significant ($p < 0.05$) continuous effect, bottom temperature, as well as three class effects, estuary location, depth and relative estuarine density of English sole (Table 4.5). English sole density anomalies decreased with increasing bottom temperature, although variability in density anomalies was high. English sole density anomalies also decreased with increasing depth in the smaller size class (Figure 4.5), with positive anomalies occurring only at the shallowest depths (1 to 3-m). Significantly higher density anomalies were observed at lower side channel locations than at all other locations within the study estuaries (Figure 4.6), while at the upper estuary sites, density anomalies were significantly lower than at all other locations. The relative density term was significant with higher density anomalies at all locations in years of relatively high densities, however, the density-location interaction term was not significant, indicating that no disproportionate expansion among locations was occurring at higher densities of small English sole. The index of relative predation pressure measured by age 1+ crab density at each site was also not significant in the analysis. Approximately 17% of the total variation in density anomalies for small English sole was explained in the statistical analysis, thus a large proportion of the variation in English sole density anomalies was not explained by the habitat variables examined.

For analyses of the large size class of English sole density anomalies, the estuary location variable based on the cluster analyses of the static habitat variables, bottom temperature and depth were included as factors. The two ephemeral variables, bottom temperature and depth were included based on the results of the PCA of the total set of ephemeral variables, The relative density variable was also utilized in the analysis.

Factorial analyses of the large size class (50 < TL <150) English sole density anomalies resulted in only one significant effect (Table 4.5). The anomalies of English sole density at different locations in the estuaries were significantly higher in lower side channel sites than in either lower main channel or upper estuary sites (Figure 4.7). This pattern was much the same as with the small cohort English sole, but the differences in density anomalies were not as large. Although the factorial analysis model for large sole was statistically significant, it explained only about 5% of the variation in the data set. There was substantial variation in the density anomalies for large English sole that was not explained by the habitat variables we examined. Much of this variation was caused by large density differences occurring among sites within the same location. For example many times the density of one or two lower side channel sites was very large, while the adjacent lower side channel sites were of average magnitude (Figure 4.8).

4.4. Discussion

The principle components analysis of the habitat variables across the study estuaries, yielded some commonalties among the trawl survey sites. The distinction between lower main channel and lower side channel sites resulted in a reasonably clear boundary between deeper sites close to the mouth with little surrounding tidal flat and shallow sites with large surrounding intertidal areas. The distinction between lower side channel sites and upper estuary sites was less distinct. The distance from the mouth of the estuary, the amount of woody debris and the relatively low surrounding intertidal area were the primary distinguishing features of upper estuary sites. Interestingly, within both the lower side channel and lower main channel designations there was approximately equal representation by all estuaries. This indicates that with regard to the static habitat variables examined, the estuaries shared common characteristics.

The upper estuary designation sites in the two Washington estuaries were somewhat different from the sites in Oregon. This distinction between Oregon and Washington is primarily due to the larger amounts of woody debris that were found in Oregon estuaries. The distinction may also be related to relative size of the area sampled within each estuary. The distance from the furthest upstream trawl survey site in Yaquina Bay was approximately 11 km from the mouth, while the furthest upstream trawl survey site in Grays Harbor was also 11 km from the mouth. However, the relative distance up an estuarine gradient of salinity was much farther for the Yaquina Bay site than the Grays Harbor site because of the smaller size of Yaquina Bay. To illustrate this, at the farthest site from the mouth of Yaquina Bay the lowest recorded salinity was 9.8-ppt, while the lowest salinity recorded for Grays Harbor was 18.8 ppt at the site farthest from the mouth of that bay. This was also true for Coos Bay where the uppermost sites were probably higher on an estuarine gradient than the upper sites in Willapa Bay or Grays Harbor.

The analysis of juvenile English sole density anomalies in estuaries revealed consistent patterns across estuaries on the Oregon and Washington coast. Juvenile

English sole were found to utilize lower side channel locations at significantly higher densities than either lower main channels or upper estuary areas. Small English sole also showed significant relationships with both bottom temperature and depth. Although it was not specifically tested in the analyses, the location effect was consistent across all estuaries that were studied (Figure 4.9). Both models of habitat use explained only a fraction of the variability in density anomalies for both size classes.

Sediment characteristics are thought to be an important factor regulating demersal fish distribution. A consistent feature of all the habitat types in the four Oregon and Washington nursery estuaries was the uniformity in sediment size. Of the 68 estuarine sites where sediment samples were taken, the dominant sediment type at 64 was either medium sand (grainsize from 500 um to 1 mm) or very fine sand (grainsize from 250 to 500 um). Previous laboratory studies revealed that when given the choice, juvenile flatfishes prefer a select range of sediment sizes that allow burying (Moles and Norcross 1995), presumably to avoid predation. Field studies have also indicated flatfish have substantial preferences for specific sizes of bottom sediments that vary with fish size (Rogers 1992, Neuman and Able 1998, Norcross et al. 1999, Phelan et al. 2001). In adult English sole there is even evidence for sex segregation by sediment type (Becker 1988). Thus, the absence of substantial variation in sediment type at our study sites may have contributed to the ubiquity of juvenile English sole throughout their nursery estuaries.

The substantial effect of depth on the distribution of small size English sole is not unexpected. Many previous studies of juvenile flatfishes have indicated substantial depth related habitat associations (i.e. Steves et al. 1999, Norcross et al. 1999). Newly settled flatfish are often found at shallower depths than their older conspecifics (Burke et al. 1991). Segregation of English sole juveniles by size class has previously been observed for populations in Puget Sound, Washington, although large fish were found at shallower depths than small fish (Thornburgh 1980). The lack of the depth effect for large size class English sole in this study may reflect a difference between estuarine nurseries and those found in more marine environments such as Puget Sound.

The four nursery estuaries surveyed in the current study are all influenced to some degree by the seasonality of runoff and oceanic conditions. This is evident in the seasonal temperature change, as temperatures increased from June to August at upriver sites and salinity increased due to surface heating and reduced runoff during the late summer. In Willapa Bay the Washington Department of Ecology has deployed a number of continuous temperature and salinity data loggers from 1998-2000 (Jan Newton and Eric Siegal, Washington Department of Ecology, Lacey, Washington, personal communication). These data indicate that the variability in both temperature and salinity at the most upstream location (at site WB-53 on Figure 4.2) on a daily basis is less than at more downstream locations. The average daily temperature maximums are about 19 ^{0}C and average daily salinity minimums are 30 ppt at this station in August. In June, daily maximum temperatures average 15 ^{0}C and salinity minima occur at about 20 ppt.

There is no available information from the literature that gives an indication of the salinity tolerance of English sole juveniles. A number of studies have found that flatfish distribution can be restricted by salinity (Marchand 1988, Kerstan 1991, Gibson 1994), but no specific information for English sole exists. Salinity data from this study was available only for the last three years of the trawl surveys, so an accurate picture of the effect of salinity on juvenile English sole distribution was difficult to attain. With the limited data set available, it can be seen that the average density of small English sole decreases with decreasing salinity (Figure 4.10). For larger English sole, the decline in density with decreasing salinity is most evident for densities less than 18 ppt (Figure 4.10). The only site from our study where no English sole were ever captured was site number 34 in Yaquina Bay, Oregon. This was the farthest site from the mouth of Yaquina Bay (11 km upstream), and June salinity averaged 18 ppt, while August salinity averaged 24 ppt over the three years of data collection.

The temperature tolerance of English sole is quite wide, ranging from 9 to 21 ^{0}C, as indicated by collections from this study. The more important effect of temperature may be observed in growth rates, rather than as a limiting factor on distribution of the flatfish. Yoklavich (1982) found that English sole growth rates were lower at high temperatures (17 ^{0}C) than at lower temperatures (13 ^{0}C). The significant negative relationship ($p = 0.01$) between English sole density and bottom temperature found in this study may be indicative of the reduced growth potential at the extreme estuarine temperatures. At Yaquina Bay site 34 the June temperature values averaged 18 ^{0}C, while August temperature was 21 ^{0}C over the three years of the study. It is unclear if either the high temperatures or low salinities resulted in zero catches of juvenile English sole at this site since the two variables are confounded.

Although not statistically significant in the analyses, there was some indication that large juvenile English sole expanded their range during years of high abundance.

Negative anomalies of large English sole in both lower main channels and the upper estuary decreased with increasing density of this size class (Figure 4.11). This indicates that as overall density increased throughout the estuary, the average density in each of the locations converged (the anomalies trended towards zero). This pattern differs from that for small English sole, where the relative anomalies among the three estuarine locations remained constant with increasing small fish density (Figure 4.11). According to the basin hypothesis, changes in distribution in flatfish stocks are caused by changes in overall abundance (MacCall 1990). Thus, in years of high abundance juvenile sole would have been expected to extend their range within the estuary to areas that may not be as suitable for development, maintaining a relatively constant density over the nursery area. This has previously been hypothesized for adult flatfish species in the Bering Sea (McConnaughey 1994). For adult English sole over the continental shelf of Oregon, population densities have been found to increase with increasing total abundance while distributions remained the same (Sampson 1994). The current trawl surveys were probably conducted on a fine enough scale to detect changes in distribution of juvenile English sole, and there is some indication of widening of the range of large sole with increasing density. The absence of range expansion for small English sole with increasing density suggests small English sole may be limited in their range of habitat tolerances. Since small English sole also showed significant relationships with both bottom temperature and depth, habitat requirements for juvenile sole may become less restrictive as the sole grow.

The pattern of changing distribution of large size class English sole may suggest that a carrying capacity for these fish could exist within nursery estuaries. If so, this would help to explain the relatively constant density of English sole in August that has been observed for our nursery estuaries (Chapter 2). In turn this may also serve as to help dampen recruitment variability caused by variation in survival through the pelagic egg and larval phases as suggested by Iles and Beverton (2000). If a carrying capacity for large size class English sole exists, the prolonged spawning season and the ability of English sole stocks to produce multiple estuarine cohorts would be a distinct ecological advantage because fish could maximize the nursery space available over a temporal scale thereby reducing intraspecific competition.

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Table 4.1. Habitat variables, classifications and source of information used in principle component analyses to define habitat types in nursery estuaries.

Habitat variable	Classification	Source of information
Depth relative to mean low water (m)	*Static*	Nautical charts
Shell substrate (kg/ha)	*Static*	Trawl survey data
Woody debris substrate (kg/ha)	*Static*	Trawl survey data
Salinity (ppt)	*Ephemeral*	Trawl survey data
Temperature (°C)	*Ephemeral*	Trawl survey data
Sediment grainsize (um)	*Static*	Sediment collections, 1998
Macroalgal substrate (kg/ha)	*Ephemeral*	Trawl survey data
Distance from mouth of estuary	*Static*	Calculated from nautical chart
Percentage of surrounding tidal flat	*Static*	Calculated from nautical chart
Age 1+ Dungeness crab density (no/ha)	*Ephemeral*	Trawl survey data
Depth at trawl (m)	*Ephemeral*	Trawl survey data
Crangonid shrimp biomass (kg/ha)	*Ephemeral*	Trawl survey data

Table 4.2. Results of principle components analysis of static habitat variables at 73 estuarine sites.

	Correlation coefficients		
Habitat variable	Principle component #1	Principle component #2	Principle component #3
Depth relative to mean low water	-0.6051	-0.2065	0.5245
Shell substrate (kg/ha)	0.5582	-0.1687	-0.3798
Woody debris substrate (kg/ha)	0.8480	-0.1167	0.3546
Distance from the estuary mouth	0.4650	0.5710	0.6108
Average sediment grainsize	0.4696	-0.5881	-0.0410
Percentage of surrounding tidal flats	0.0996	0.7915	-0.3629
Cumulative variance explained	0.3072	0.5377	0.7130

Table 4.3. Average value (SE) of static habitat variables within each location category used to classify trawl survey sites.

Static habitat variable	Lower main channel	Lower side channel	Upper estuary
Depth relative to mean low water (m)	5.1 (0.14)	3.7 (0.17)	4.0 (0.17)
Shell substrate (kg/ha)	55 (14.2)	182 (17.9)	191 (43.6)
Woody debris substrate (kg/ha)	15 (2.3)	32 (4.7)	155 (22.8)
Distance from the estuary mouth	0.33 (0.02)	0.46 (0.02)	0.80 (0.02)
Average sediment grainsize (um)	263 (8.3)	223 (5.7)	275 (10.0)
Percentage of surrounding tidal flats	20.6 (1.8)	53.1 (2.6)	39.8 (2.5)

Table 4.4. Results of principle components analysis of the ephemeral habitat variables.

	Correlation coefficients		
Variable	Principle component #1	Principle component #2	Principle component #3
Depth (m)	0.3232	-0.7295	0.1389
Bottom temperature (^{0}C)	-0.7484	0.2726	-0.3019
Bottom salinity (ppt)	0.8863	0.0761	-0.0937
Crangonid shrimp biomass (kg/ha)	-0.4976	-0.4102	0.6182
Age 1+ D. crab density (no/ha)	0.0424	0.4747	0.6352
Macroalgae (kg/ha)	0.3103	0.4770	0.2994
Cumulative variance explained	0.2993	0.5049	0.6706

Table 4.5. Results of factorial analysis of variance of small and large age 0+ English sole density anomalies. Significant ($p < 0.05$) variables are shown, as well as the squared correlation coefficient, * denotes $p < 0.01$.

Cohort of English sole	Significant factors	n	R^2
Small (TL < 50 mm)	Location*	400	0.17
	Bottom temperature*		
	Depth		
	Relative density of small English sole		
Large (50 mm < TL <150 mm)	Location*	800	0.05

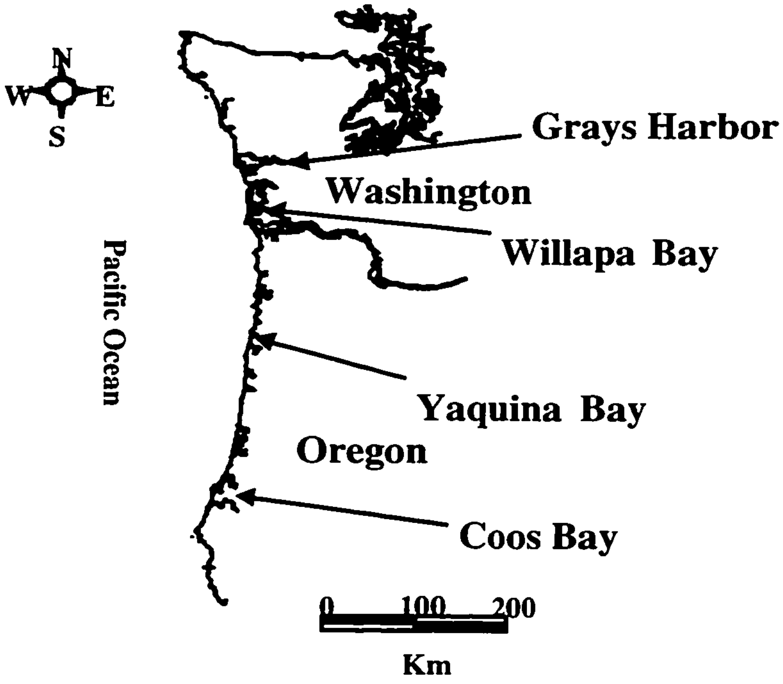


Figure 4.1. Coastline of Oregon and Washington showing each of the study areas; Grays Harbor, Willapa Bay, Yaquina Bay and Coos Bay.

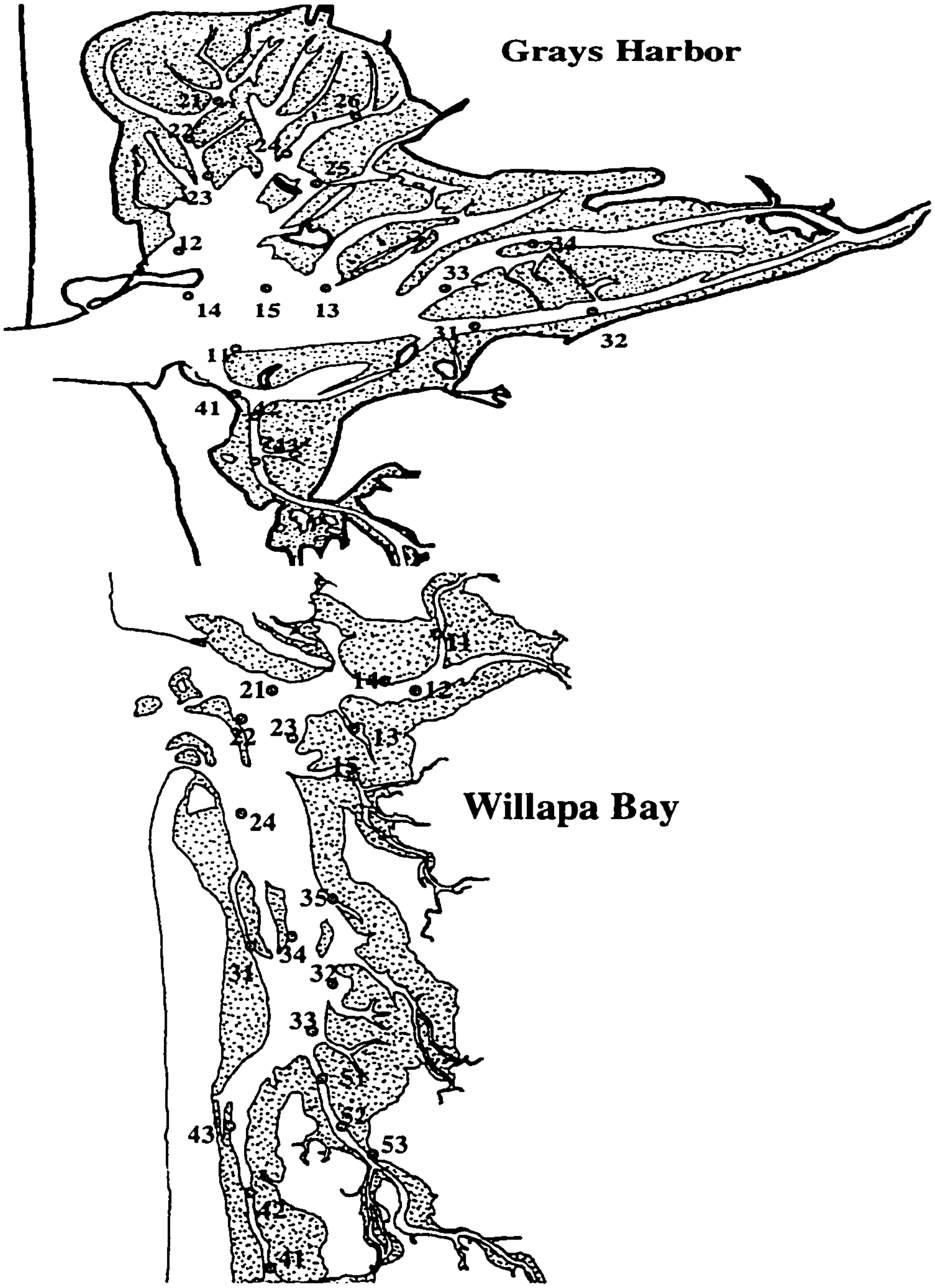
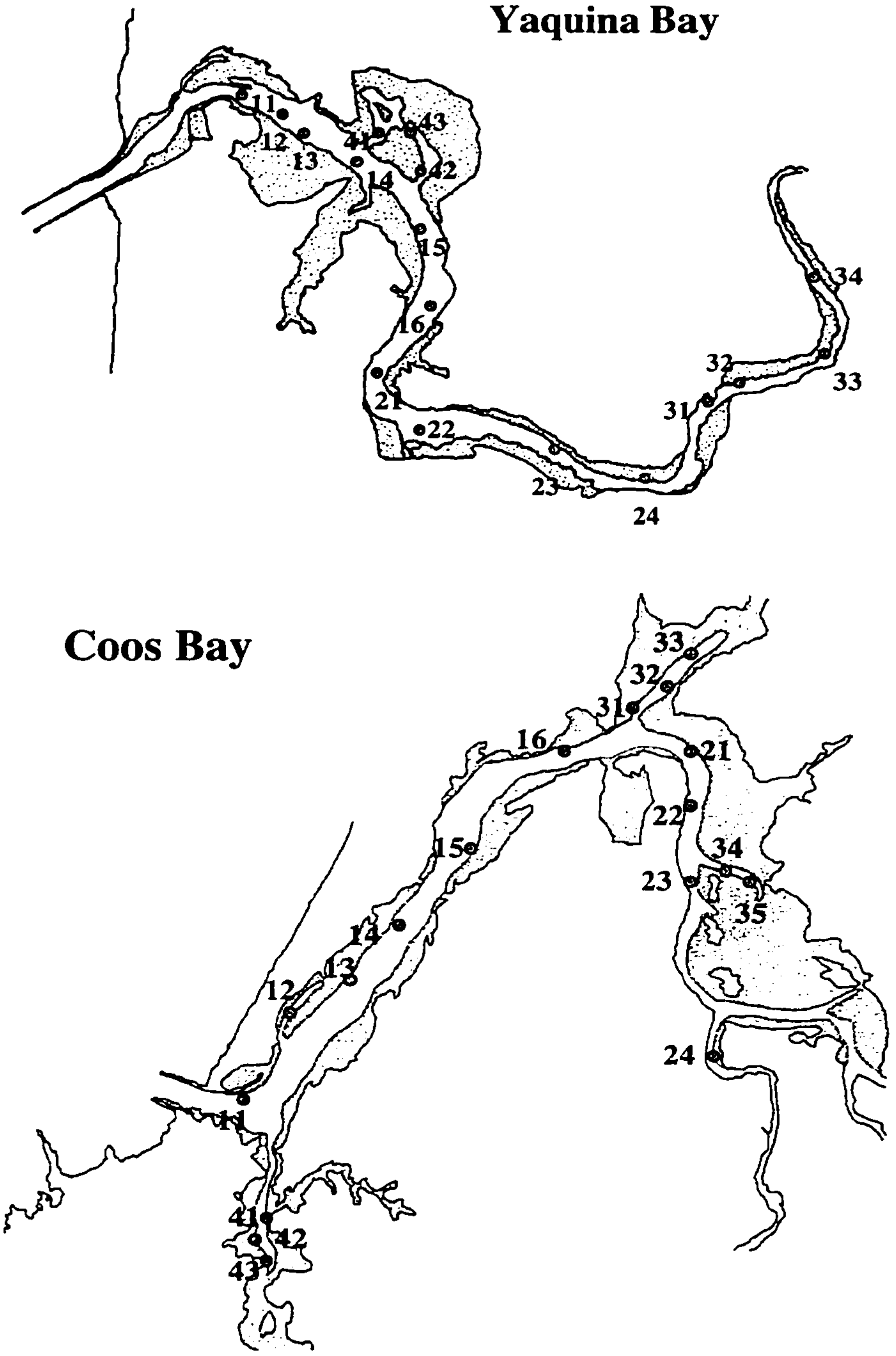


Figure 4.2. Map of the four study areas showing station locations and number designations.



Yaquina Bay

Coos Bay

Figure 4.2 (cont.). Map of the four study areas showing station locations and number designations.

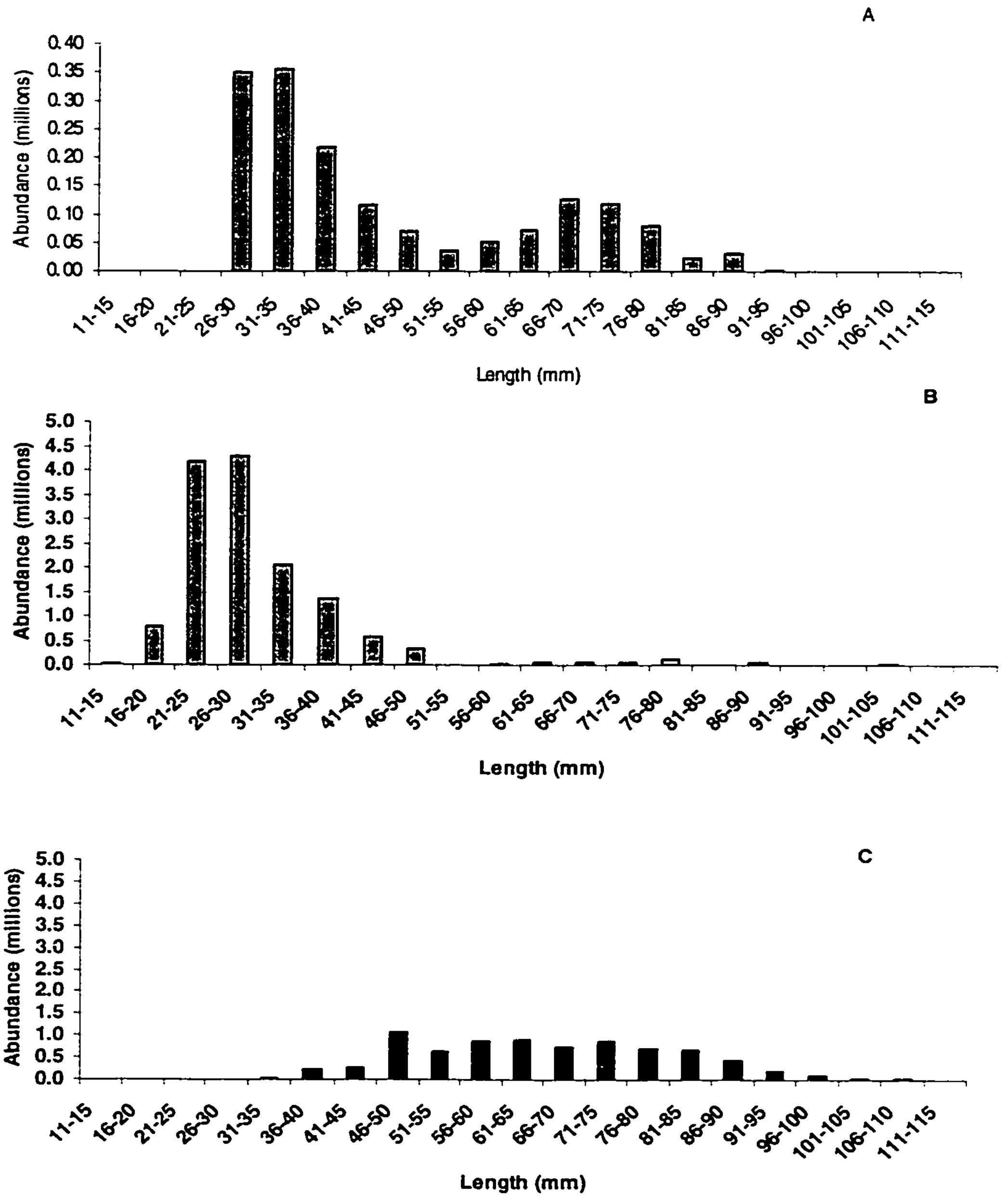


Figure 4.3. Length frequency plots for English sole captured in trawl surveys. Panel A depicts the bimodal length frequency of fish captured in the June 1998 survey of Coos Bay. Panels B and C are from Grays Harbor, 1998 from June (B) and August (C) surveys. The bottom two panels show the more typical length frequencies of fish captured in the June and August trawl surveys.

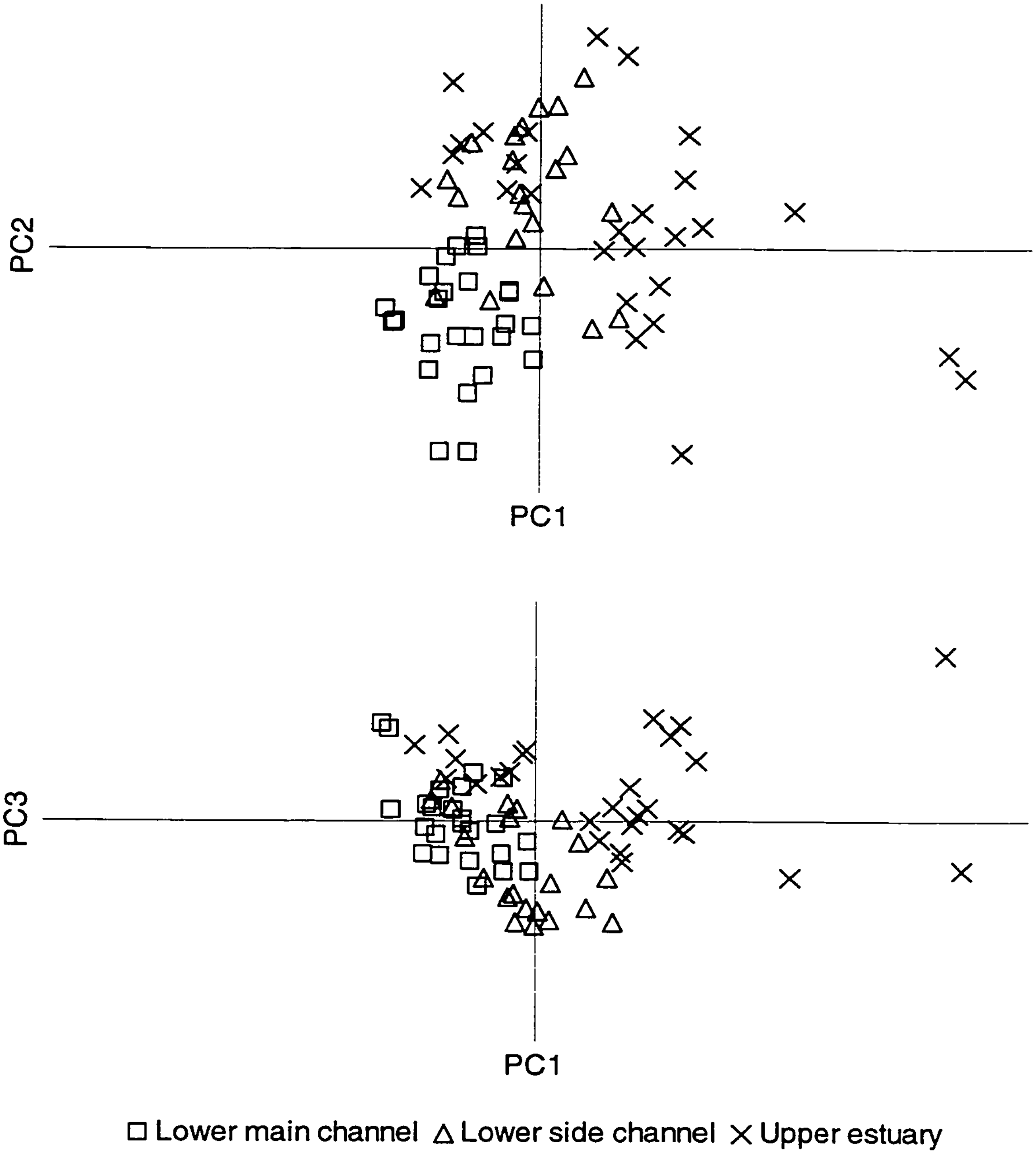


Figure 4.4. Scatter-plots depicting the significant principle components (PC1, PC2 and PC3) values for each trawl survey site. This principle components analysis was completed on the static habitat variables.

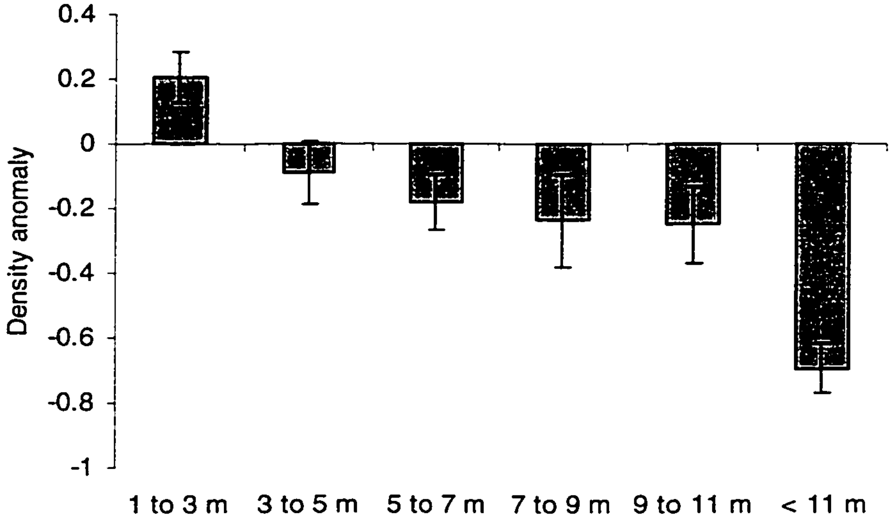


Figure 4.5. Density anomalies of small English sole at depths of trawling from 1983-1988 and 1998-2000 surveys. The depths were compiled into two meter bins for the analysis.

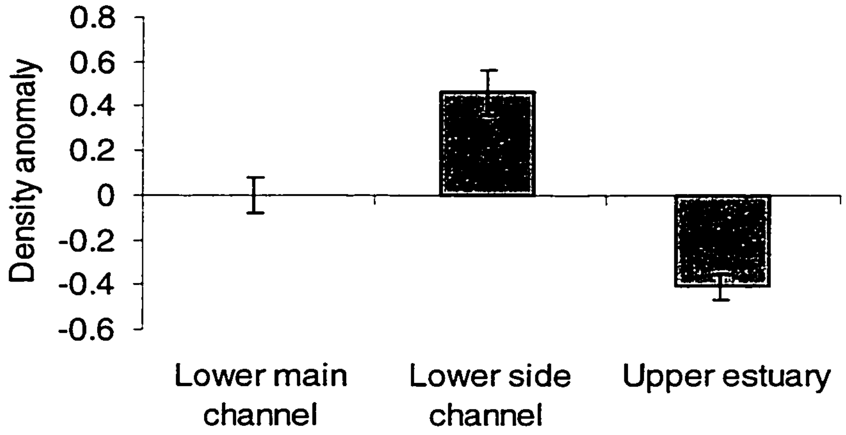


Figure 4.6. Average density anomalies of small English sole (total length < 50 mm) at locations within the study estuaries

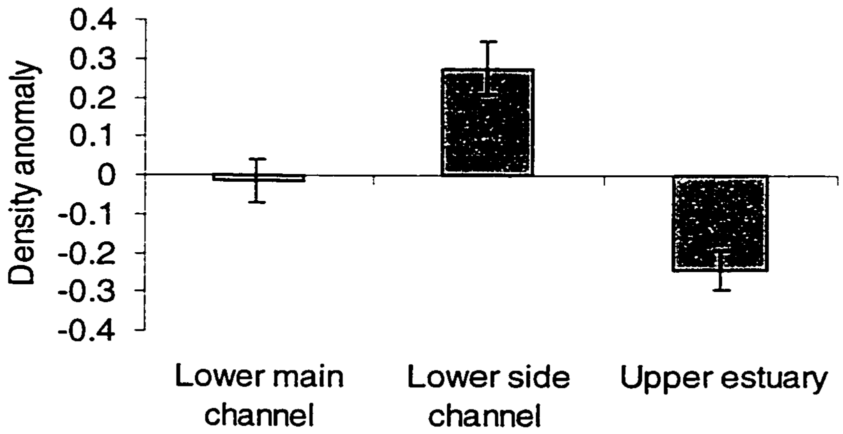


Figure 4.7. Average density anomalies of large English sole (50 mm < Total length <150 mm) at locations within estuaries.

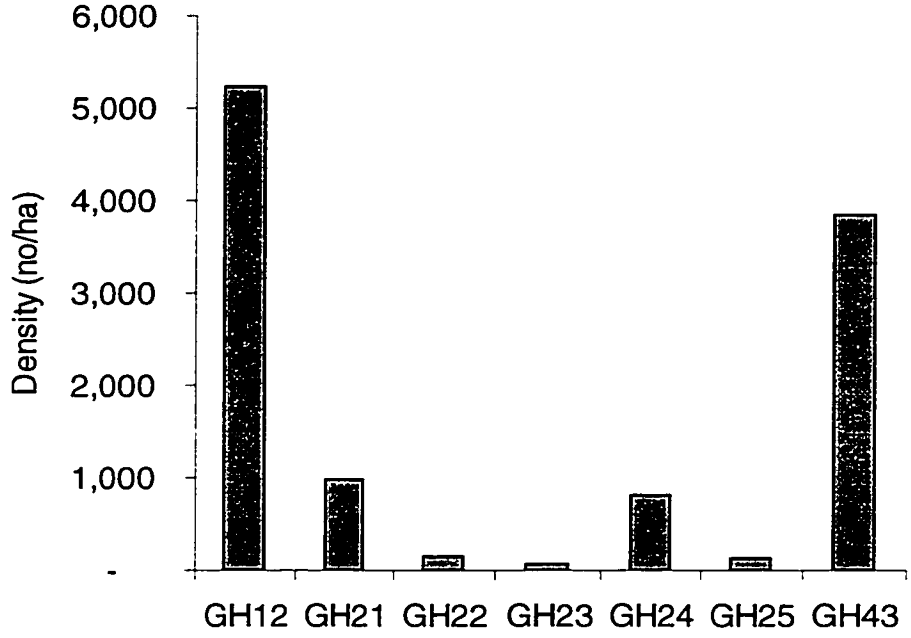
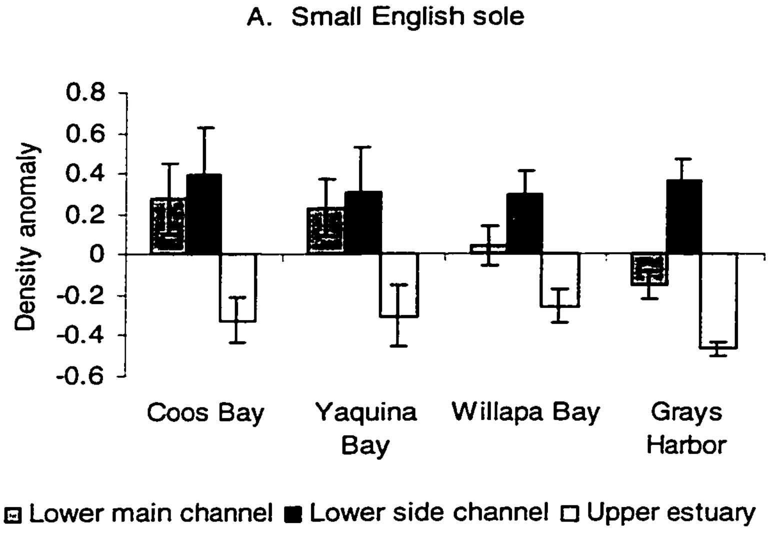
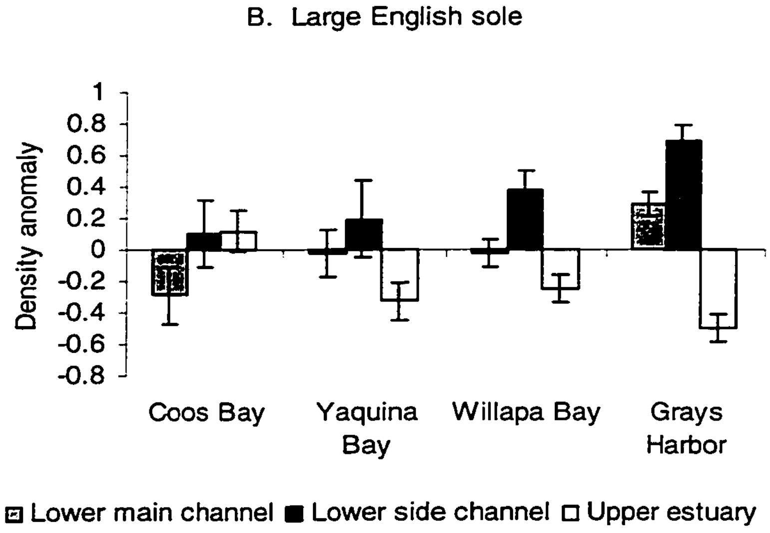


Figure 4.8. Density of large cohort English sole in Grays Harbor during the June 2000 trawl survey. The depicted stations constitute the lower side channel location sites for Grays Harbor.



A. Small English sole



B. Large English sole

Figure 4.9. Average density anomaly across all years for the four estuaries for small (upper panel) and large English sole (lower panel).

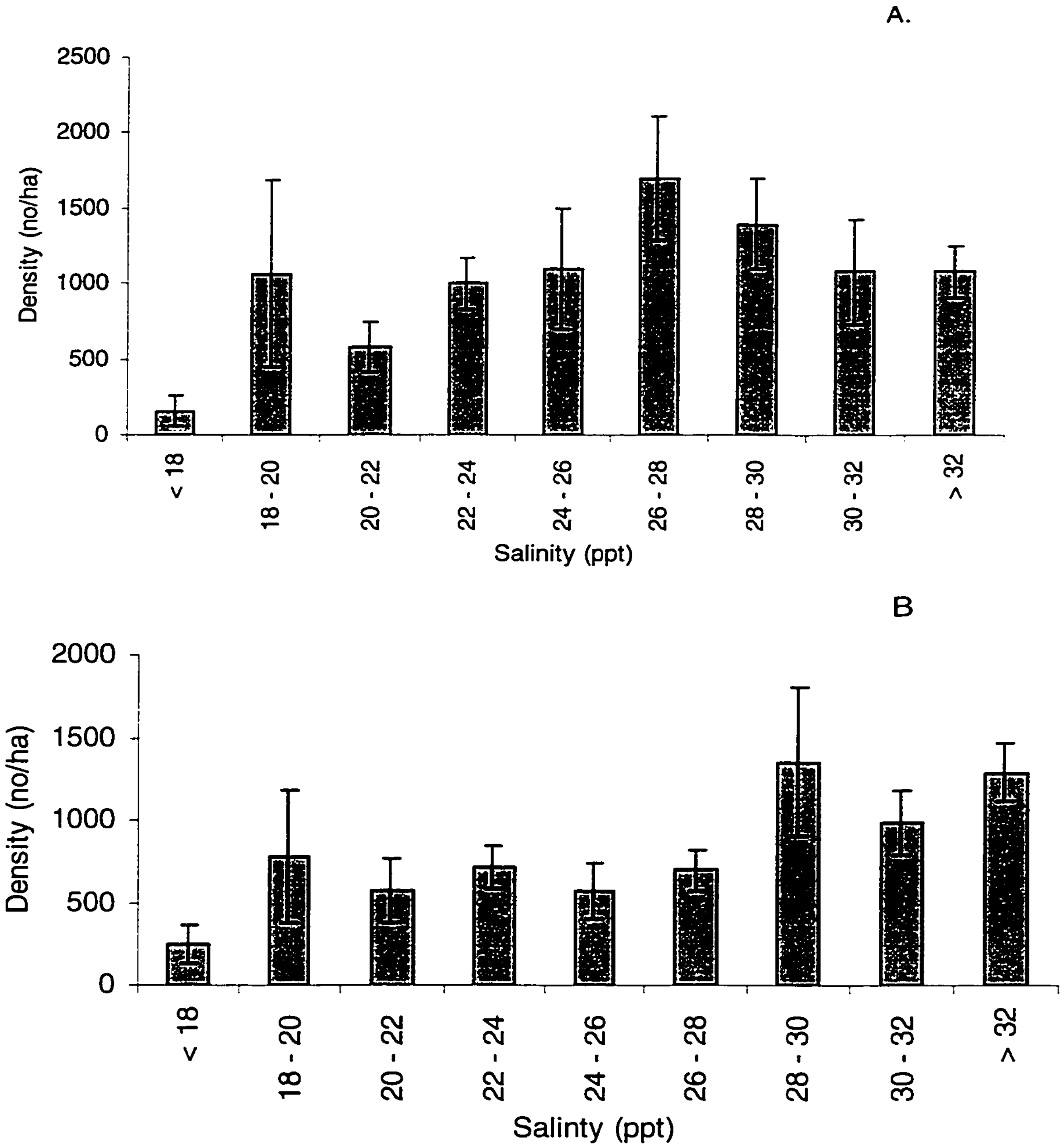


Figure 4.10. Average density of small (panel A) and large (panel B) juvenile English sole plotted against salinity measured during trawl surveys in 1998-2000. Densities are averaged over all estuaries and years, and combined into salinity increments of two ppt.

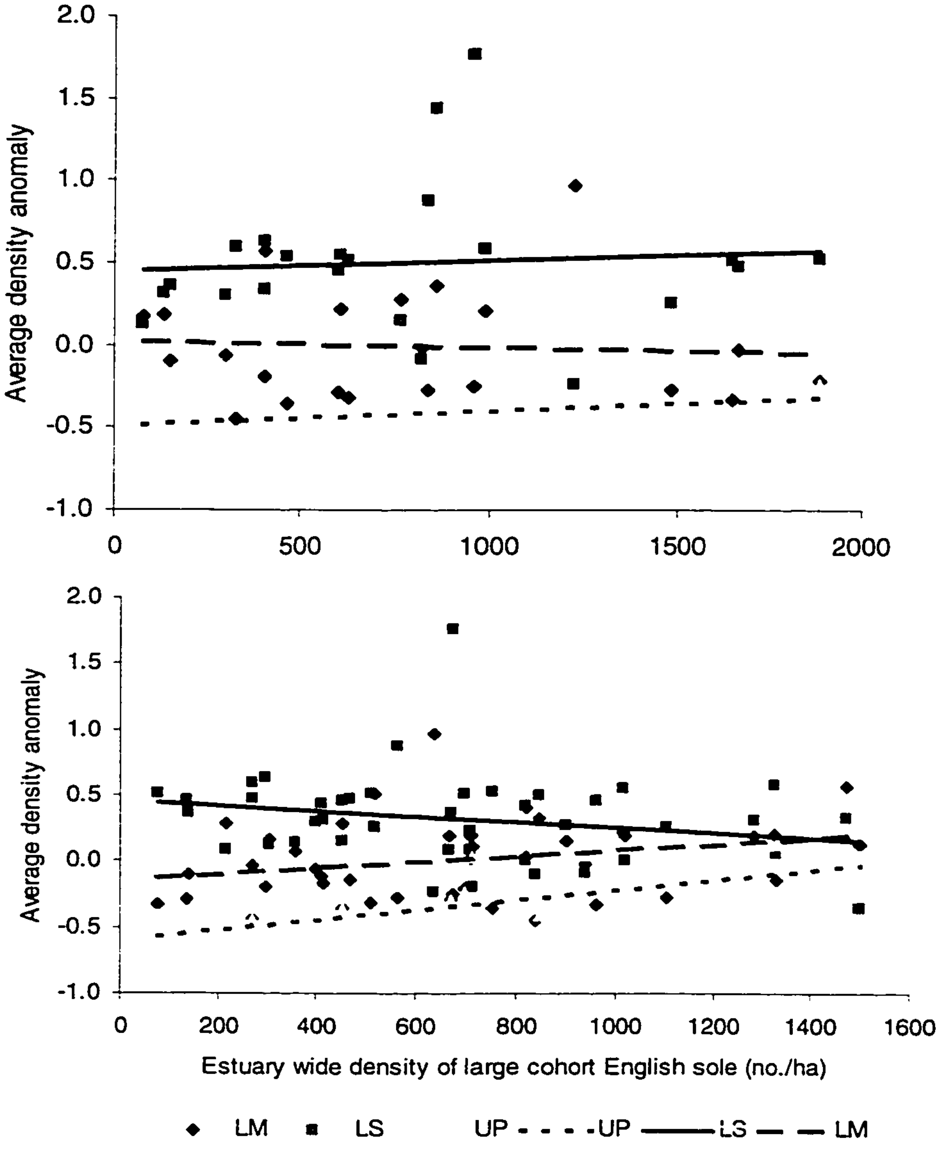


Figure 4.11. Average density anomaly for small (top panel) and large (bottom panel) English sole in each estuarine location plotted against the overall density in each year-estuary-month of sampling. Lower side channel (LS), Lower main channel (LM), and Upper estuarine (UP) sites are depicted. In the large English sole plot the set of samples for Yaquina Bay in June of 2000 was removed, since the density was almost three times greater than that found for the other estuary-month-year combinations.

Chapter 5. Distribution of juvenile flatfishes in Oregon and Washington coastal estuaries.

5.1. Introduction

Juvenile nursery areas separate from the range of the adult population are a common feature in flatfish species that co-occur in nursery areas throughout the worlds oceans. In most cases juveniles utilize shallow nearshore habitats as nursery areas (Gibson 1994, Van der Veer et al. 2000). Juveniles of multiple species have been observed to coexist in a single nursery area (e.g. Burke et al. 1991, Henderson and Holmes 1991, Reichert and Van der Veer 1991, Norcross et al. 1997). For example, 10 species of flatfish were reported to occur in two North Carolina, U.S.A. estuaries (Walsh et al. 1999). Seven of these 10 species occurred as juveniles. Since limitation in nursery habitat has been implicated in the control of recruitment for many species that concentrate during juvenile phases (Iles and Beverton 2000), the interactions and distributional differences among juvenile flatfish in nursery estuaries is an important feature of their life history.

On the Pacific coast of North America estuaries are typically smaller and occur less frequently than in other areas, such as the Atlantic coast of North America. Possibly because of the limited nursery estuaries on the west coast fewer species of marine fish and invertebrates utilize coastal estuaries for nursery areas. Only four flatfish species were captured during this study in Oregon and Washington coastal estuaries; English sole

(*Pleuronectes vetulus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*) and starry flounder (*Platichthyes stellatus*). All four species occur as juveniles in estuaries. Adults of all four species occur offshore on the continental shelf, and with the exception of starry flounder, are not found in estuaries during adult stages.

Starry flounder occurs commonly in estuaries at all sizes and has been identified as an euryhaline species able to stand salinities less than one part per thousand (Orcutt 1950). Commercial data suggests relatively large concentrations of adult fish from 20 to 300-m depths over the continental shelf, but most are found at depths < 150-m (Orcutt 1950, Hart 1973). Spawning occurs in December and January in northern California, and in February to April in Washington (Hart 1973). Spawning occurs in shallow water at river mouths and sloughs along the coast from San Francisco to the tip of Washington state (Orcutt 1950, Garrison and Miller 1982). Juvenile starry flounder are common in shallow estuaries and bays and appear to be estuarine dependent (Moyle 1976).

Pacific sanddab spawning appears to occur prior to October in California (Arora 1951). They also have pelagic eggs and larvae (Ahlstrom and Moser 1975). Juvenile sanddab have been reported in both nearshore estuaries and along the open coast (Calliet et al. 1978). Adults are found offshore at depths of 18 to 600-m, but more typically at depths from 40 to 100-m (Kramer et al. 1995). Juveniles are found both in shallow water along the open coast and in estuaries (Rogers et al. 1988).

Sand sole are known to inhabit the continental shelf from nearshore to depths of about 360-m, but are usually found at depths to ~80-m (Kramer et al. 1995). Spawning occurs from January to March in Washington and eggs and larvae are known to be pelagic (Hart 1973). Little is known of its use of nearshore or estuarine nurseries, although juvenile sand sole have been found in both estuaries and along the open coast (Rogers et al. 1988).

The main objective of this study was to compare the distribution and abundance of juvenile starry flounder, sand sole and sanddab across four west coast estuaries in three years. A further objective was to examine the distributions of these three co-occuring flatfish within nursery areas. The numerically dominant species of juvenile flatfish in these estuaries was English sole (Chapter 2), however the other three species were also found in each of the nursery areas. A primary focus of this analysis was to compare the distributional patterns for English sole found in Chapter 4 to those of starry flounder, sanddab and sand sole to determine if the four flatfish species were partitioning the nursery estuary spatially to minimize interspecific interactions.

5.2. Methods

This study was carried out at four estuaries on the Oregon and Washington coasts, Grays Harbor, Willapa Bay, Coos Bay, and Yaquina Bay (Figure 5.1). All four estuaries were originally divided into 4-5 strata based loosely on degree of oceanic influence (i.e. distance from estuary mouth). Trawl stations were chosen by random sampling within each strata with the caveat that no two stations were adjacent (Figure 5.2). Stations were allocated based on abundance of English sole and Dungeness crab within the stratum, with strata of higher abundance receiving more stations (Shi et al. 1994). Seventeen to

20 sites were chosen within each estuary, and a constant location for each of the trawl survey sites was maintained throughout the study. Sites were located using a combination of landmarks and global positioning system (GPS) readings. Thus, the exact site location varied somewhat from sampling period to sampling period roughly on a scale of 50 m.

Survey data collection

Trawl surveys of all four estuaries were conducted in both June and August from 1998-2000. Benthic organisms including the four flatfish species, English sole, starry flounder, Pacific sanddab and sand sole were collected during daylight using a 3-m beam trawl (Gunderson and Ellis 1986). The beam trawl had an effective opening width of 2.3-m and a height of 0.6-m. The net was towed at a speed of 0.8 to 0.9 $m*s^{-1}$ behind a 6.4-m research vessel with a minimum 5:1 scope of line out to depth. The distance towed averaged 139-m in 1998-2000. Trawls were made against the prevailing current over a variety of tide stages, although efforts were made to conduct trawling near the time of daylight low tides. Sampling was not conducted at high current velocities during maximum ebb and flood to allow the greatest adherence of the beam trawl to the substrate. All fish and invertebrates captured were identified, and English sole caught during the surveys were measured for total length to the closest mm. Other species of flatfish were measured for total length only in 1999 and 2000.

Data analysis

Analysis of variance techniques were used to detect differences in density of flatfishes among estuaries, years and months of surveys (Zar 1974). The density data was log+1 transformed for each species to best meet the assumptions of normality. The density analyses for each species included all main effects (year, estuary and month) and interactions. Post hoc tests to determine differences among levels for each significant category were performed using the least squares mean approach with a Tukey adjustment for multiple comparisons (SAS 1987).

The initial analysis of flatfish densities across estuaries, months and years showed that significant differences existed. Additionally, there were large differences in the overall density when comparing the three species. To standardize for this variation, I used the anomaly of flatfish densities as the dependent variable in further analyses to compare use of habitats within estuaries. The mean density of each species of flatfish for each estuary in each of the years and months where sampling occurred was calculated and removed from each individual density estimate. The values were then normalized by dividing by the standard deviation of the densities in each period so that

$$a_i = \frac{x_i - \bar{x}_{emy}}{sd_{emy}}.$$

In this equation the subscript *i* refers to an individual density from a trawl survey site within an estuary-month-year combination. Thus, *emy* refers to the estuary-month-year combination where a trawl survey occurred, and $\bar{x}$ and *sd* are the mean and standard deviation of all trawl surveys occurring in that estuary-month-year combination. By using the anomaly of the densities I attempted to reduce the variation in the dataset that was attributed to interannual, estuarine and seasonal sources in order to concentrate solely on the within estuary component of variation.

The density anomalies were analyzed using analysis of variance techniques. Density anomalies were compared among three spatial locations in the estuary, lower main channel, lower side channel and upper estuary sites (see Chapter 4 for area descriptions and development of categories). In addition to analyzing distributions of each species with regard to location within the estuary, I was interested in determining whether interannual or inter-estuarine differences in locations utilized by each flatfish species occurred. Therefore, the total model used to analyze spatial distributions of each species included the main effects of location, month of survey, year of survey, and estuary, as well as estuary-location, year-location and month-location interaction terms. The interaction terms were specifically included to test the hypotheses that spatial distribution of each flatfish species was consistent across estuaries, years and months. The results of the analyses for Pacific sanddab, sand sole and starry flounder were compared to the results of analysis of English sole spatial distribution from Chapter 4. All significant interaction and main effects were compared for significant differences among effect levels using the least squares mean approach as a post-hoc test with a Tukeys' adjustment (SAS 1987).

5.3. Results

Pacific sanddab

Pacific sanddab were found in all estuaries during every trawl survey conducted from 1998 to 2000. Catches of sanddab ranged from 0 (at 124 of 431 trawls) to 6,578/ha at a site in Yaquina Bay in June of 1999. Lengths of sanddab ranged from 23 mm to 150 mm. This is a comparable range to the range of lengths of English sole (Chapter 2). Analysis of variance of sanddab density revealed significant differences ($p < 0.05$) among years and estuaries as well as significant estuary*month and estuary*year interactions (Table 5.1). The estuary*month interaction was primarily driven by one data point, where overall densities were significantly higher in June than in August for Grays Harbor. In the rest of the estuaries the densities were not significantly different between the two months. Density of sanddab was higher in 1999 than in other years, however, the two northern estuaries (Willapa Bay and Grays Harbor) densities were also high in 1998 (Figure 5.3). Densities of sanddab were uniformly lower in 2000 than in other years.

The analysis of sanddab density anomalies for spatial locations within estuaries resulted in significant differences among habitats in the estuaries (Table 5.2). There were significantly higher density anomalies in lower main channel locations and significantly lower densities in upper estuary sites. Lower side channels often had negative density anomalies, the most notable exceptions being Willapa Bay and Grays Harbor in 1998. This produced a significant interactions between location and both year and estuary. During the 1998 Willapa Bay and Grays Harbor surveys, density anomalies for sanddab were highest at lower side channel sites (Figure 5.4), although not significantly greater than at lower main channel sites. In Grays Harbor in 1999, density anomalies for sanddab were similar throughout the estuary. In all other cases sanddab density anomalies were higher in lower main channel sites than in other locations in the estuaries.

Sand sole

Only 585 sand sole were captured during three years of trawling in the four estuaries. The lengths of sand sole captured by trawling was comparable to those for sanddab and English sole, ranging from 20 to 234-mm, with only 12 specimens of length greater than 150-mm. Analysis of variance of sand sole densities resulted in a significant three way interaction among estuary, year and month (Table 5.3). The sand sole were highly variable across all systems, and there were 318 zero catches over the 431 trawls in three years of sampling. Sand sole densities were highest in Grays Harbor in June of 2000, and were lowest in all months in Yaquina Bay with zero catches during four of six sampling periods (Figure 5.5). Catches were somewhat higher in June than in August, although this varied between years and estuaries. Overall, catches were significantly lower in 1998 than in all other years. Catches of sand sole were significantly different in all estuaries, with densities highest in Grays Harbor and lowest in Yaquina Bay.

Sand sole density anomalies followed a similar pattern to those of sanddab. Density anomalies were significantly higher at lower main channel sites than at other sites within the estuary (Figure 5.6). Density anomalies were similar between upper estuary sites and lower side channel sites. There were no significant interaction terms between estuary or year and location (Table 5.4), implying that the pattern in spatial distribution of sand sole was consistent across estuaries and years.

Starry Flounder

Starry flounder catches ranged from 999 (site CB-24 in Coos Bay, 1998) to zero fish at 329 of 431 trawls over the three years of trawling. The total catch of starry flounder over these three years was 311, making them the least common species of flatfish captured in the study estuaries. The total lengths of starry flounder captured were larger than for the other species of flatfish, ranging from 49 to 376-mm, with 44 individuals of length >150-mm. Analysis of variance of starry flounder densities resulted in significant differences among years and estuaries (Table 5.5). There was also a significant interaction between year and estuary which was driven primarily by higher densities observed in Coos Bay, Grays Harbor and Willapa Bay in 1998 (Figure 5.7). Yaquina Bay had significantly higher densities of starry flounder than other estuaries. Significantly higher densities of starry flounder were observed across all estuaries in 1998 than the other two years.

Spatial locations with positive density anomalies were different for starry flounder than the other species of juvenile flatfish in Northwest estuaries. Starry flounder density anomalies were significantly higher at upper estuary sites than at lower estuary sites (Figure 5.8). Density anomalies were also significantly less at lower main channel sites than at lower side channel sites. As with sand sole, there were no significant interaction terms between spatial location and estuary or year (Table 5.6). The effect of spatial location on starry flounder densities was thus a consistent effect observed across all estuaries and years.

Comparison of flatfish distributions

An interesting pattern emerged from the analysis of density anomalies for the three species of flatfish, especially when compared to the results from the English sole results in Chapter 4. The average density anomaly within each of the spatial locations for the four species of flatfish followed different patterns (Figure 5.9). English sole were distributed throughout the estuaries, but exhibited highest densities at lower side channel locations and lower densities at other locations in the estuaries. Starry flounder densities were highest in upper estuarine locations, with fewer starry flounder observed in the lower reaches of estuaries. Pacific sanddab density anomalies were highest in lower main channel locations and were significantly lower in other sections of the estuaries. Sand sole density anomalies were greatest in the lower main channel. While English sole are dominant throughout the estuaries, the other species appear to be spatially segregating throughout these estuaries utilizing different habitats.

In Chapter 4 it was observed that large cohort (early settling) English sole expanded their use of estuaries during periods of high densities. The expansion of English sole corresponds to a decrease in the distribution of Pacific sanddab (Figure 5.10). As large cohort English sole densities increase, there is a tendency for sanddab density anomalies to increase in lower main channel locations and decrease in other parts of the estuary. Thus, sanddab are more likely to be found at lower main channel locations when English sole densities are high throughout the estuary. This may indicate a restriction of the range of Pacific sanddab when juvenile English sole are abundant.

This phenomena does not apply to starry flounder (Figure 5.11). The starry flounder distribution pattern remains the same regardless of the density of English sole. Starry flounder are distributed throughout the estuary with positive density anomalies at upper estuary locations and negative density anomalies in the lower estuary even at the highest English sole densities.

5.4. Discussion

Juvenile English sole are by far the most abundant flatfish in Pacific Northwest coastal estuaries (Chapters 2 and 4). Pacific sanddab are also common as juveniles, and typically seem to be most abundant in deeper waters closer to the estuary mouth than English sole. There was significant interannual variation in sanddab densities among estuaries, however there was no discernable pattern to this variation (mean densities ranged from ~100/ha to ~600/ha). Sand sole were less common than sanddab in the trawl surveys, and their densities varied significantly by estuary, year and month. The most apparent difference among estuaries was the very low abundance of sand sole in Yaquina Bay. Starry flounder were the least common of the four flatfish species captured during trawl surveys, but they occurred as both juveniles and adults. The starry flounder was most often found in the upper sections of the estuaries, a pattern much different from that of the other flatfish. Interesting interannual variation was observed for starry flounder, with much higher densities observed in 1998 than all other years in all estuaries except Yaquina Bay. Mean density of starry flounder was highest in Yaquina Bay in all years. This is probably a function of the low salinity found at upper estuary sites in Yaquina Bay (Chapter 4). The coverage of trawl survey sites in the upper estuary of Yaquina Bay reached farther up the estuarine salinity gradient than in other estuaries. Average salinity in June was 16-18 ppt at the uppermost Yaquina Bay sites, while the average June salinity at sites in other estuaries was not less than 19 ppt.

The analysis of density anomalies indicated that the four flatfish species were exploiting different sections of each estuary. Highest densities of sanddab and sand sole were found in lower main channel sites close to the estuary mouth which were primarily deeper, colder and more saline than other parts of the estuary (Table 5.7). Starry flounder were more common in the upper sections of the estuary where salinities were typically lower and temperatures warmer. English sole were more common in lower side channels where temperatures were optimal for their growth and large expanses of tidal flats were available (Chapter 4).

Even in lower main channel areas where density anomalies for English sole were negative and density anomalies for sanddab were positive, English sole was still the numerically dominant species in that section of the estuary. Densities of English sole in lower main channel areas ranged from 0 to 10,377 (mean = 1,467, SE = 140), while densities of sanddab ranged only from 0 to 6,578 (mean = 453, SE = 57). The overwhelming abundance of English sole within these nursery areas clouds the picture of distinctive use of spatial locations in the estuaries. However, as the density anomaly analysis shows, sanddab were only found at relatively high densities at these lower main channel sections of the estuaries, where English sole densities were low relative to other parts of the estuary.

Surveys of flatfish assemblages in Puget Sound have found similar divisions of space by juvenile flatfish (Kendall 1966, Thornburgh 1980). Thornburgh (1980), found that four species of juvenile flatfish were partitioning space using depth in Puget Sound Washington, although the pattern was not consistent among sites. In Thornburgh's study spatial segregation among the species may have been driven by differences in sediment type among the sites, and differences in settling times among the four dominant species; English sole, sand sole, Pacific sanddab and rock sole (*Lepidopsetta bilineata*). Thornburgh (1980) also found distinctions between the diets of the four species, with English sole consuming the widest range of prey items. Kendall (1966) found that the smallest juvenile English sole sampled in intertidal zones of Puget Sound had a more limited depth distribution than that of larger juveniles.

For juvenile flatfish assemblages beyond the Pacific Northwest, distinct patterns in spatial distribution have also been observed. In estuaries in the California Bight, Diamond turbot (*Hypsopsetta guttulata*) settle in the upper portions of bays during January and March, while California halibut (*Paralichthys californicus*) are closer to bay entrances and the open coast, settling from March to September (Kramer 1991). Settlement timing has also been found to be an important partitioning factor for common dab (*Limanda limanda* L.) and plaice (*Pleuronectes platessa* L.) in a small Scottish bay, where plaice settle earlier in the year than dab (Steele and Edwards 1970). However, the authors concluded that distinctions in settlement time were not enough to prevent competition from occurring because the limited depth in the nursery area did not allow the populations to spatially segregate. Depth has been identified as an important factor in partitioning nursery areas for the common dab and age-0 plaice (Edwards and Steele 1968, Gibson 1973). Juvenile flatfish in Alaskan inlets have also been found to segregate with depth and a number of other factors including temperature and sediment type (Norcross et al. 1997). Habitat type has also been found to be important in determining the spatial segregration of flatfish assemblages, with ontogenetic shifts in habitat use occurring for some species (Walsh et al. 1999, Chapter 4). All of these studies suggest that flatfish species that co-occur in nursery areas can partition resources a number of ways including division by biological (i.e. diet) and/or physical (i.e. depth) factors.

The implications of the current analyses are that distinctions in habitat use occur among the four species. It is beyond the scope of this study to determine the root cause of the flatfish distributions. However, it seems that starry flounder are very salinity tolerant (Orcutt 1950), and should therefore be able to exploit areas in the upper reaches of the estuary to a greater degree than the other species. Salinity seems to be an important determinant of the distribution of English sole (Chapter 4) as well as other species of flatfish (Coggan and Dando 1988, Marchand 1988, Kerstan 1991, Gibson 1994, Marshall and Elliot 1998). The patterns in flatfish distribution observed in the four estuaries studied here suggest salinity may be determining the upper limit of English sole distribution. The absence of other species of flatfish in upper reaches of the estuaries due to a salinity barrier probably allows starry flounder to dominate in this region.

Competition between butter sole (*Isopsetta isolepis*) and English sole has previously been suggested as a reason English sole utilize estuaries as nursery areas (Hogue and Carey 1982). They found diet overlap among speckled sanddab *Citharichthys stigmaeus*, sand sole and English sole to be less than overlap between butter sole and English sole on the continental shelf. Studies of shallow water habitats have generally suggested that flatfish in nursery areas are not limited by competition for food (Evans 1983). In West Coast estuaries food resources can be quite high, especially in intertidal areas (Gunderson et al. 1990). Based on the diet studies documenting feeding differences among sanddab and English sole (Hogue and Carey 1982, Thornburgh 1980), as well as the abundance of food within the nursery area, it is unlikely that direct competition for food is responsible for the apparent pattern in estuarine distributions between the two species. However, competition with offshore species may be influencing the apparent dependence on estuaries for nursery areas by English sole.

The temperature and salinity tolerances of English sole may allow them some advantage within estuaries, which allows them to exploit areas of the estuary not utilized extensively by sanddab. In the speckled sanddab, a close relative of the Pacific sanddab maximum growth has been observed to occur from 8-13 ^{0}C (Ehrlich et al. 1979). This is lower than the temperature found in lower side channels (Table 5.7), and in the range of temperatures found in lower main channels in our study area. Thus, the Pacific sanddab, if it has temperature tolerances similar to those of its congener, may be limited to lower main channel locations in order to optimize growth rates. English sole grow fastest at temperatures less than 17.5 ^{0}C (Yoklavich 1982), which is consistent with temperatures found in the lower side channel locations of the study estuaries (Table 5.7).

The restriction of sanddab to lower main channel locations at high English sole densities suggests that high densities of English sole may restrict the distribution of sanddab within estuaries. However, more study of the interactions between the two species is needed to confirm or dismiss the possibility of competitive interactions or physiological conditions as a mediating factor in determining the distributions of these two species.

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Table 5.1. Results of analysis of variance of Pacific sanddab densities. Data was log + 1 transformed and combined across all estuaries 1998-2000. R^2 value for this analysis was 0.26, n = 431. Degrees of freedom (DF), sum of squared error (SS), mean squared error (MSE), and calculated F statistic are shown for each variable.

Source	DF	SS	MSE	F	Pr>F
Month	1	3	3	0.49	0.4826
Year	2	267	133	25.37	<0.001
Estuary	3	279	93	17.69	<0.001
Month*Year	2	14	7	1.31	0.2708
Month*Estuary	3	78	26	4.97	0.0021
Estuary*Year	6	80	13	2.54	0.0199
Month*Estuary*Year	6	4	1	0.14	0.9912
Error	407	2140	5		

Table 5.2. Partial ANOVA table for analysis of Pacific sanddab density anomalies. Data was combined for all estuaries from 1998-2000. R^2 value for this analysis was 0.20, n = 431. Degrees of freedom (DF), sum of squared error (SS), mean squared error (MSE), and calculated F statistic are shown for each variable.

Source	DF	SS	MSE	F	Pr>F
Location	2	78.63	39.31	53.85	<0.001
Location*Month	2	0.18	0.09	0.12	0.8834
Location*Estuary	6	14.30	2.38	3.26	0.0038
Location*Year	4	12.49	3.12	4.28	0.0021
Error	410	299.31	0.73		

Table 5.3. Results of analysis of variance of sand sole densities. Data was log + 1 transformed and combined across all estuaries in 1998-2000. R^2 value for this analysis was 0.21, n = 431. Degrees of freedom (DF), sum of squared error (SS), mean squared error (MSE), and calculated F statistic are shown for each variable.

Source	DF	SS	MSE	F	Pr>F
Month	1	16	16	4.59	0.0328
Year	2	25	12	3.67	0.0264
Estuary	3	187	62	18.42	<0.001
Month*Year	2	10	5	1.45	0.2359
Month*Estuary	3	15	5	1.49	0.2154
Estuary*Year	6	48	8	2.36	0.0299
Month*Estuary*Year	6	63	11	3.11	0.0055
Error	407	1378	3		

Table 5.4. Partial ANOVA table for analysis of sand sole density anomalies. Data was combined for all estuaries from 1998-2000. R^2 value for this analysis was 0.09, n = 431. Degrees of freedom (DF), sum of squared error (SS), mean squared error (MSE), and calculated F statistic are shown for each variable.

Source	DF	SS	MSE	F	Pr>F
Location	2	16.74	8.37	11.01	<0.001
Location*Month	2	0.03	0.01	0.02	0.9817
Location*Estuary	6	7.89	1.32	1.73	0.1125
Location*Year	4	3.07	0.77	1.01	0.4029
Error	410	311.60	0.76		

Table 5.5. Results of analysis of variance of starry flounder densities. Data was log + 1 transformed and combined across all estuaries in 1998-2000. R^2 value for this analysis was 0.20, n = 431. Degrees of freedom (DF), sum of squared error (SS), mean squared error (MSE), and calculated F statistic are shown for each variable.

Source	DF	SS	MSE	F	Pr>F
Month	1	5	5	1.95	0.1632
Year	2	26	13	4.61	0.0105
Estuary	3	178	59	21.11	<0.001
Month*Year	2	6	3	1.12	0.3268
Month*Estuary	3	7	2	0.80	0.4925
Estuary*Year	6	39	7	2.32	0.0328
Month*Estuary*Year	6	14	2	0.82	0.5527
Error	407	1144	3		

Table 5.6. Partial ANOVA table for analysis of starry flounder density anomalies. Data was combined for all estuaries from 1998-2000. R^2 value for this analysis was 0.09, n = 431. Degrees of freedom (DF), sum of squared error (SS), mean squared error (MSE), and calculated F statistic are shown for each variable.

Source	DF	SS	MSE	F	Pr>F
Location	2	17.31	8.65	11.59	<0.001
Location*Month	2	1.52	0.76	1.02	0.3614
Location*Estuary	6	5.39	0.90	1.20	0.3029
Location*Year	4	6.64	1.66	2.23	0.0655
Error	410	305.96	0.75		

Table 5.7. Average value (SE) of habitat variables within each of the location categories used to classify trawl survey sites.

Static habitat variable	Lower main channel	Lower side channel	Upper estuary
Depth relative to mean low water	5.1 (0.14)	3.7 (0.17)	4.0 (0.17)
Salinity (ppt)	28.5 (0.46)	26.1 (0.58)	25.1 (0.48)
Temperature (^{0}C)	13.6 (0.21)	15.6 (0.18)	17.0 (0.19)
Distance from the estuary mouth	0.33 (0.02)	0.46 (0.02)	0.80 (0.02)
Average sediment grainsize (um)	263 (8.3)	223 (5.7)	275 (10.0)
Percentage of surrounding tidal flats	20.6 (1.8)	53.1 (2.6)	39.8 (2.5)

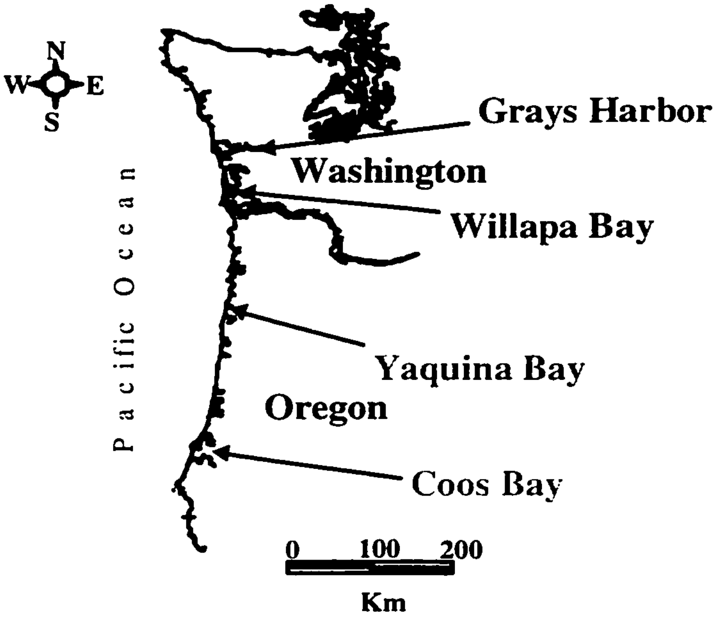

Figure 5.1. Coastline of Oregon and Washington showing each of the four study areas; Grays Harbor, Willapa Bay, Yaquina Bay and Coos Bay.

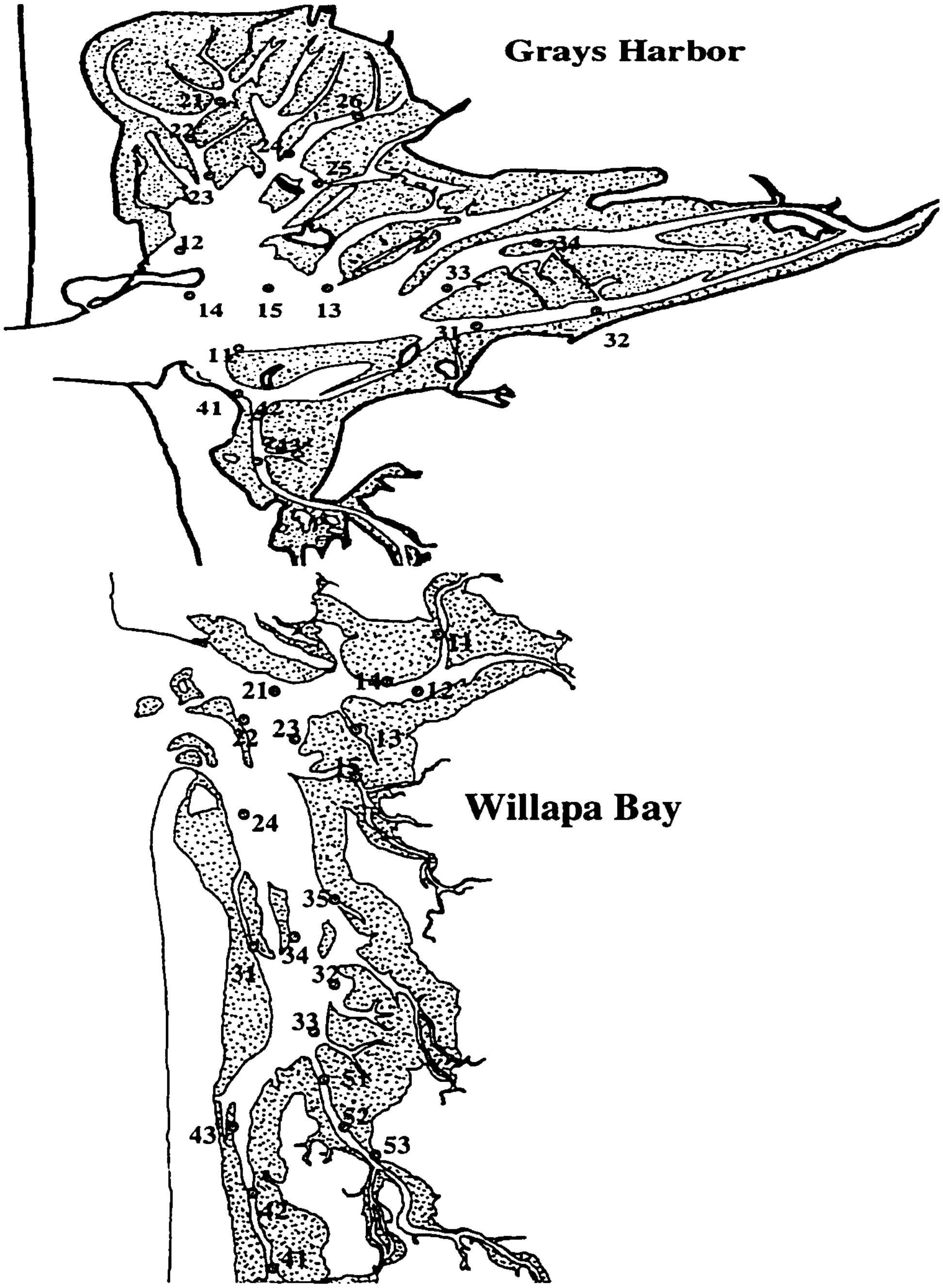

Figure 5.2. Map of the four study areas showing station locations and number designations.

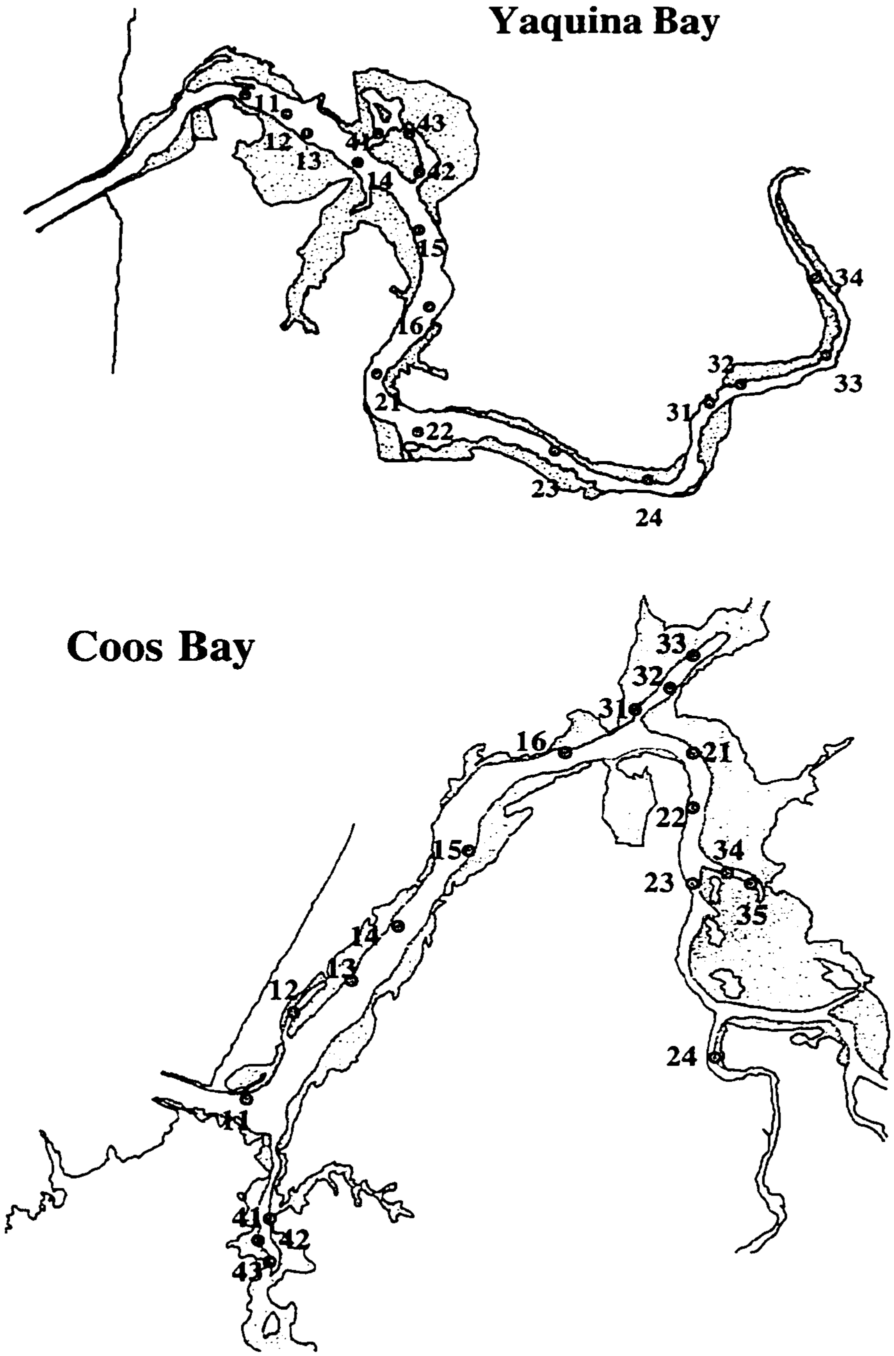

Figure 5.2 (continued). Map of the four study areas showing station locations and number designations.

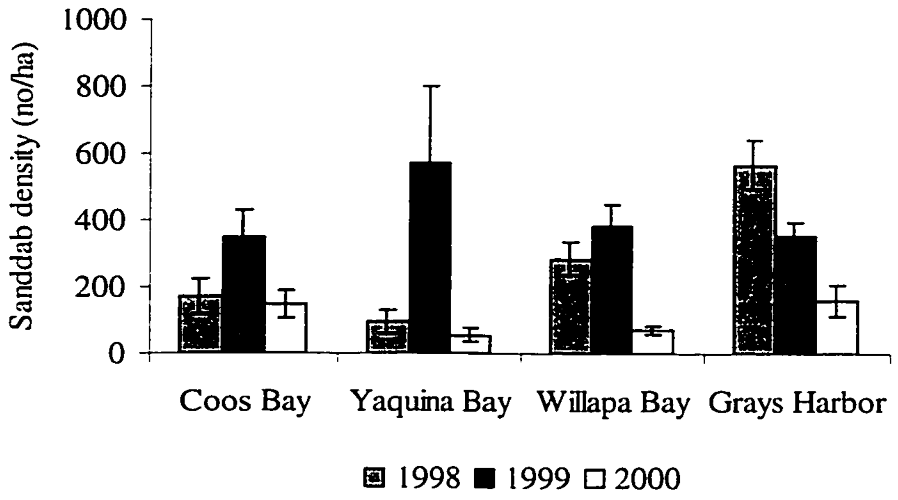

Figure 5.3. Mean (+/- SE) density of sanddab for each estuary from 1998-2000.

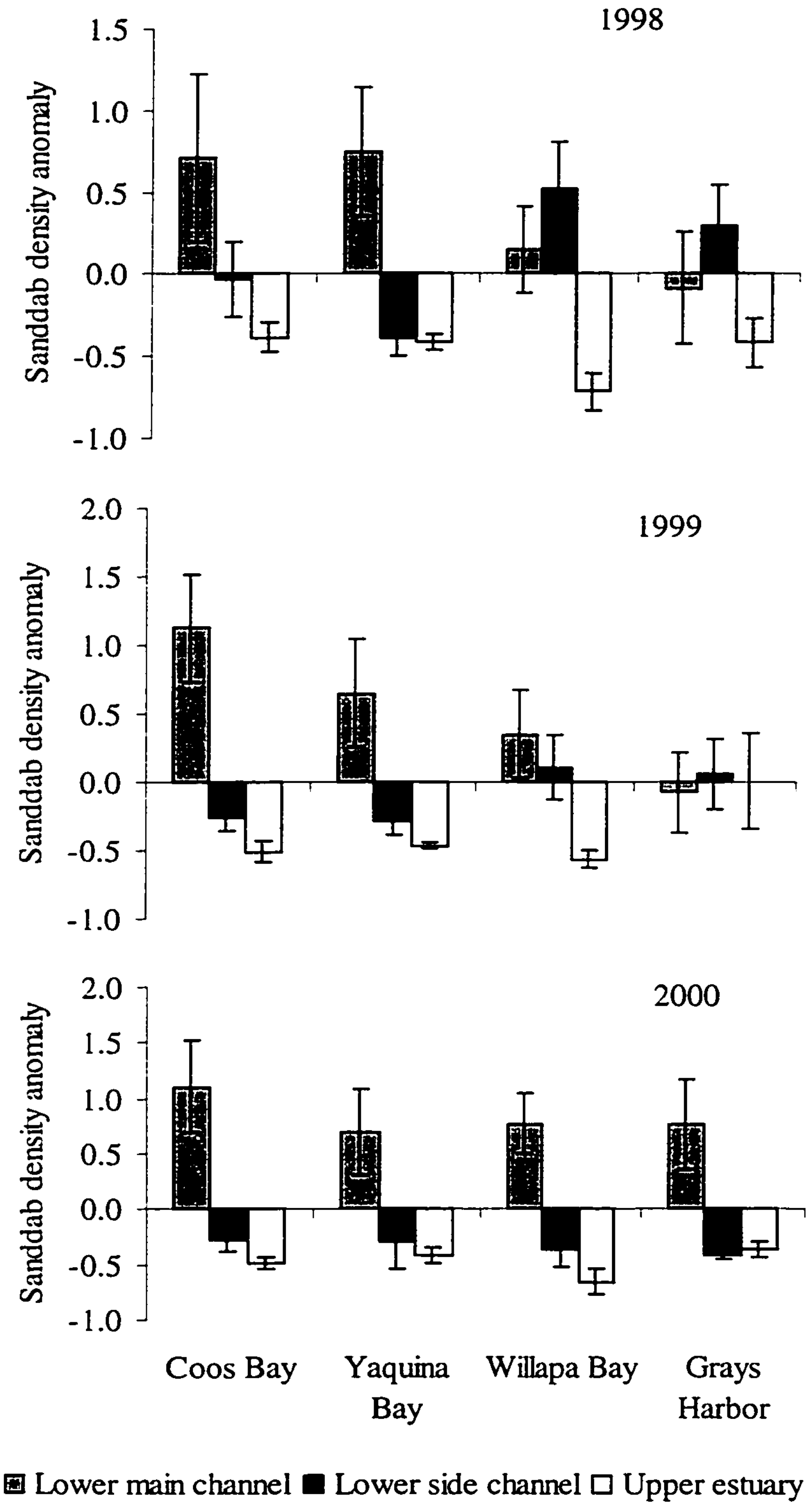

Figure 5.4. Sanddab density anomalies by estuary and location from 1998-2000.

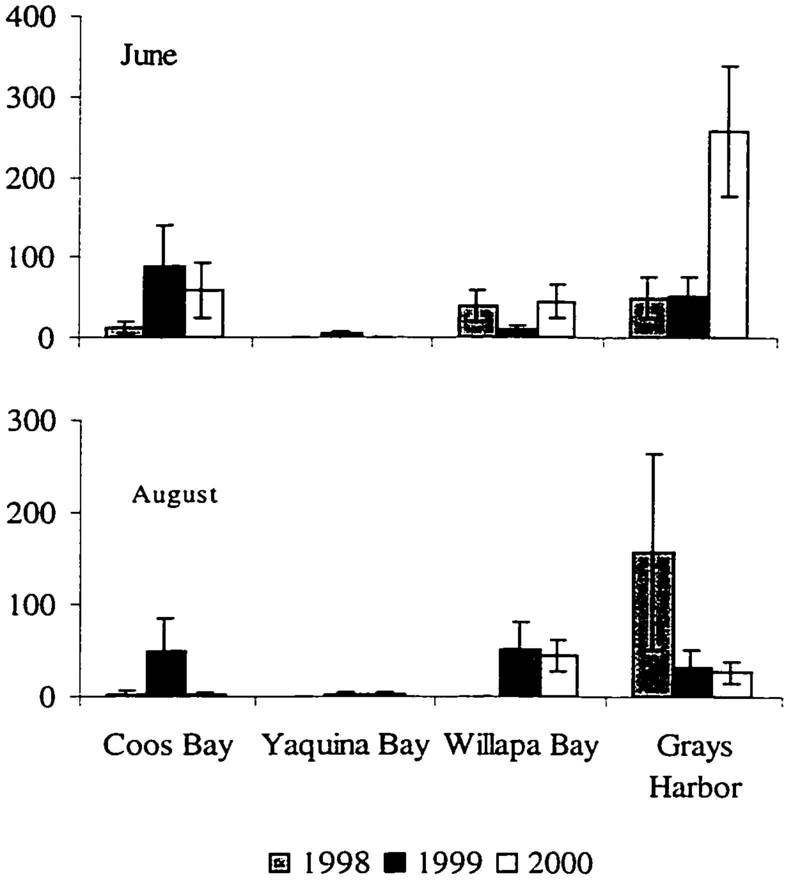

Figure 5.5. Mean (+/- SE) density of sand sole for June and August in each estuary from 1998-2000.

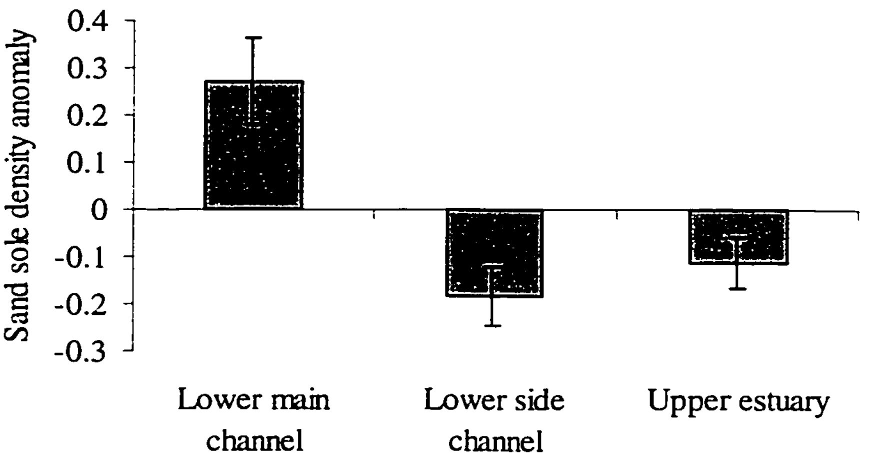

Figure 5.6. Average density anomaly (+/- SE) for sand sole at estuary locations. Mean is calculated for all estuaries, months and years of trawl surveys from 1998-2000.

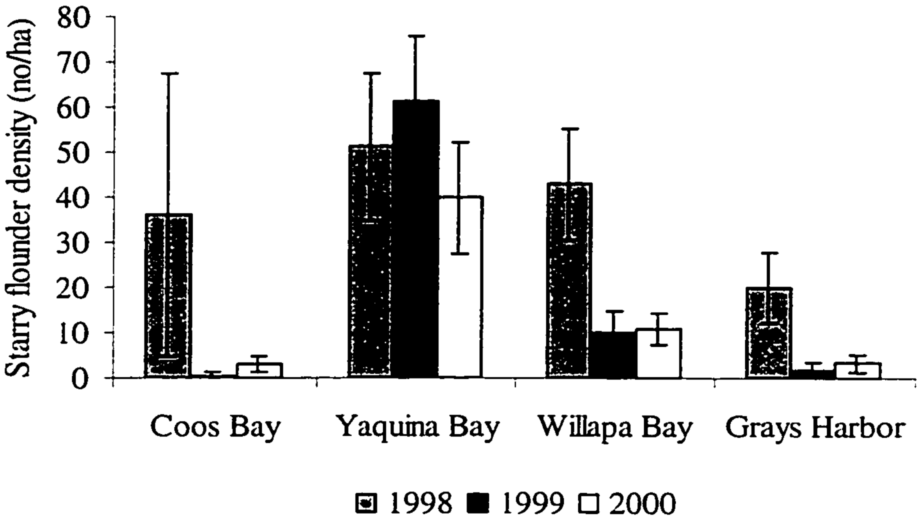

Figure 5.7. Mean (+/- SE) density of starry flounder for each estuary from 1998-2000.

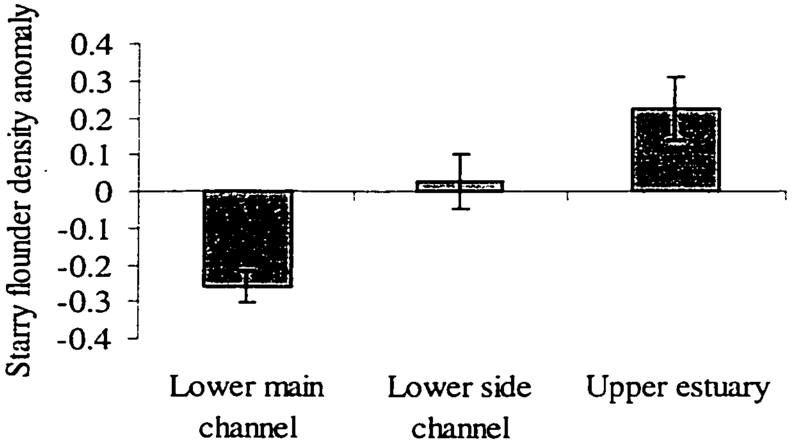

Figure 5.8. Average density anomaly (+/- SE) for starry flounder at estuary locations. Mean is calculated for all estuaries, months and years of trawl surveys from 1998-2000.

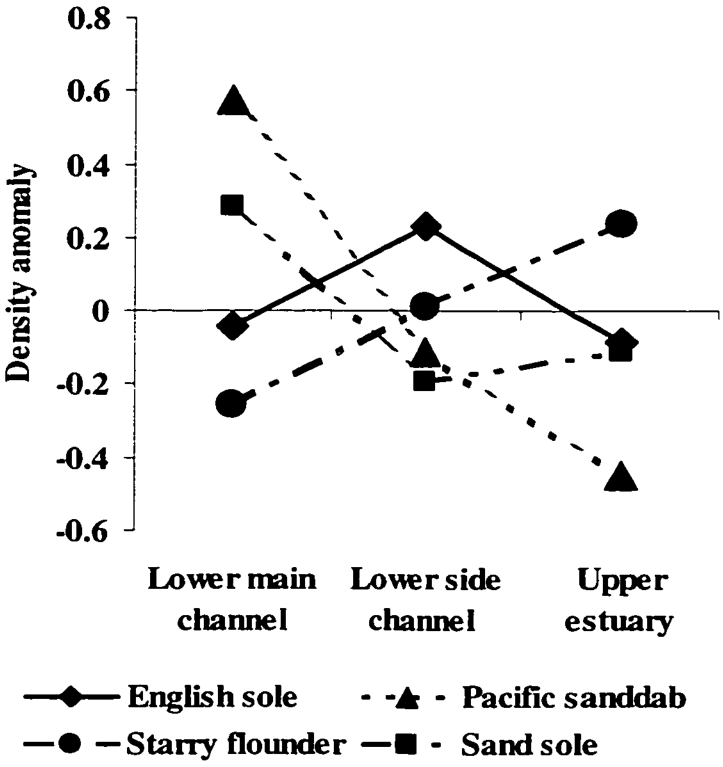

Figure 5.9. Average density anomaly of English sole, Pacific sanddab, sand sole and starry flounder from 1998-2000 by spatial location across all estuaries.

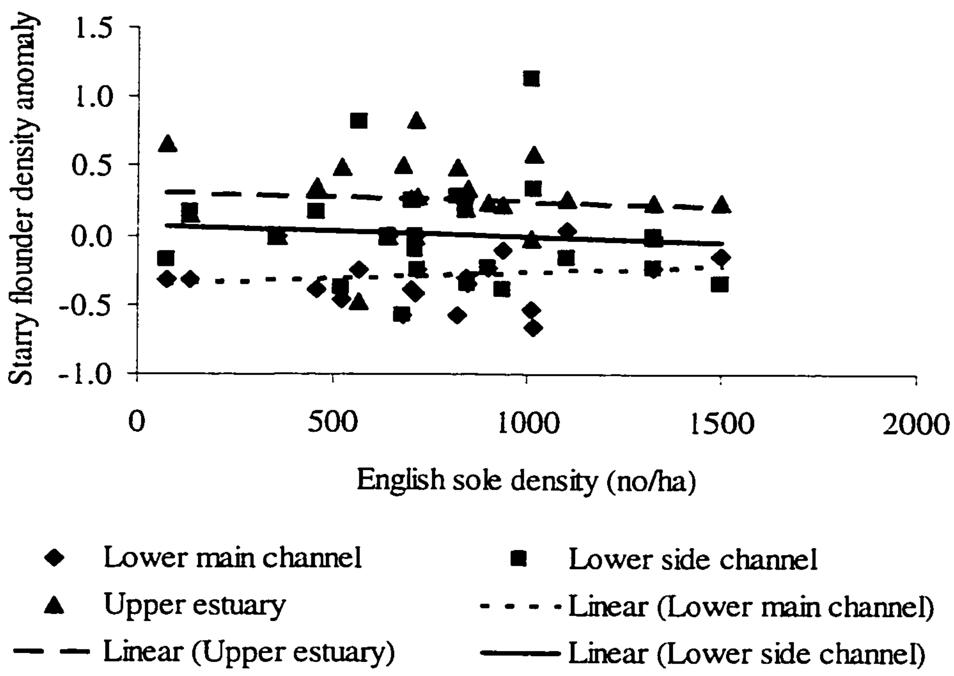

Figure 5.10. Average sanddab density anomaly compared to English sole density in each spatial location of estuaries from 1998-2000.

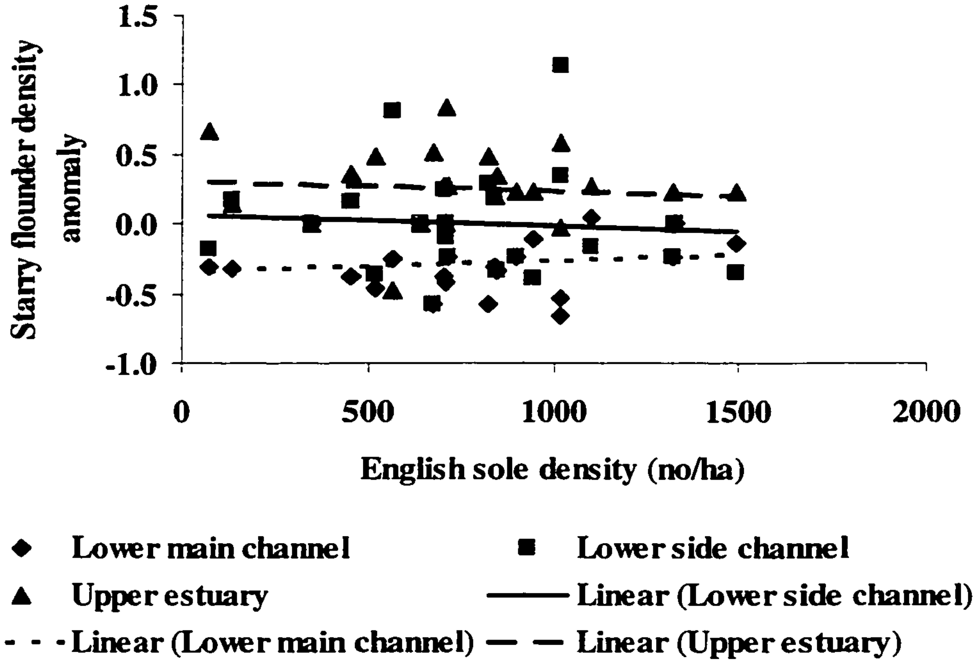

Figure 5.11. Average starry flounder density anomaly compared to English sole density in each spatial location of estuaries from 1998-2000.

Chapter 6. Summary

In Chapter 2 I found that density of English sole in all study areas varied significantly on an interannual basis, but were generally in the range of 1000-2000 fish*ha^{-1} across all estuaries. The analyses presented in Chapter 2 also suggested interannual differences in settlement timing as implied by the length frequency of English sole observed during the June surveys. In some years and estuaries there was both an early and late settling cohort of English sole in June, while more typically June surveys were dominated by a single late settling cohort. By August densities of English sole were similar across all estuaries, and generally a single mode of fish in the 60-100 mm length class was observed. Patterns in spatial distribution of English sole were apparent within estuaries, as some strata had consistently higher densities of English sole. The more upriver strata had significantly lower densities in both Willapa Bay and Grays Harbor.

The results of Chapter 2 suggested that:

1) Supply of larvae and juvenile English sole to nursery estuaries can vary in both timing and strength on an interannual basis, and
2) English sole juveniles exhibited persistent patterns in use of estuaries, with relatively consistent August densities across all estuaries and years.

In Chapter 3 interannual variability in juvenile English sole abundance and the appearance of multiple cohorts in nursery areas was addressed by examining transport of eggs and larvae by coastal currents. A model was constructed to uncover the mechanisms responsible for patterns in juvenile English sole abundance by taking into account prevailing currents during the pelagic period and spawn timing. The model utilized observed currents from three locations to estimate alongshore flow at 10-m depth. The larval trajectories of English sole demonstrated that passive larval drift could not account for the distribution of sole observed in northwest estuaries. The early cohorts of English sole moved north, while the late cohorts generally moved northward then south. Both early and late cohorts moved out of the system prior to the conclusion of full development in all but four cases. Based on model trajectories, the egg stage was carried inshore before hatching for 13 of 19 cohorts examined.

The major findings of Chapter 3 were:

1) Passive transport of English sole eggs and larvae alone cannot explain the patterns of density and length frequency observed in nursery estuaries,
2) Multiple cohorts of English sole occurring in estuaries probably result from multiple spawning events during the winter, although differential survival may occur as well.

Chapter 4 assessed the relationships of estuarine habitat types to large (TL > 50-mm) and small (TL <50-mm) size cohorts of English sole. Principle components analysis of the habitat variables across the study estuaries, yielded commonalties among the trawl survey stations as a basis for classifying the sites. Each site was grouped into one of three categories; lower main channel, lower side channel, or upper estuary sites. The analysis of juvenile English sole density anomalies across all estuaries revealed consistent patterns in habitat use. Juvenile English sole utilized lower side channel locations at significantly higher densities than either lower main channels or upper estuary areas.

The results of Chapter 4 indicate that

1) English sole in both small and large size classes utilize lower side channel habitat where there are shallow depths, temperatures are optimal for growth, and more tidal flats relative to other sections of the nursery estuary,
2) Small English sole have a more restricted range in terms of temperature and depth than larger English sole, and
3) Large English sole ranges expand at high densities, suggesting there may be carrying capacity for English sole in nursery estuaries.

In Chapter 5 the distribution of three additional species of flatfish were analyzed to determine whether and how juvenile flatfish partition nursery estuaries. Significant interannual variation was observed in sanddab, starry flounder and sand sole densities among estuaries. While English sole were the dominant species throughout the estuaries, the analysis of density anomalies indicated that the other three flatfish species were exploiting different sections of each estuary. Densities of sanddab and sand sole were higher in lower main channel sites close to the estuary mouth which were more oceanic than other parts of the estuary, while starry flounder were more common in the upper sections of the estuary where salinities were typically lower and temperatures warmer.

The primary conclusions from the analyses presented in Chapter 5 were

1) Juvenile flatfish partition nursery estuaries by segregating themselves spatially,
2) This segregation is consistent with the suspected temperature preferences for growth of sanddab and English sole and the salinity tolerances of starry flounder, and
3) High densities of English sole are correlated with restriction of sanddab range within the estuary, although it is unclear if this is a function of biological interactions or variation in physical conditions.

This study is the first broad scale survey (covering ~400-km of coastline and four estuaries) to examine patterns of nursery area use by juvenile flatfish in the Pacific Northwest. The results indicate that Oregon and Washington estuaries have similar habitats in common, and thus similar patterns in habitat use by juvenile flatfish occurred within the estuaries.

The results presented here fill a gap in the existing knowledge of English sole life history previously unexamined. The results also point to future work that is needed including the resolution of stock structure for coastal populations of English sole both temporally and spatially. Another important topic for future study is the characterization of local oceanographic features and larval behavior that may enhance English sole larval retention. Resolution of the interannual and seasonal variability in local oceanographic features appears to be important in determining the larval supply that is available to settle in nursery areas, both estuarine and offshore. Thus, although much work has been accomplished for English sole populations and flatfish in general, there is still much to be done in order to account for variations in both life history strategies and recruitment for these species.

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Appendix 1. Results of test trawling for calculating area swept.

A1.1. Methods

On October 14 1999, from 13:00 to 16:00, eight tows of the 2.3 m beam trawl used in PNCERS sampling were completed (see Chapter 2 for description of the gear). The trawling was carried out in Puget Sound in Shilshole Bay. These tows were designed to 1) test the adherence of the beam trawl to the bottom during the tow, and 2) enable calculation of a correction factor for distance towed that allowed for net movement during retrieval and deployment when the net was not on the bottom. Attached to the beam was a time-depth-temperature recorder (TDR) which recorded these three variables at five-second intervals. Test trawls were carried out at depths ranging from 7 to 21.5 m. During tows #3-8 the speed was also varied by increasing the boat speed for the last half of each tow from approximately 0.69 to 1.25 $m*s^{-1}$. Both depth and speed were varied to determine the effects of these factors on the adherence of the net to the bottom.

The continuous data from the TDR was graphed to determine the data where tows occurred (Figure A1.1). Then each tow was isolated from the surrounding data and plotted (Figures A1.2-A1.9). During the test trawls depth, time and wire out were periodically recorded to obtain a bottom profile and document times when gear was deployed and retrieved. In order to match the time and depth recorded in the boat to the time and depth recorded by the TDR a correction of two minutes and –2.0 m depth was applied to the TDR data. For each tow the data summarized in Table A1.1 were obtained from the TDR data.

During PNCERS trawl surveys of Grays Harbor, Willapa Bay, Yaquina Bay and Coos Bay in 1998 and 1999 no consistent distance measurement for estimating the area swept was collected. In 1999 however, data was collected to enable calculation of the area swept at 97 of the 143 sampling stations. The information including distances, depths and times that were collected at these 97 stations are summarized in Table A1.2. At the remaining 1999 sampling stations the total distance traveled from net deployment to net surfacing and the average depth were recorded. In 1998 the distance from the point where 20 m of wire had been deployed to the point where the net surfaced was collected at all stations but one. At that station, the average distance recorded for stations in the same stratum was used in calculations. Average depth was also recorded at most stations in 1998. Where this information was not collected, the average depth from other sites in the same stratum was used in the calculations.

The distance the net was in contact with the bottom during each trawl can be calculated by subtracting two components of the total distance traveled by the vessel from the point where the net was deployed to the point where the net is retrieved at the surface. These two components are the distance the net traveled before hitting the bottom during net deployment and the distance the net traveled after it came off the bottom during retrieval. A separate method is used to calculate each component. The following formulae refer to the 97 samples with complete data collected in 1999. Modifications of these basic formulae and assumptions used to calculate corrections for the remaining stations are discussed in the results section.

The distance the net travels while it is being deployed can be calculated from the relationships found in Figure A1.10. Here w is the length of wire out, x_d is the distance traveled from the beginning of net deployment to the end of net deployment, and d_d is the depth where the net was deployed. The correction for the distance the net travels while it is being deployed is calculated by the formula

$$x_c = x_d - x_1 \quad (1)$$

where

$$x_1 = \sqrt{w^2 - d_d^2} \quad (2)$$

Calculation of a correction for the retrieval of the net is a two step process. In the first step the distance traveled by the vessel from the point when the net comes off the bottom to the point when the net is at the surface, y_2, must be calculated (Figure A1.10). Since the amount of wire out when the net comes off the bottom during net retrieval can be found from the formula

$$w_x = 15.1 + 1.54 * d_r \quad (3)$$

(a linear regression of the wire out when the net comes off the bottom and the depth developed from TDR data found below). The distance, y_2, is calculated by multiplying the ratio of the distance traveled by the boat while the full amount of wire was being retrieved y_i to the total amount of wire retrieved w_i by w_x so that;

$$y_2 = \frac{y_i}{w_i} * w_x \quad (4)$$

In the second step the distance the net travels while the last 20 m of wire is being retrieved, y_l, is calculated by

$$y_1 = \sqrt{w_x^{\,2} - d_r^2} \tag{5}$$

where d_r is the depth of the net when it comes off the bottom and w_x is the amount of wire out when the net comes off the bottom. These two corrections are summed to obtain the total distance the net traveled while it was off the bottom during retrieval.

Thus, the total distance fished during trawling calculated by applying the two corrections for net retrieval and deployment is

$$T_D = D_m - (y_2 + y_1) - x_c \tag{6}$$

where D_m is the distance measured on the boat from the point of net deployment to the point where the net reaches the surface during retrieval.

A1.2. Results

Net adherence

In general there seemed to be little problem with the net coming off the bottom during test trawling (Figures A1.2-A1.9). However, the bottom bathymetry measured on the boat may have been inaccurate due to wave action, the fact that the net was behind the boat by 50 to 100 m, and the general error associated with depth sounders of the type used. The effect of towing speed seemed also to have little effect on bottom adherence. When towing speed increased by from 0.69 to 1.25 $m*s^{-1}$ no obvious gaps in contact between the net and the bottom were observed. In addition both flatfish and bottom material (woody debris, mud, etc.) were observed in all trawls during testing, further confirming bottom contact. During 1999 PNCERS sampling, the towing speed averaged 0.63 $m*s^{-1}$, ranging from 0.36 to 1.53 $m*s^{-1}$ (Figure A1.11). Since these are comparable to the range of speeds during test trawling, it is reasonable to conclude that loss of bottom contact was probably not a problem during sampling.

Corrections for distance

Trials with the TDR showed that in most cases the net first touched bottom with approximately 40 m of wire out (Table A1.3). This result was fairly consistent over the range of depths from 8 to 13 m (Figure A1.12). At 20 m depth the net hit the bottom at 60 to 90 m of wire out. During 1999 sampling the maximum depth at which the net was deployed was 12.4 m and the average was 5.1 m.

The correction calculated for net deployment averaged –3.45 m. The value ranged from –64.8 to 42.1 m over the 97 transects in 1999. There were no apparent trends in the correction over the depths deployed at in 1999 (Figure A1.13). There were also no trends in the net deployment correction with the amount of wire that was deployed (Figure A1.14).

Test trawls with the TDR showed that the net came off the bottom when the amount of wire out was between 20 and 60 m during retrieval (Figure A1.15). A linear regression of the amount of wire out when the net came off the bottom against depth resulted in equation 3.

Based on this regression, the average distance correction calculated for net retrieval was –23.75 m, ranging from –97.3 to 1.3 m. There was an increasing trend in the correction with increasing depth (Figure A1.16), however, this trend was largely driven by one point where the depth at retrieval was over 15 m. Removal of this point resulted in no trend evident in the correction as depth at net retrieval increased. A slight increase in the correction was also evident with an increasing amount of wire out (Figure A1.17).

When both components of the distance correction were compiled, the average total correction for the distance trawled was –27.2 m, ranging from –116.0 to 15.7 m.

Application to survey data

For 1999 trawls where only total distance from net deployment to net surfacing and average depth were recorded equation 6 will be modified so that

$$T_D = D_m - y_1 - 3.45 \tag{7}$$

In this case the distance the boat travels while the net is off the bottom ,y_2,will be assumed to be zero, and the average net deployment correction (-3.45 m) will be employed in the calculation. The average y_2 value for 1999 trawls was 1.7 m (SE=1.7), indicating that the assumption of zero movement of the boat during net retrieval is appropriate (Figure A1.18).

For 1998 trawls D_m was not recorded during sampling. Instead D_{m20} was recorded as the distance between the point where 20 m of wire had been deployed to the point where the net reached the surface during retrieval. To correct for this it is necessary to assume that the net reached the bottom when 20 m of line had been let out during net deployment, then

$$D_m = D_{m20} + \sqrt{20^2 - d_d^2} \tag{8}$$

where d_d is the depth at net deployment. Then assuming zero movement of the boat (y_2) during net retrieval, the total distance trawled is calculated by equation 7.

A1.3. Recommendations

Based on the results of the 1999 PNCERS sampling and the test trawling conducted in Puget Sound the following data must be collected during any additional sampling with the beam trawl.

1) The distance from the start of net deployment to the end of net deployment (x_d)
2) The depth where the net was deployed (d_d)
3) The amount of wire out (w)
4) The distance when net retrieval begins (d_i)
5) The distance when the net reaches the surface (D_m)
6) The depth where the net is retrieved (d_r)

Table A1.1. Measurements inferred from time-depth recorder data during test trawling.

Measurement
Depth at net deployment
Depth where net came off the bottom during retrieval
Time from net deployment to contact with bottom
Time spent on the bottom during the trawl
Time from on bottom to surface during retrieval
Wire out when net contacted bottom during deployment
Wire out when net came off bottom during retrieval

Table A1.2. Measurements collected during PNCERS trawl surveys in 1999 to determine the correct distance swept by the trawl during surveys. Symbols refer to Figure A1.10 and formulae found in the text.

Measurement	Symbol
Total wire let out at beginning of tow	w
Depth at which net was deployed	d_d
Distance from the start point to the point all wire is out	x_d
Distance traveled during net retrieval	y_i
retrieval	D_m
retrieval	d_e

Table A1.3. Summary of time-depth recorder data from test trawls.

Trawl #	Depth at net deployment (m)	Depth at net off bottom (m)	Line out (m)	Time to bottom	Total time on bottom	Time to surface	Line out when first on bottom (m)	when first off bottom (m)	Distance towed (m)
1	8.5	10.0	100	0:00:40	0:05:20	0:00:40	44	40	263
2	8.5	10.0	100	0:00:45	0:05:05	0:00:40	45	37	223
3	11.5	8.0	50	0:01:00	0:04:50	0:00:25	34	26	326
4	21.5	19.5	100	0:01:50	0:05:10	0:00:35	63	32	305
5	19.5	19.5	100	0:01:55	0:03:45	0:01:10	88	60	329
6	10.5	9.5	100	0:00:50	0:06:25	0:00:20	38	21	366+
7	12.1	11.0	100	0:01:10	0:06:50	0:00:20	40	20	
8	8.0	7.0	50	0:00:30	0:04:05	0:00:25	42	30	214
Average	12.5	11.8		0:01:05	0:05:11	0:00:34	49.25	33.25	276.635

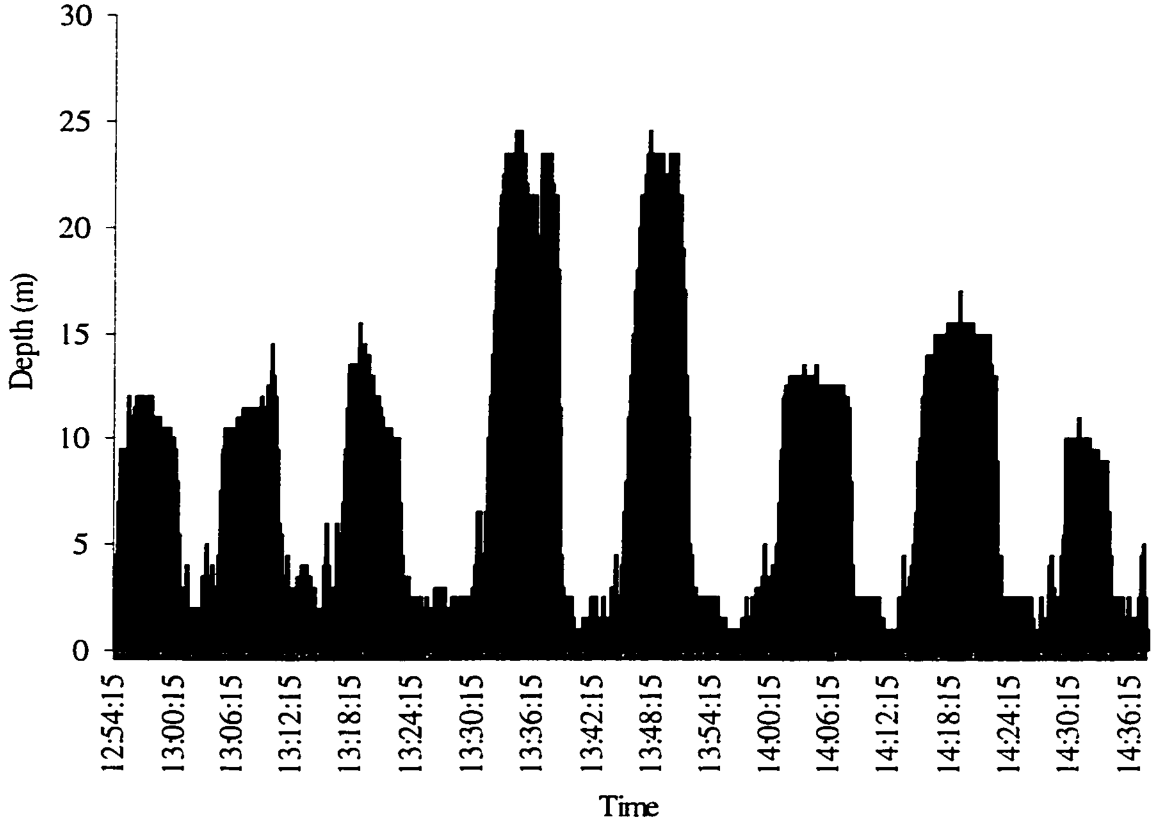

Figure A1.1. Raw data from time-depth recorder showing the profiles of the eight test trawls carried out on October 14, 1999.

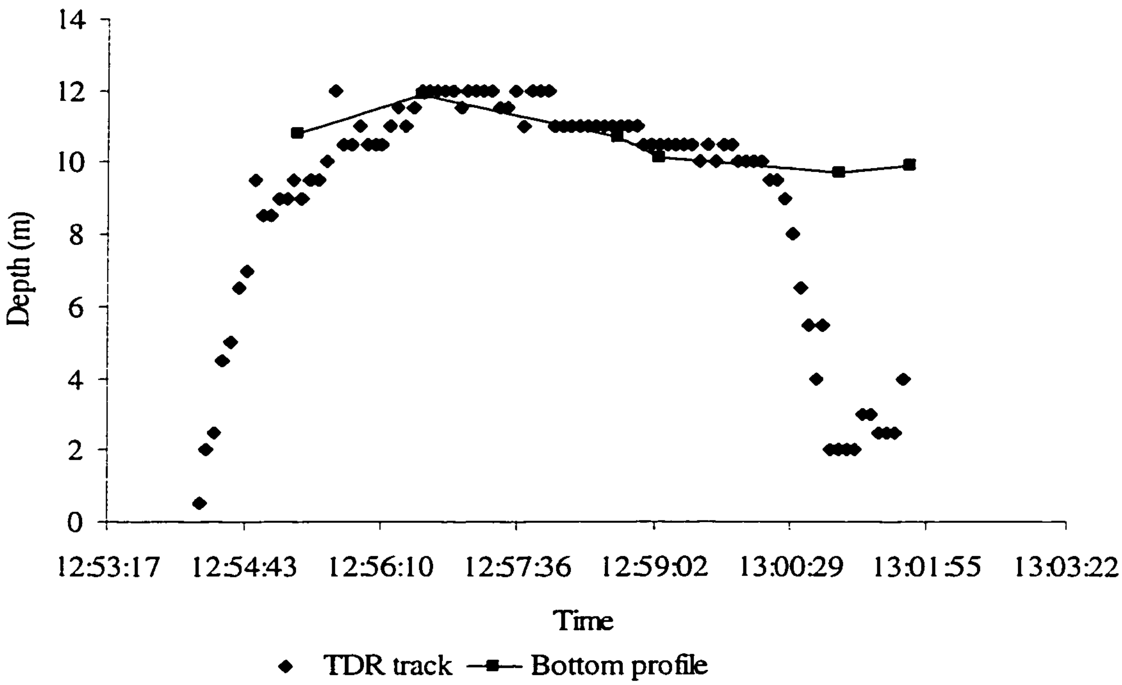

Figure A1.2. Time-depth profile of trawl #1 showing approximate bottom profile.

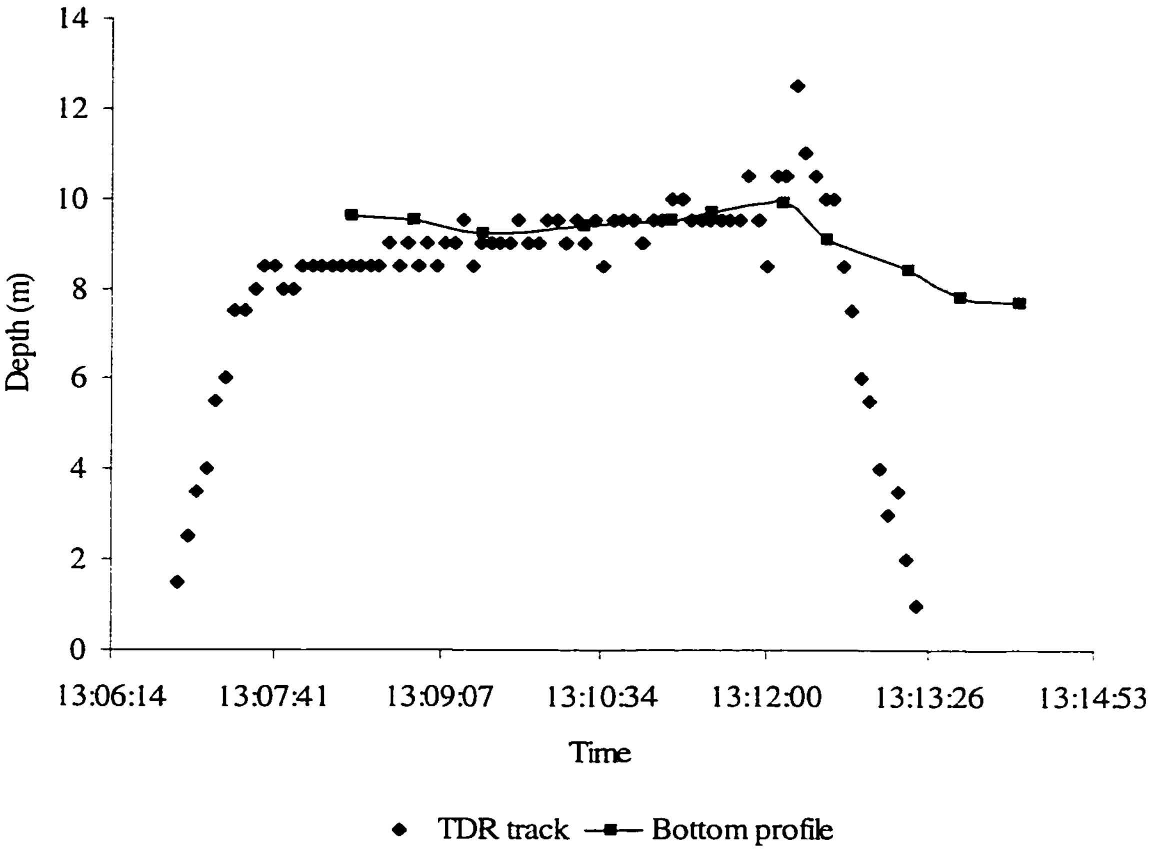

Figure A1.3. Time-depth profile of trawl #2 showing approximate bottom profile.

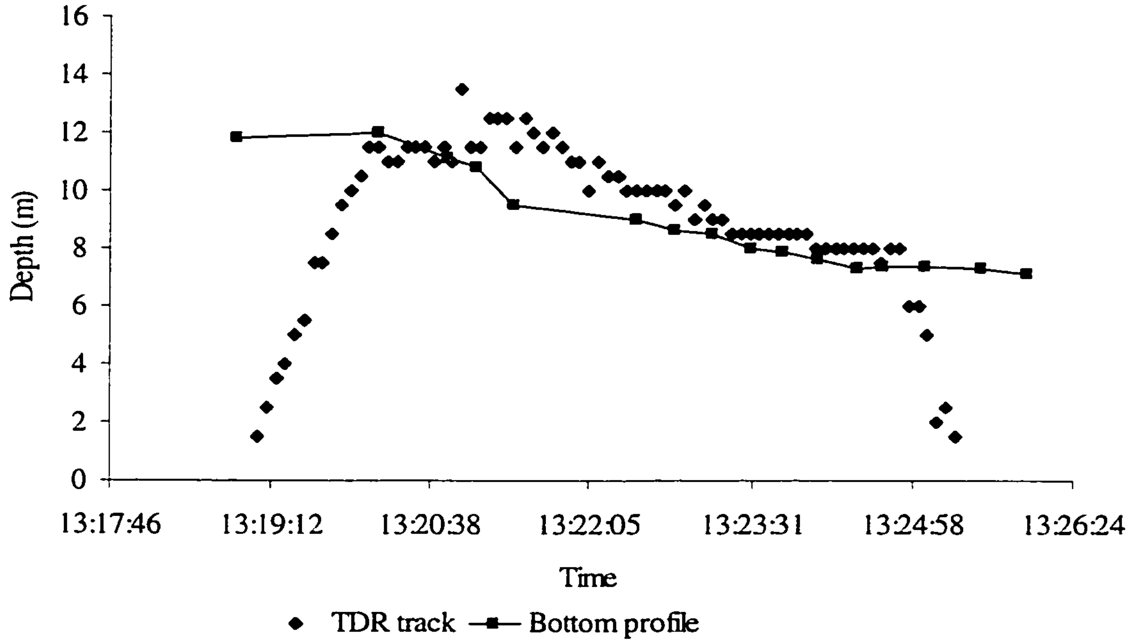

Figure A1.4. Time depth profile of trawl #3 showing approximate bottom profile.

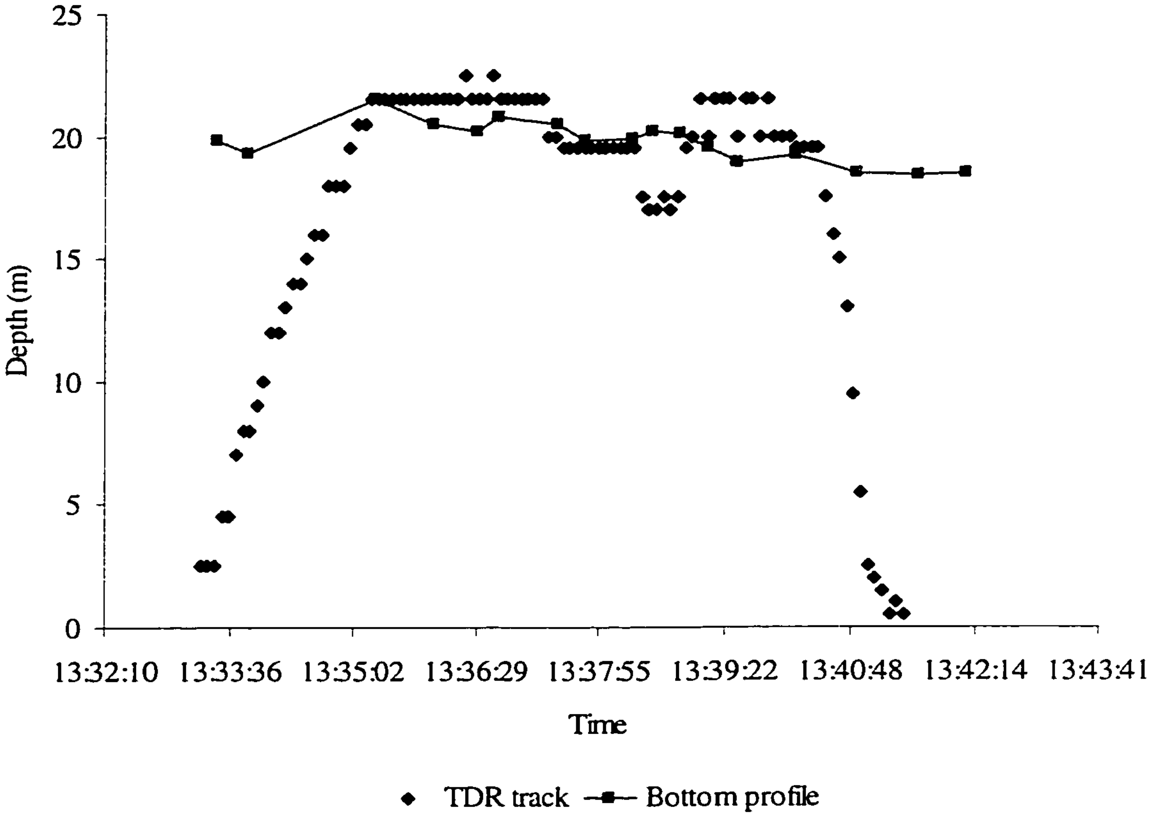

Figure A1.5. Time depth profile of trawl #4 showing approximate bottom profile.

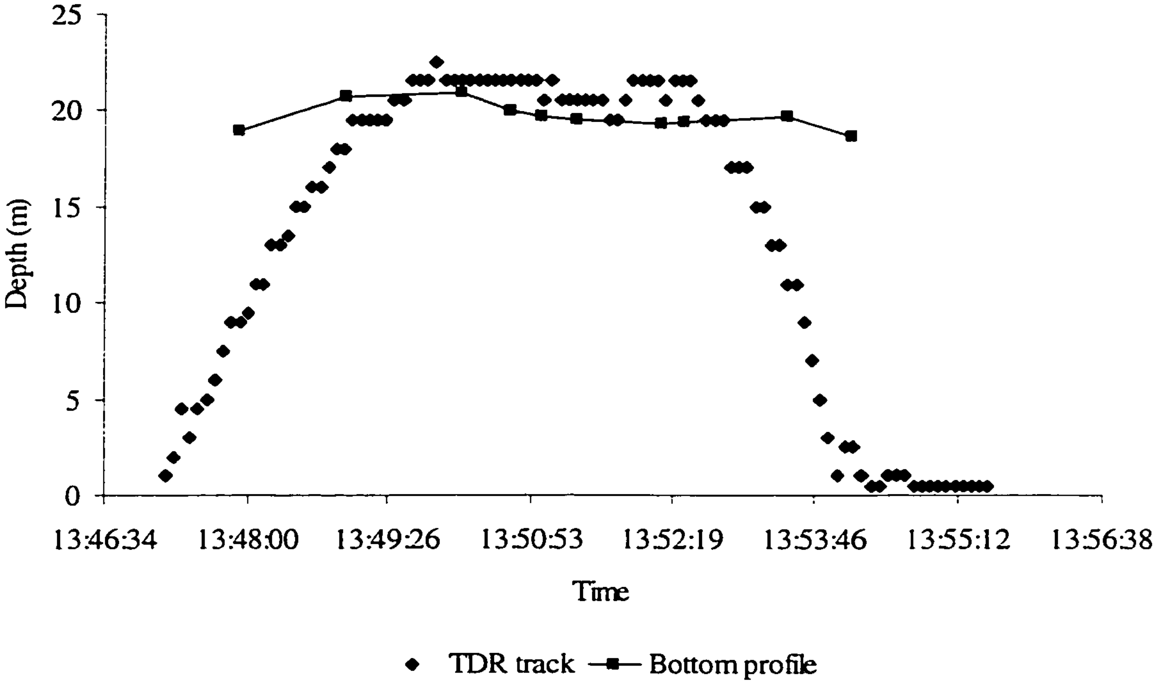

Figure A1.6. Time depth profile of trawl #5 showing approximate bottom profile.

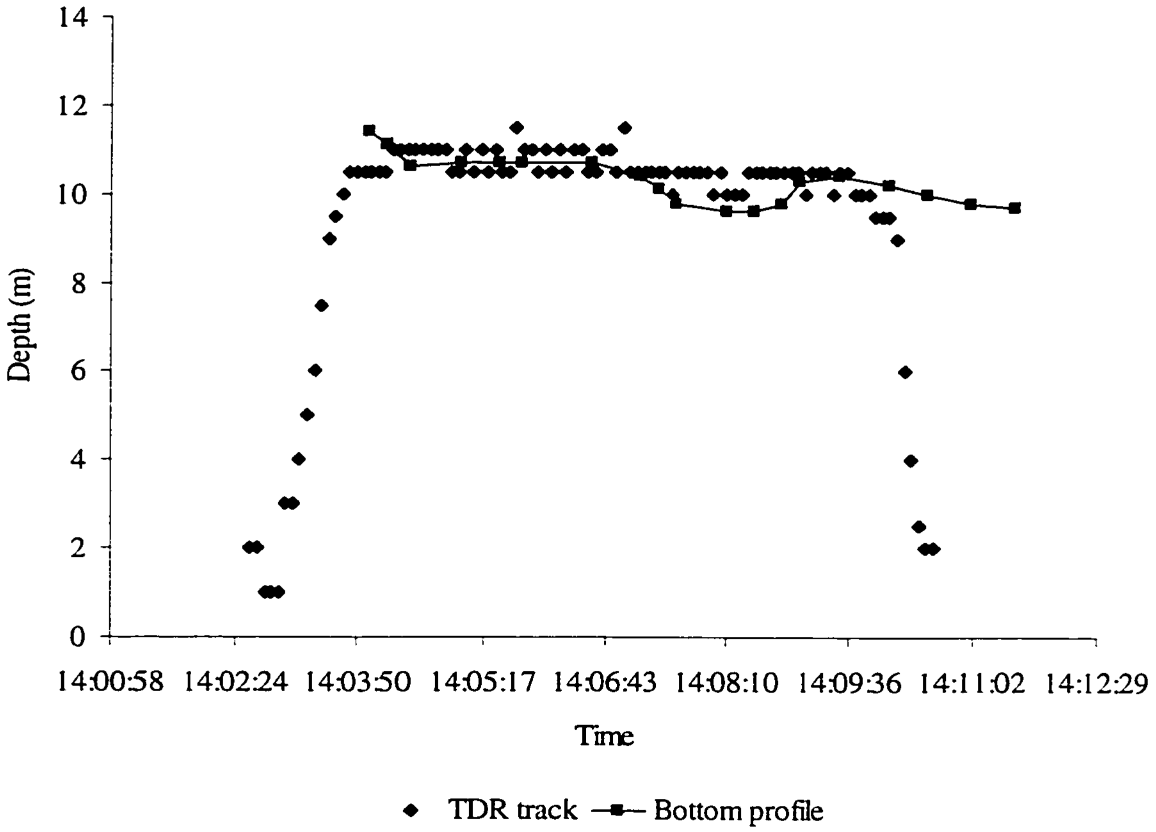

Figure A1.7. Time-depth profile of trawl #6 showing approximate bottom profile.

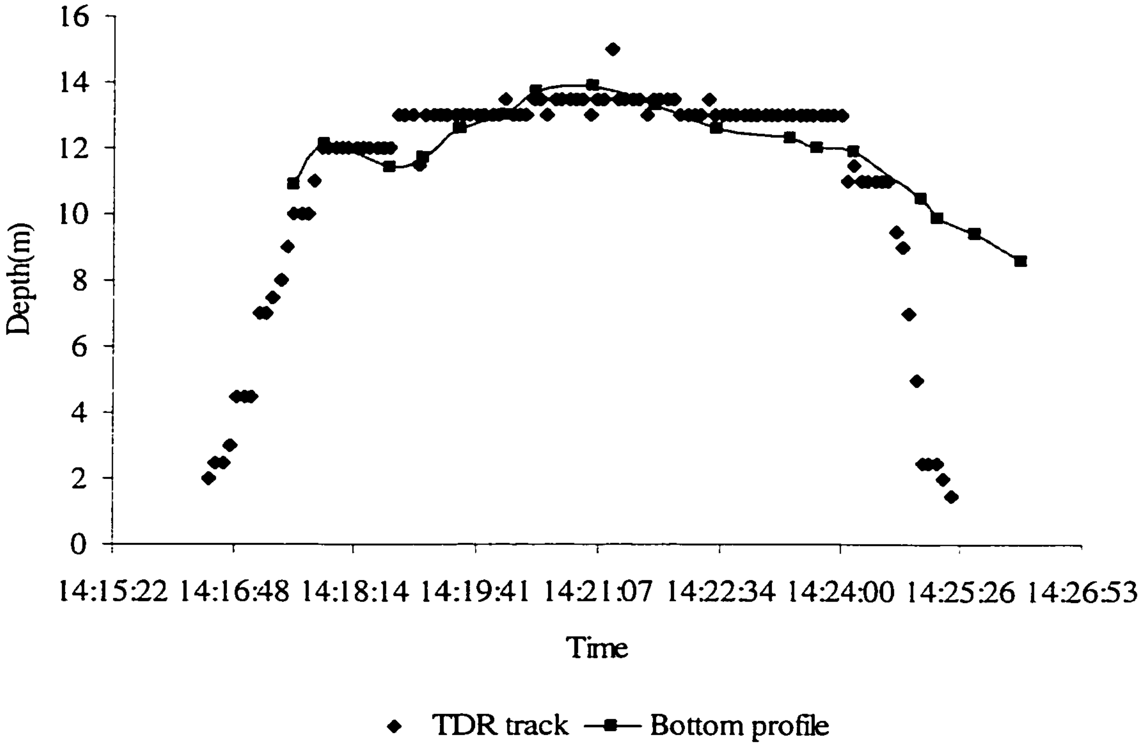

Figure A1.8. Time-depth profile of trawl #7 showing approximate bottom profile.

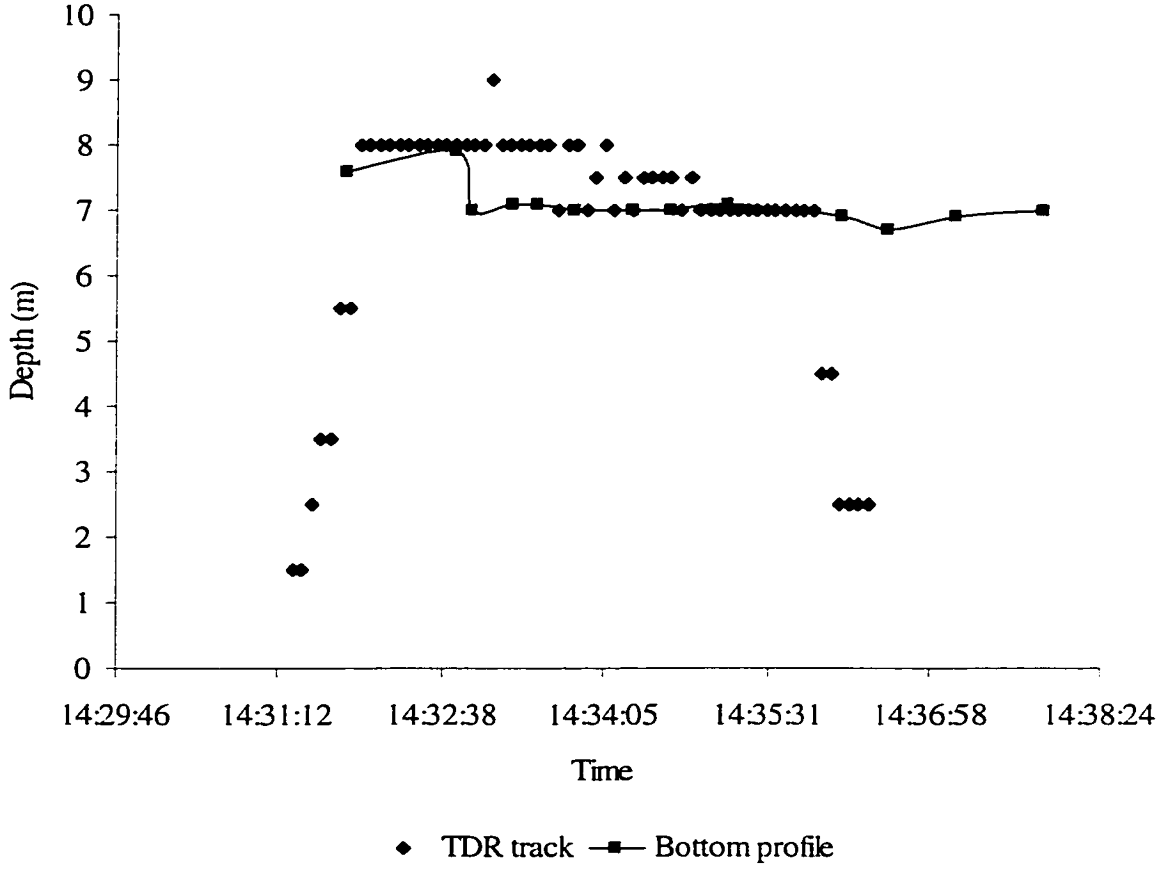

Figure A1.9. Time-depth profile of trawl #8 showing approximate bottom profile.

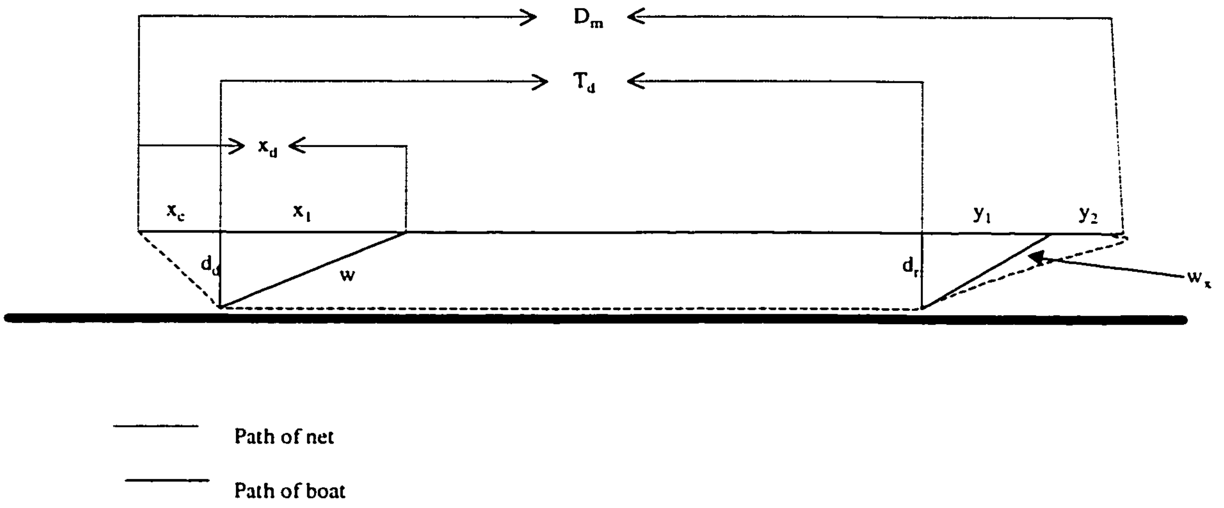

Figure A1.10. Physical description of equation terms used to correct for the distance during net deployment and retrieval when the net is not in contact with the bottom. See text for definitions.

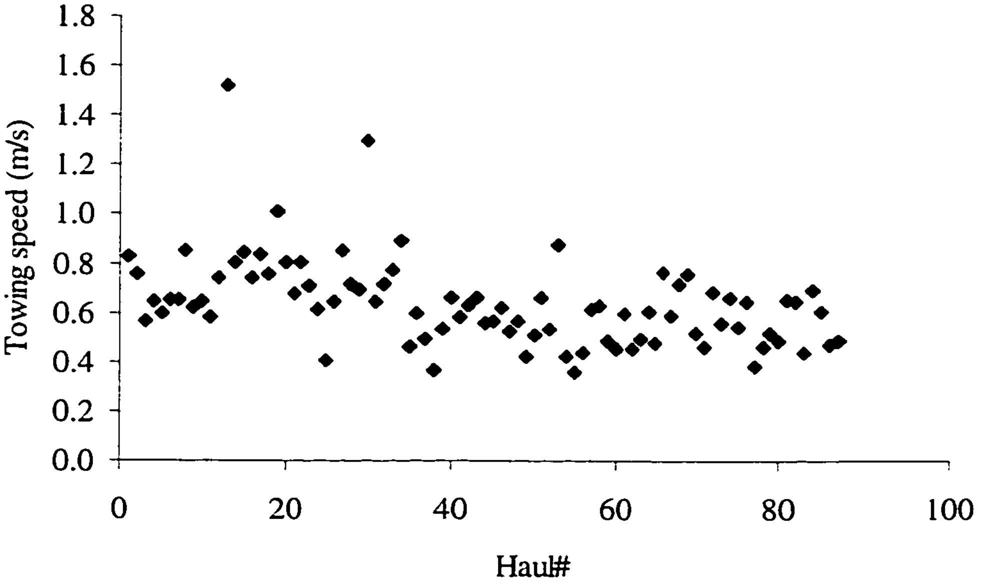

Figure A1.11. Towing speeds during 1999 PNCERS sampling at estuarine stations.

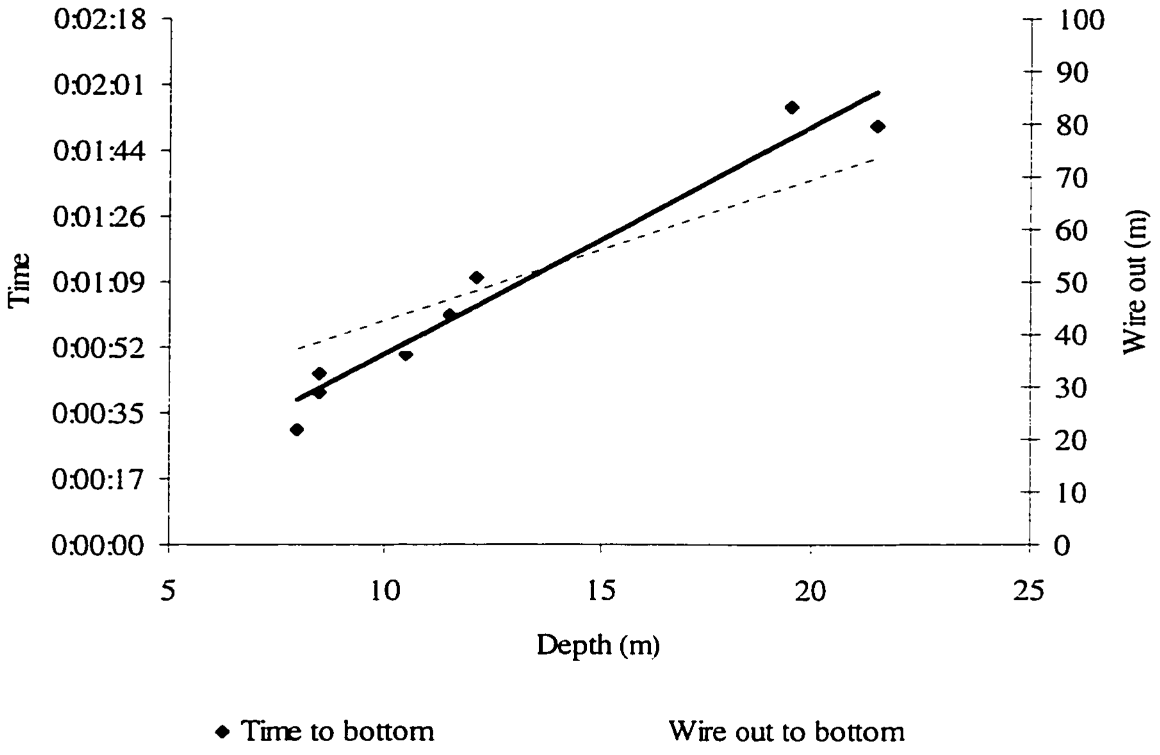

Figure A1.12. Time and amount of wire out when the net hit the bottom during deployment during test trawling.

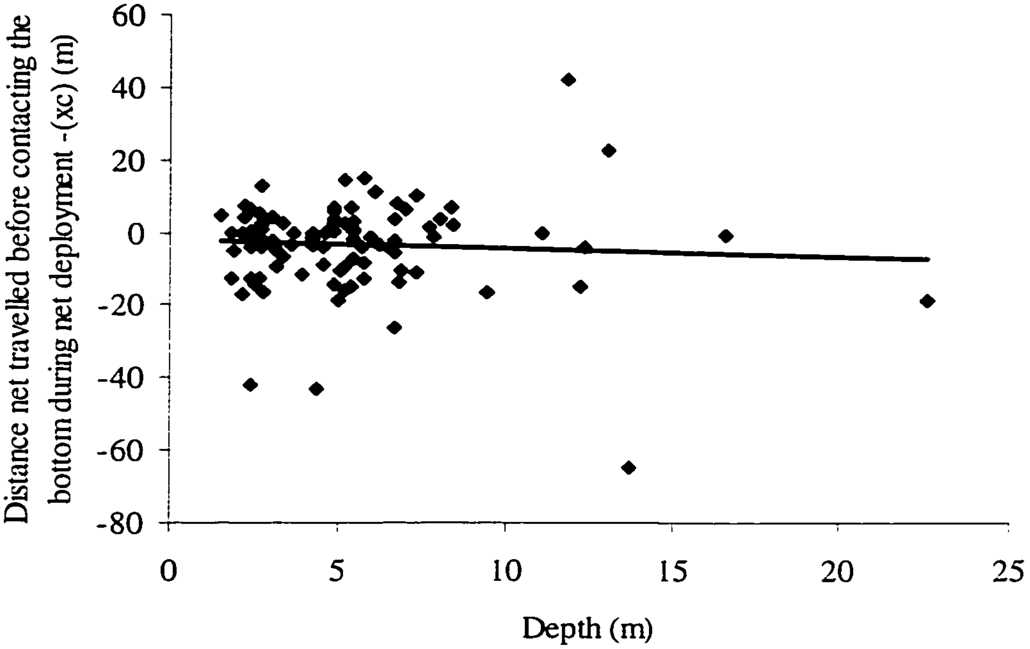

Figure A1.13. Correction for the distance the net traveled off the bottom during net deployment against the depth at which the net was deployed. Data is from 97 stations during 1999 PNCERS sampling.

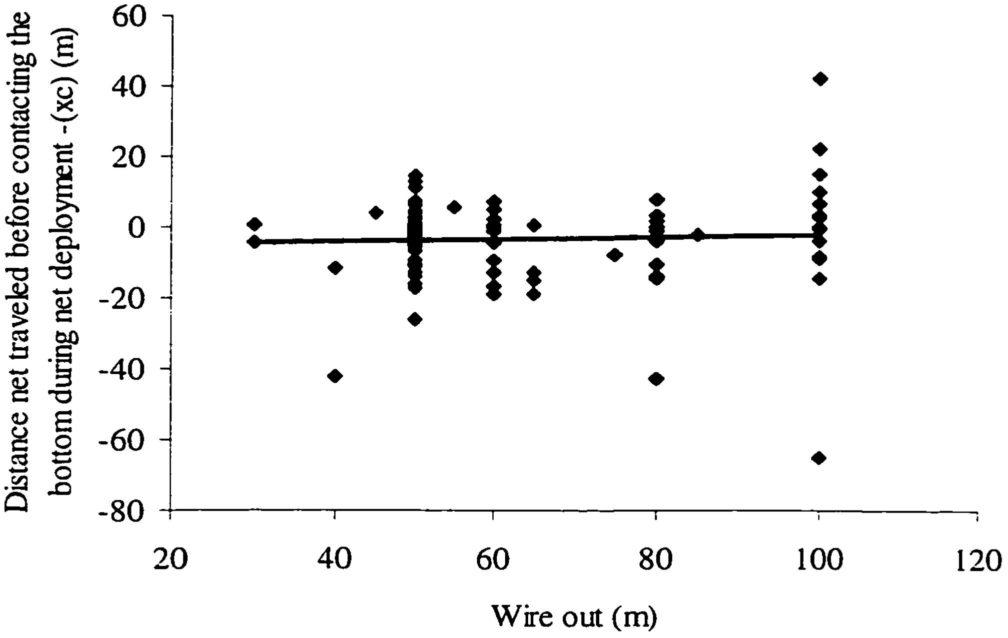

Figure A1.14. Correction for the distance the net traveled off the bottom during net deployment plotted against the amount of wire that was let out. Data is from 97 stations during PNCERS sampling in 1999.

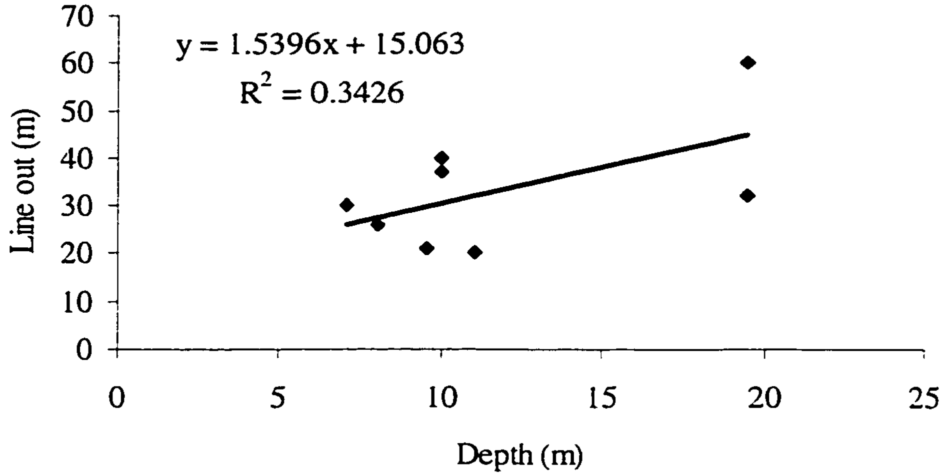

Figure A1.15. Amount of wire out when the net came off the bottom during net retrieval in eight test trawls.

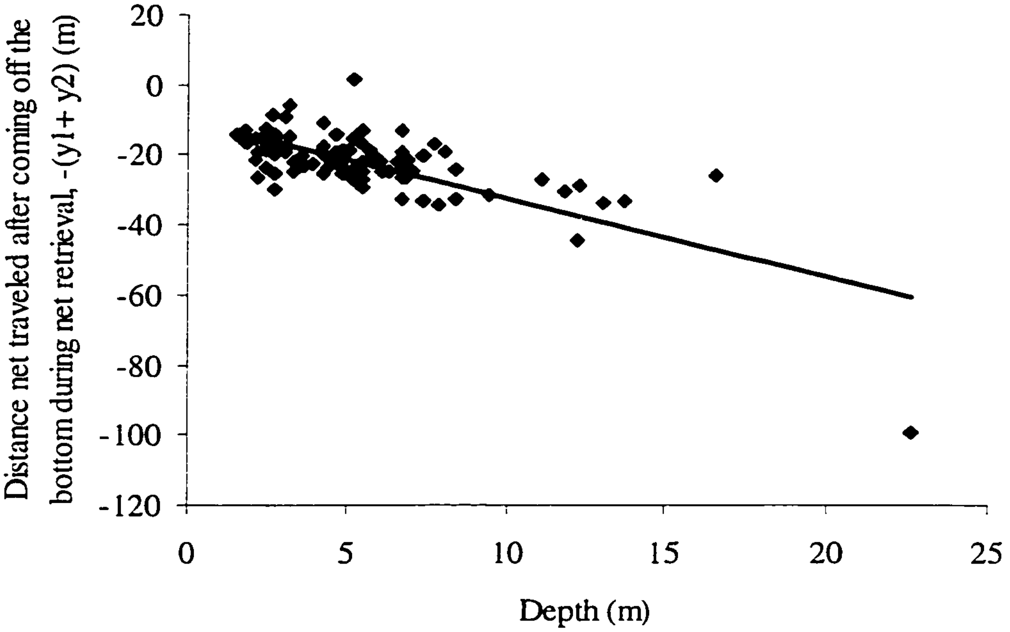

Figure A1.16. Correction for the distance the net traveled during retrieval from the point it left the bottom to the point where it reached the surface. Data is from 97 stations during 1999 PNCERS sampling.

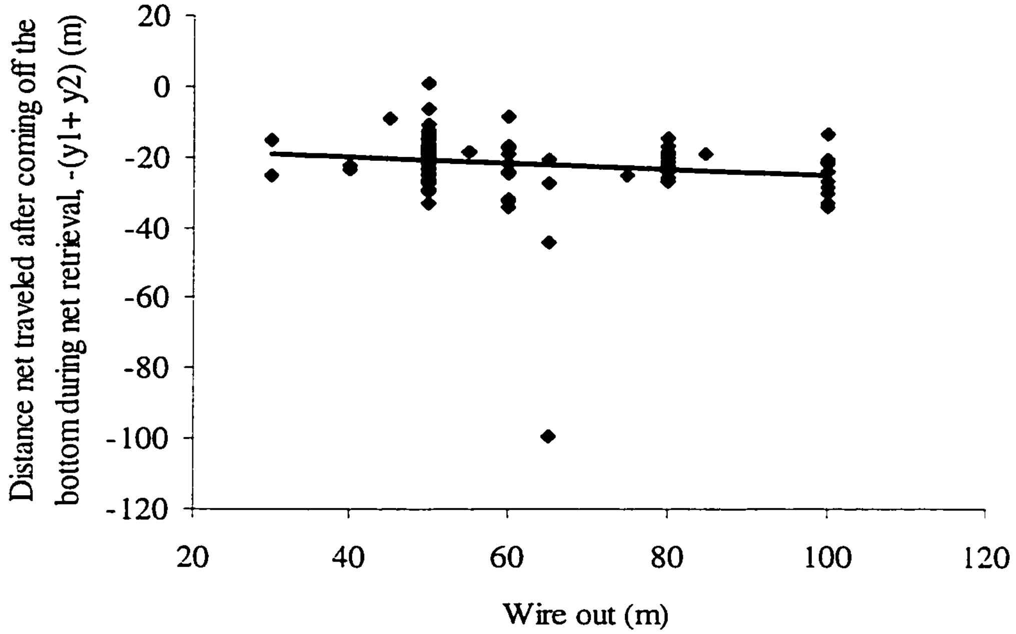

Figure A1.17. Correction for the distance the net traveled from the point it left the bottom to the point it reached the surface during net retrieval. Data is from 97 stations during 1999 PNCERS sampling.

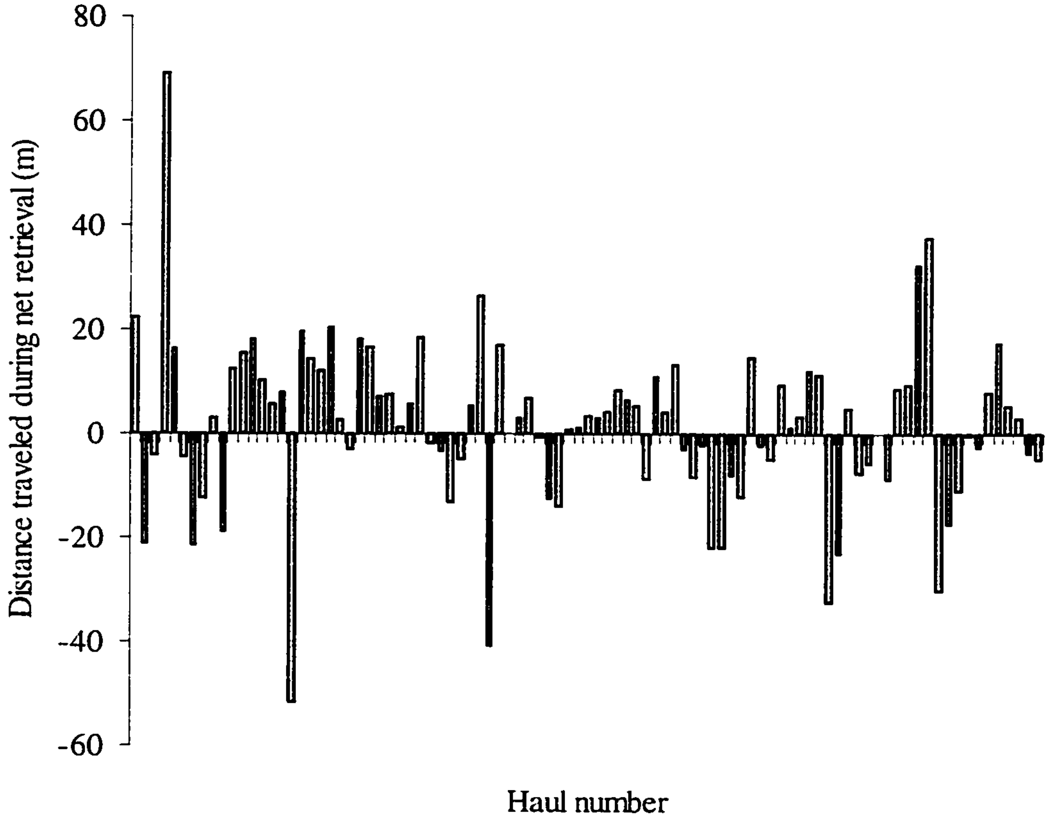

Figure A1.18. Distance the net traveled while off bottom during retrieval. Values are calculated from 97 tows during 1999 PNCERS sampling.

Appendix 2. Current meter data from Coos Bay, 1997-1999.

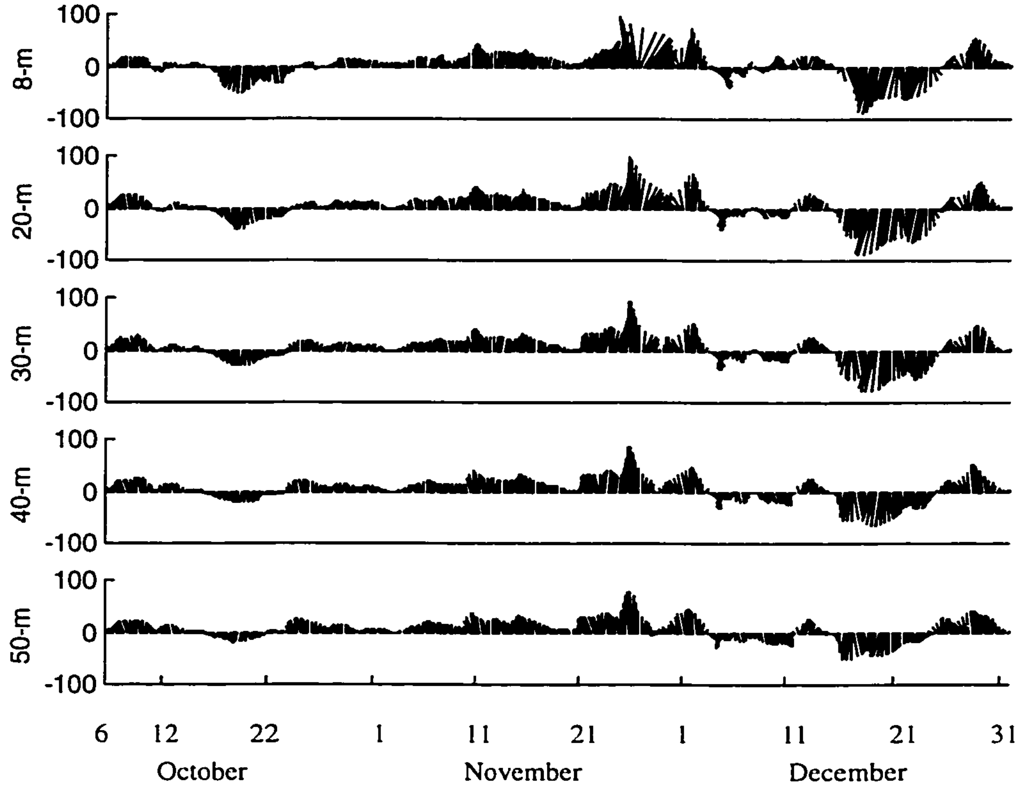

Figure A2.1. Currents from October 6, 1998 to December 31, 1998 measured at Coos Bay in depths from 8-50 meters. Current speeds on the y-axis are in cm per second.

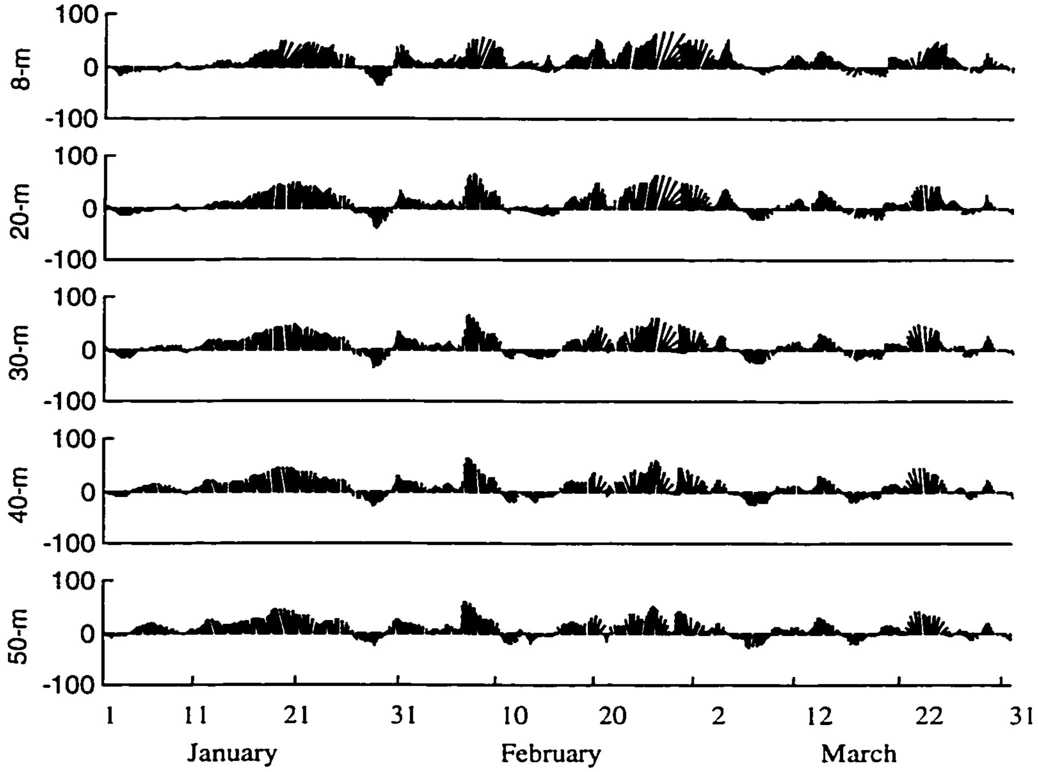

Figure A2.2. Currents from January 1, 1999 to March 31, 1999 measured at Coos Bay in depths from 8-50 meters. Current speeds on the y-axis are in cm per second.

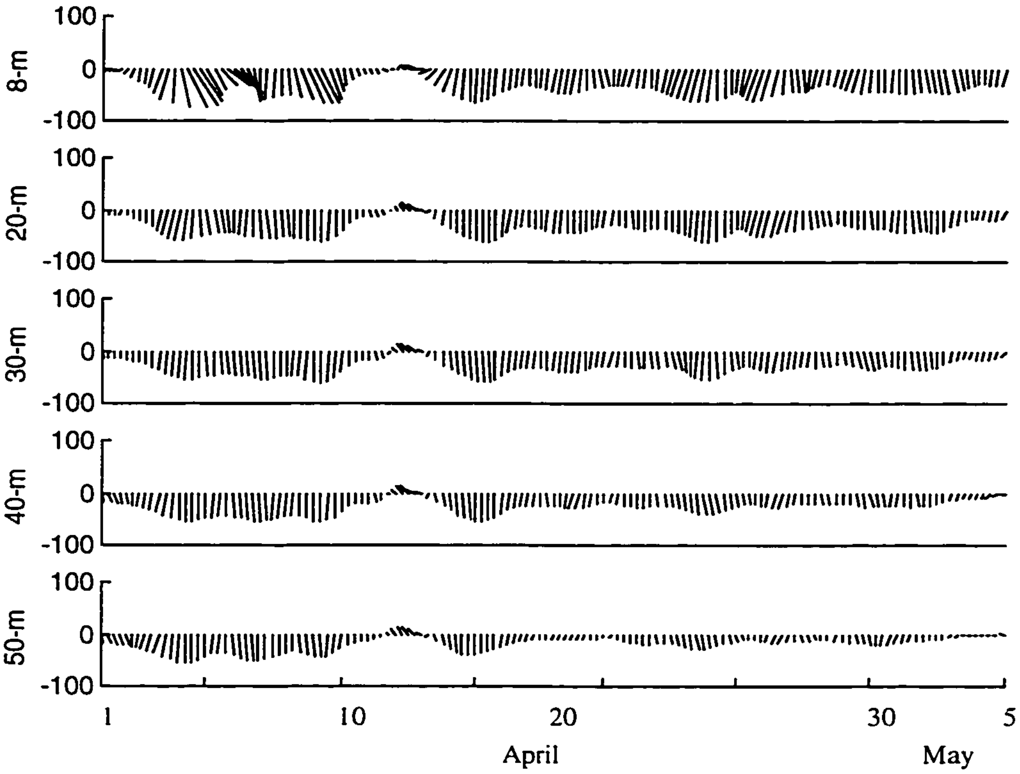

Figure A2.3. Currents from April 1, 1999 to May 5, 1999 measured at Coos Bay in depths from 8-50 meters. Current speeds on the y-axis are in cm per second.

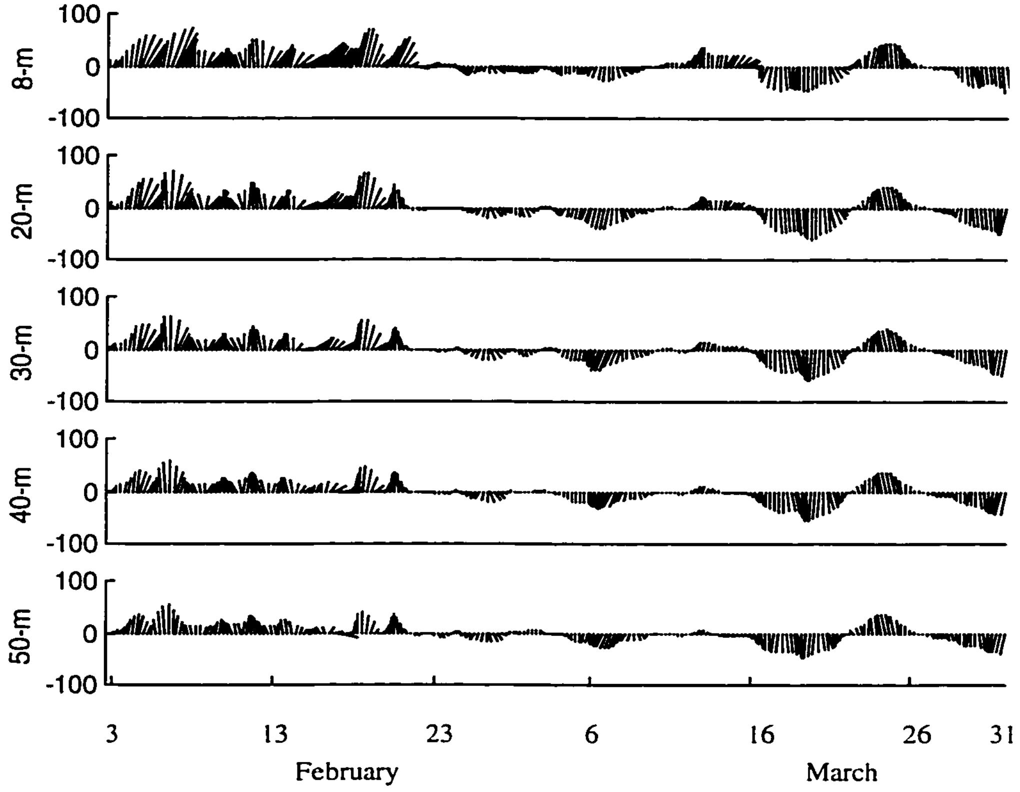

Figure A2.4. Currents from February 3, 1998 to March 31, 1998 measured at Coos Bay in depths from 8-50 meters. Current speeds on the y-axis are in cm per second.

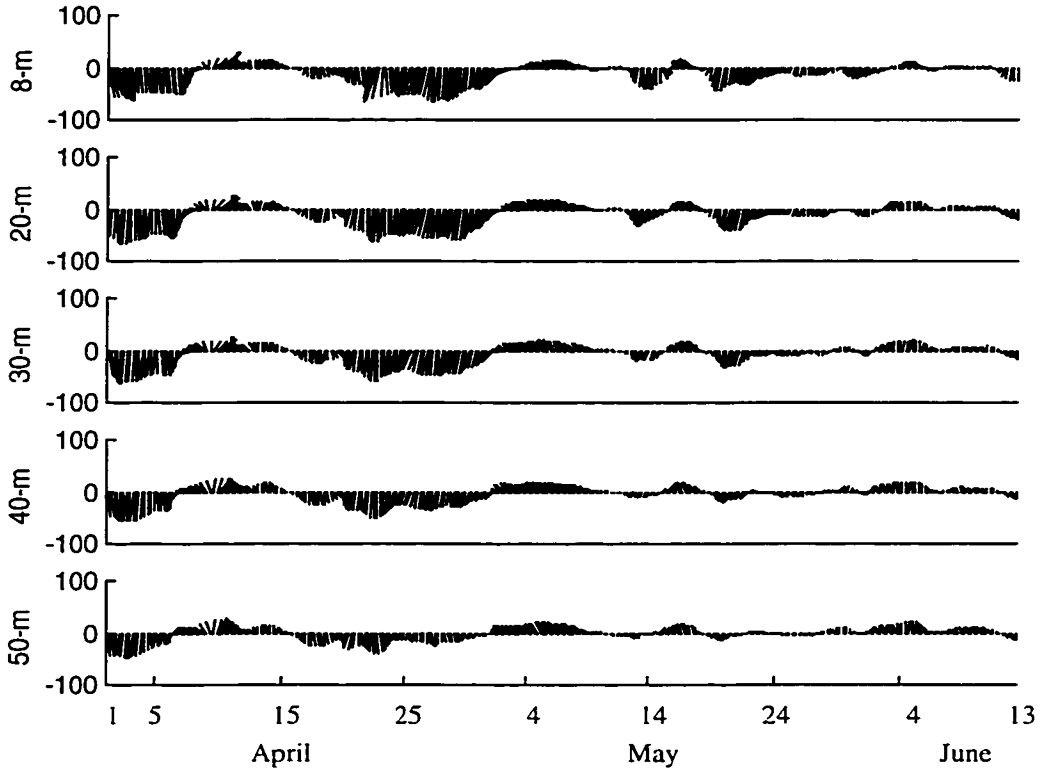

Figure A2.5. Currents from April 1, 1998 to June 13, 1998 measured at Coos Bay in depths from 8-50 meters. Current speeds on the y-axis are in cm per second.

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