

AN ABSTRACT OF THE THESIS OF

Christopher J. Donohoe for the degree of Doctor of Philosophy in Fisheries Science presented on August 2, 2000. Title: Metamorphosis, Growth, and Settlement of Pacific Sanddab (*Citharichthys sordidus*) to a Continental Shelf Nursery, Inferred from Otolith Microstructure.

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Douglas F. Markle

Processes of metamorphosis, settlement, and growth were examined in Pacific sanddab using field studies and otolith microstructure. This flatfish transforms at large sizes, has a gradual metamorphosis, and settles to a nursery on the middle continental shelf. Eye migration takes 3 months and "metamorphosis proper" which begins after completion of eye migration (CEM) takes an additional 1-2 months. Larvae at CEM ranged from 30-46 mm SL and were 125-224 d old. Coefficients of variation in length and age at CEM were 0.081 and 0.122, similar to flatfishes that transform at smaller sizes. Accessory primordia (AP) and an opaque region formed in the sagitta 14-49 d before CEM and 2-3 months before the start of the juvenile period.

Depth stratified benthic surveys were conducted on the continental shelf and upper slope off central Oregon bimonthly in 1989 and in March 1990-1994. Peak settlement occurred in late fall and winter. Larvae initially landed on the upper slope but continued inshore to the middle shelf, a process that takes ~50-60 d. The nursery is centered at 80-119 m in winter and 50-99 m in summer. Abundance of settling Pacific sanddab on the upper slope in March 1989-1994 was strongly correlated to onshore Ekman transport during the preceding 30 d ($r=0.91$, $P=0.013$, $n=6$).

Electron microprobe analysis revealed strong cross-otolith trends in concentrations of Sr, K, and P in Pacific sanddab and Dover sole, but trends were not related to settlement,

thermal experience, or otolith and somatic growth. Margin concentrations of Cl and K differed among stations as little as 5-8 km apart, potentially indicating meso-scale patchiness. Patterns also imply long term cohesion of pelagic larvae, a surprising result given the 9 month to 2 year pelagic period of Dover sole.

Time series of daily increment widths revealed ontogenetic, seasonal, and individual variation in otolith growth rate. Otolith growth rates were correlated with SST in 1992 and 1994, but were largely determined by timing of settlement. Otolith growth was synchronous among a small portion of each year class. Distinct growth histories acted as natural tags that allowed study of patch dynamics and settlement.

Metamorphosis, Growth, and Settlement of Pacific Sanddab (*Citharichthys sordidus*)
to a Continental Shelf Nursery, Inferred from Otolith Microstructure

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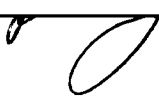
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Metamorphosis, Growth, and Settlement of Pacific Sanddab (*Citharichthys sordidus*) to a Continental Shelf Nursery, Inferred from Otolith Microstructure

CHAPTER 1

Introduction

OVERVIEW

Life history strategies

Most marine fishes have complex life histories with distinct larval and juvenile phases. The transition between phases represents a major ecological shift and includes changes in morphology, habitat, behavior, diet, and growth rate. Many species have transparent pelagic larvae that metamorphose into pigmented benthic juveniles. Metamorphosis is particularly pronounced in flatfishes and includes migration of one eye across the top of the head resulting in an asymmetrical juvenile (Brewster, 1987). Pelagic larvae generally occur offshore and must move inshore to reach juvenile nurseries (Minami and Tanaka, 1992). This inshore movement may depend upon favorable currents (Nelson et al., 1977; Boehlert and Mundy, 1988; Miller, 1988). Recent studies suggest that survival of late larval and early juvenile stages may be critical determinants of year class success (Sissenwine, 1984; Peterman et al., 1988; Bradford, 1992).

The early life history strategies of flatfishes are quite variable (Moser, 1981). Most flatfishes metamorphose at relatively small sizes of 10-25 mm SL, have short pelagic periods on the order of 1-3 months, and settle to shallow nearshore and estuarine nursery areas (Ahlstrom et al., 1984; Miller et al., 1991; Chambers and Leggett, 1992). Research on recruitment of flatfishes has focused on species with this life history strategy, and is particularly well documented for temperate flatfishes in the North Atlantic (Lockwood, 1980; Van der Veer, 1986; Bergman et al., 1988; Van der Veer et al., 1990; Beverton and Iles, 1992; Leggett and Frank, 1997). A smaller number of flatfishes transform at large sizes, have long pelagic

durations, and settle to nursery areas on the mid-continental shelf (Pearcy et al., 1977; Miller et al., 1991; Markle et al., 1992; Minami and Tanaka, 1992; Toole et al., 1997). The early life history of these species, including the processes which affect settlement and recruitment to deep nurseries, are not well understood.

Otolith analysis

Research on the early life history of fishes has profited greatly from otolith analysis. Fish otoliths contain a variety of detailed life history information. Several properties of otolith growth make otoliths valuable information storage structures. Otolith growth is incremental, producing daily marks that can be used to estimate age. Otolith growth rate, microstructure, and composition are affected by the environment and life history events, and thus record experience and timing of development. Because otolith material is not resorbed or reworked after deposition (Campana and Neilson, 1985), the otolith contains a complete permanent daily record of early life.

Since the discovery of daily increments in fish otoliths (Pannella, 1971), counts of increments have been widely used to estimate age and average growth rates of larval and juvenile fishes. In addition to average growth, the width of daily increments provide a record of otolith growth rate for the entire life of the fish. A few studies have demonstrated a direct correlation between otolith increment width and somatic growth (Volk et al., 1984; Karakiri and von Westernhagen, 1989; Sogard, 1991). However other studies have shown that the relationship between otolith growth and somatic growth is more complex (Reznick et al., 1989; Secor and Dean, 1989, 1992). Microstructural features in the otolith have been shown to correspond to specific life history events such as hatching, yolk absorption, metamorphosis, and settlement (Victor, 1983; Campana, 1984; Hare and Cowen, 1994; Wilson and McCormick, 1997). The timing and location of these landmarks, when combined with age and size

information from the otolith, allow backcalculation of the age and size of an individual at important life history events.

Otoliths may also contain individual environmental histories stored in chemical form. Otoliths are composed primarily of calcium carbonate in the aragonite form (Degens et al., 1969), but numerous elements are also incorporated into the otolith matrix. Concentrations of these elements can be influenced by environmental conditions at the time of deposition (Radtke and Shafer, 1992). Cross-otolith variation in element concentrations has been used to infer the temperature histories of individual fish (Radtke, 1989; Townsend et al., 1989, 1995; Radtke et al., 1990) and the timing of migrations among habitats (Tzeng and Tsai, 1994; Radtke et al., 1996; Secor and Piccoli, 1996). Differences in otolith composition or 'elemental fingerprints' among geographic groups of fish have been used to infer or confirm stock or population structure (Mulligan et al., 1987; Edmonds et al., 1989, 1992; Campana and Gagne, 1994; Campana et al., 1994).

Scope

This dissertation focuses on the transition period during the early life of Pacific sanddab (*Citharichthys sordidus*), and briefly that of Dover sole (*Microstomus pacificus*). Both species transform at large sizes and appear to settle to nurseries on the continental shelf (Matarese et al., 1989; Markle et al., 1992; Toole et al., 1997). Benthic Pacific sanddab used in these studies were collected during stratified surveys of continental shelf and upper slope off central Oregon in 1989-1994, and pelagic Pacific sanddab were obtained from midwater collections off central California in 1994. Although distribution and abundance patterns were derived from this survey data, much of the life history data was derived from analysis of otolith microstructure and microchemistry. The overall goal of the research was to gain a better understanding of the transitional period during early life of Pacific sanddab and other flatfishes with similar life history strategies.

This dissertation consists of four main chapters. Chapter 2, "Relationship between otolith microstructure, growth, and metamorphosis in Pacific sanddab (*Citharichthys sordidus*)", describes the process of metamorphosis with emphasis on developmental rate, variation in size and age at metamorphosis, and describes relationships between the otolith record, somatic growth, and events during metamorphosis. Chapter 3, "Settlement, distribution, and abundance of age-0 Pacific sanddab (*Citharichthys sordidus*) on the Oregon continental shelf", describes the settlement process, including timing of settlement, depth of the nursery, inshore movement, and annual variation in settlement abundance and its relationship to Ekman transport. Chapter 4, "Ontogenetic and individual variation in otolith microchemistry in two recently-settled flatfishes, Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*)", examines whether cross-otolith patterns in microchemistry represent an environmental record of settlement and inshore movement, then tests for and uses fixed differences in otolith composition as natural tags to discriminate among settling cohorts and infer patterns of settlement and larval patch dynamics. Chapter 5, "Sources of variation in time series of otolith growth of settling Pacific sanddab, *Citharichthys sordidus* (Paralichthyidae)", examines the relationship between mean daily otolith growth (growth histories) and seasonal variation in broad-scale sea surface temperature. Growth histories of individual fish are tested for synchrony to determine if the large "unexplained" variation was random or due to the presence of a few subgroups with distinct but asynchronous growth histories. Growth histories were related to mesoscale features and used as natural tags to examine patterns of settlement and larval patch dynamics. Finally, Chapter 6 summarizes the major conclusions of the dissertation and suggests directions for future research.

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CHAPTER 2

Metamorphosis and Relationships to Otolith Microstructure and Growth in Pacific Sanddab, *Citharichthys sordidus* (Paralichthyidae)

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ABSTRACT

Most flatfishes metamorphose at lengths of 10-25 mm SL. We describe metamorphosis in Pacific sanddab (*Citharichthys sordidus*) which transform at larger sizes and relate metamorphosis to changes in otolith microstructure and growth. Metamorphosis consists of two phases: eye migration which takes 3 months and "metamorphosis proper" which takes an additional 1-2 months. Eye migration began at 16-22 mm SL, then halted while larvae continued to grow. As a result, the right eye was partially migrated for 3 months or half the larval period. Larvae that had recently completed eye migration (CEM) ranged from 30-46 mm SL (mean=38.2, $n=70$) and were 125-224 d old (mean=174, $n=65$), although ages were not validated. Coefficients of variation in length and age at CEM were 0.081 and 0.122, similar to flatfishes that transform at smaller sizes.

During eye migration, accessory primordia (AP) formed in the sagitta, growth from the central primordium shifted abruptly from translucent (clear) to opaque, and sagitta growth rate temporarily tripled. Otolith growth rate also doubled in the asteriscus, which lack AP, suggesting AP formed in the sagitta in response to conditions that promote rapid otolith deposition. Unlike most flatfishes, AP formed 2-3 months before the start of the juvenile period. Somatic growth did not slow during the period of rapid otolith growth. Individual growth rates of larvae 18-46 mm SL ranged from 0.14 to 0.32 mm SL/d (mean=0.21, $cv=0.157$, $n=128$).

Metamorphosis proper did not begin until after CEM. During metamorphosis proper, relative body depth decreased, relative eye diameter increased, length of 2nd and 3rd dorsal rays decreased, and pectoral fin rays, scales, and juvenile pigmentation began to develop. Somatic growth appeared to halt for about 50 d then resumed. In addition, otolith growth slowed, sagitta density decreased, a distinct translucent band formed in some sagittae, and contrast of increments decreased in some asterisci. Increments formed at the same rate in the two otoliths, but the first increment formed in the asteriscus an average of 46 d after forming in the sagitta.

INTRODUCTION

Size at metamorphosis is highly variable among flatfishes, ranging from about 5 to >120 mm SL (Moser, 1981). However, most flatfishes metamorphose at relatively small sizes of 10-25 mm SL (Ahlstrom et al., 1984; Chambers and Leggett, 1992), have a short pelagic life, and settle to shallow coastal nurseries. Metamorphosis in some of the smaller flatfishes is rapid and takes only 1-2 weeks in species such as winter flounder, *Pleuronectes americanus* (Chambers and Leggett, 1987), and plaice, *Pleuronectes platessa* (Modin et al., 1996). Rapid metamorphosis is consistent with the idea that intermediate forms are poorly adapted to either the pelagic or benthic habitat. Curiously, some flatfishes transform at large sizes, have longer pelagic periods, and settle to deep continental shelf or slope nurseries. For example, rex sole, *Errex zachirus*, complete metamorphosis at 49-89 mm SL (Pearcy et al., 1977) and Dover sole, *Microstomus pacificus*, complete metamorphosis at 49-79 mm SL (Markle et al., 1992). Both settle on the mid-continental shelf of the eastern Pacific. Dover sole metamorphosis is also unusually slow, taking 9 months to >1 year, and eye migration is uncoupled from the rest of metamorphosis resulting in optically asymmetrical planktonic larvae (Markle et al., 1992; Butler et al., 1996).

Microstructures of fish otoliths are often used to understand timing of life history events such as hatching, yolk absorption, and settlement. In many flatfishes, secondary growth centers or accessory primordia (AP) are important microstructures associated with eye migration, metamorphosis, and settlement (Campana, 1984b; Kramer, 1991; Sogard, 1991; Modin et al., 1996). The timing of AP formation has been combined with increment counts to backcalculate age at metamorphosis and settlement dates for plaice (Alhossaini et al., 1989). In Dover sole, multiple AP formation begins after eye migration and coincides with a transition from clear to opaque material and with the initiation of metamorphosis (as defined by Markle et al., 1992) (Toole, et al., 1993). Settlement in Dover sole is approximated by the otolith landmark at which growth from AP completely encloses growth from the central primordium, but no landmark is

associated with completion of metamorphosis (Toole et al., 1993). The protracted metamorphosis in Dover sole suggests that AP formation is associated with initial metamorphosis and merely confounded with eye migration and settlement in species with rapid metamorphosis.

The generality of the Dover sole results can be explored in Pacific sanddab, *Citharichthys sordidus*, which is a paralichthyid rather than a pleuronectid, and which metamorphoses at moderate sizes, 20 to >50 mm SL (Matarese et al., 1989; Sakuma and Larson, 1995). Adults inhabit the continental shelf from Baja California to the Bering Sea (Miller and Lea, 1972) in areas with sand substrates, and mostly at depths of 35 - 90 m (Demory, 1971). Early larval stages have been described (Matarese et al., 1989; Moser, 1996), but little is known about metamorphosis. Sakuma and Larson (1995) suggested there is little growth during metamorphosis and that migration of the eye from right of the midline to the left side takes 3 weeks. The duration of the larval period is not known but assumed to be long because of the large size at metamorphosis. In this paper, we describe Pacific sanddab metamorphosis, microstructure of Pacific sanddab sagittae and asterisci, and relate microstructures to the process and rate of metamorphosis and growth.

METHODS

Collections

Larval, juvenile, and adult Pacific sanddab were collected from the continental shelf and upper slope off central Oregon (43.8-45.8°N) at depths of 50 to 400 m. Benthic fishes were collected with a 27.4 m headrope commercial shrimp trawl composed of 34.9 mm mesh (stretched) and lined with 6.4 mm mesh in the cod end and were frozen at sea. Most of the Pacific sanddab examined were collected in March 1992, 1993, and 1994, but a few larger young-of-the-year juveniles were collected in September 1991 with the shrimp trawl and in May 1994 using a 7.6 m otter trawl. In addition, we examined a sample of 57 pelagic larvae

and juveniles obtained from the annual juvenile rockfish survey conducted by NMFS scientists off central California (36.7-38.0°N) in May 1994 using a 26 m x 26 m modified Cobb midwater trawl (cruise number DSJ-9406).

Sample processing

In the laboratory, standard length (SL), body depth, and eye diameter were measured to 0.1 mm on fresh, defrosted fish. Pelagic fish were preserved in ethanol, but lengths were not corrected for potential shrinkage which prior experience suggests would be small. Fish were classified into four metamorphic stages based on the position of the right (migrating) eye: stage 0- eyes symmetrical; stage 1 - eye beginning to migrate but right of midline; stage 2 - eye intersecting the midline; and stage 3 - right eye migrated to left side. Individuals classified as stage 3 have not necessarily completed metamorphosis. In addition, pigmentation pattern was classified as one of six groups (early larval to juvenile) for fish collected in 1994.

Sagittae and asterisci were removed, cleaned of adhering tissue, and mounted in thermoplastic resin. Otoliths were measured under a light microscope with the aid of either an ocular micrometer or a video camera connected to an image analysis system. Whole otoliths were ground in the sagittal plane on both faces to the level of the central primordium (core) to expose increments. Otoliths were ground on silica sandpaper and polished with 0.05 μm alumina powder. Increments were counted under a light microscope at 100-1000x magnification. For sagittae, separate counts were made in the clear central region and the opaque outer regions. Only opaque increments were counted for pelagic fish. Increments in each sagitta were counted two times on different dates without knowledge of the size of the fish and the counts were averaged. If counts differed by more than 15%, the otolith was read a third time and the two most similar counts were averaged. Asteriscus increments were counted once.

Age was estimated by adding 5 days to the total number of sagittal increments. We assumed the first sagitta increment formed at yolk absorption which we estimated to occur 5

days after hatching based on the development of English sole, *Pleuronectes vetulus* (Laroche et al., 1982). Individual growth rates were estimated by subtracting average length at hatching (2.5 mm; Moser, 1996) from standard length and dividing by age. Kruskal-Wallis non-parametric ANOVA was used to test for significant differences in length and age among stages. Post-hoc pairwise comparison α levels were adjusted using the Bonferroni inequality.

Relationships between standard length and otolith size were complex. A segmented, three-part regression model incorporating a power function for the third segment described the relationships well. Inflection points were first estimated by fitting a three part linear model to the data (Bacon and Watts, 1971; Laidig et al., 1991). Regressions were then fit sequentially to data below, between, and above the two inflection points. The general form of the model for each segment was $SL = a + b(OL - c_i)^d$ where c_i is the otolith length at the inflection point at the start of the segment. Simple linear regression ($d=1$) was used for segments 1 and 2.

RESULTS

Metamorphosis

Metamorphosis in Pacific sanddab consists of two phases: eye migration and "metamorphosis proper" (see below). Eye migration occurs first and because it was the basis of our classification system, does not adequately characterize the entire process of metamorphosis. Length increased with metamorphic stage (stage 0 - 13.9-21.5 mm SL, stage 1 - 16.0-38.1 mm SL, stage 2 - 21.2-42.5 mm SL, and stage 3 fish caught in March - 29.8-55.6 mm SL) indicating considerable growth during eye migration (Figure 2.1). Overlap of these ranges indicates that the right eye began to migrate at 16-22 mm SL, reached the midline at 21-38 mm SL, and completed migration at 30-42 mm SL. Differences among these ranges indicate that larvae grew at least 8 mm SL and perhaps as much as 26 mm SL while the eye was migrating. Benthic stage 3 fish caught in March 1992 and pelagic stage 3 fish caught in May 1994 were an average of 21.4 and 16.8 mm SL larger than stage 0 larvae (Kruskal-Wallis, $P < 0.001$, Figure 2.1).

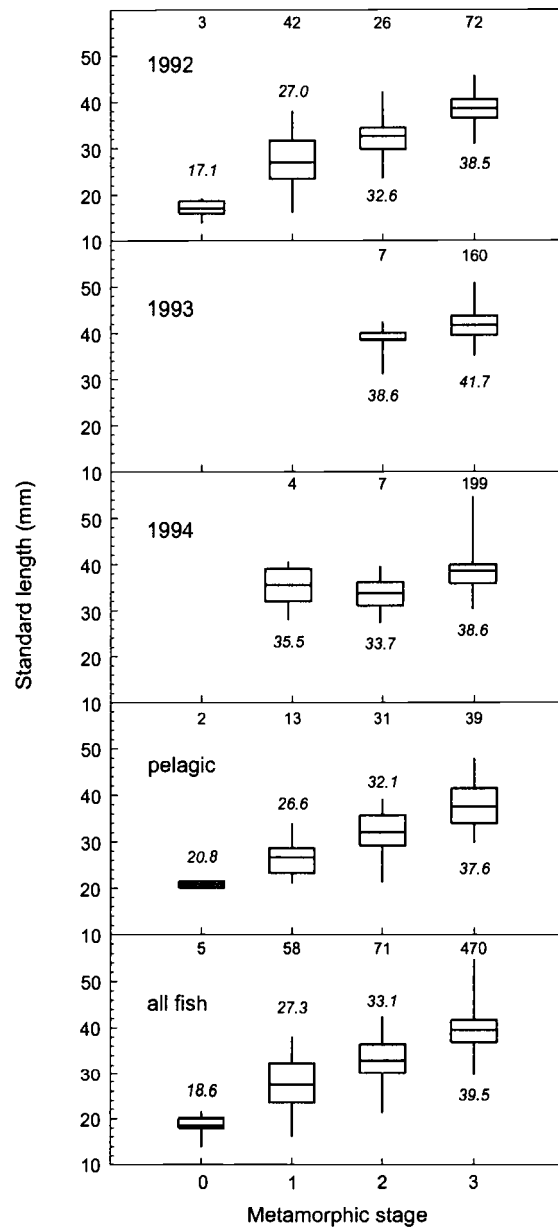


Figure 2.1. Length distribution of benthic Pacific sanddab (*Citharichthys sordidus*) collected in March 1992, 1993, and 1994 and pelagic fish collected off central California in May 1994 by metamorphic stage. Horizontal lines are the mean, boxes enclose 50% of observations, and vertical lines are the range. Means and numbers of fish are shown.

Mean age increased with metamorphic stage indicating eye migration was a gradual process. A pre-metamorphic, stage 0 larvae (18 mm SL) was 89 d old while four metamorphosing, stage 1 larvae of a similar size (16.0-21.5 mm SL) were 78-107 d old. The range in age of all stage 1 larvae was 78-165 d, stage 2 larvae was 108-196 d, and stage 3 fish 125-268 d (Figure 2.2). Overlap of these ranges indicates that the eye began to migrate at an age of approximately 78-89 d, reached the midline at 108-165 d, and completed migration at 125-196 d. Differences among these ranges indicate that larvae require 36-118 d to complete eye migration.

Mean length and age at completion of eye migration (CEM) were estimated from early stage 3 fish (those with <50 opaque sagittal increments, see below). Mean length of these early stage 3 fish was 38.2 mm SL (range=29.8-46.1 mm SL, $n=70$) and the coefficient of variation (CV) was 0.081. Mean age was 174 d (range=125-224 d, $n=65$) with a CV of 0.122. Thus length at CEM was less variable than age at CEM. If larvae begin eye migration at 16-22 mm SL (above), and these data suggest completion at about 30-46 mm SL, then larvae grew from 8-30 mm SL during eye migration. Similarly, if larvae begin eye migration at 78-89 d (above), and these data suggest completion at 125-224 d, then eye migration takes 36-146 d.

Although eye migration began at 16-22 mm SL, other major morphological changes associated with metamorphosis did not begin until after fish reached 30-42 mm SL and completed eye migration (stage 3). We refer to this period of change as "metamorphosis proper". During stage 3 relative body depth decreased from 0.37 to 0.34 SL and relative eye diameter increased from 0.07 to 0.09 SL (Figure 2.3). Juvenile pigmentation began to develop in stage 3. All stage 2 larvae and 21% of stage 3 fish ($n=120$) had larval pigmentation consisting of several large clusters of melanophores along the body (Figure 2.4 a, b, c). Melanophores were greatly reduced in other stage 3 fish (Figure 2.4 d, e) and the complete asymmetrical juvenile color pattern (not shown) was present only in fish > 60 mm SL. Other stage 3 changes include reduction in length of the 2nd and 3rd dorsal fin rays, elongation of

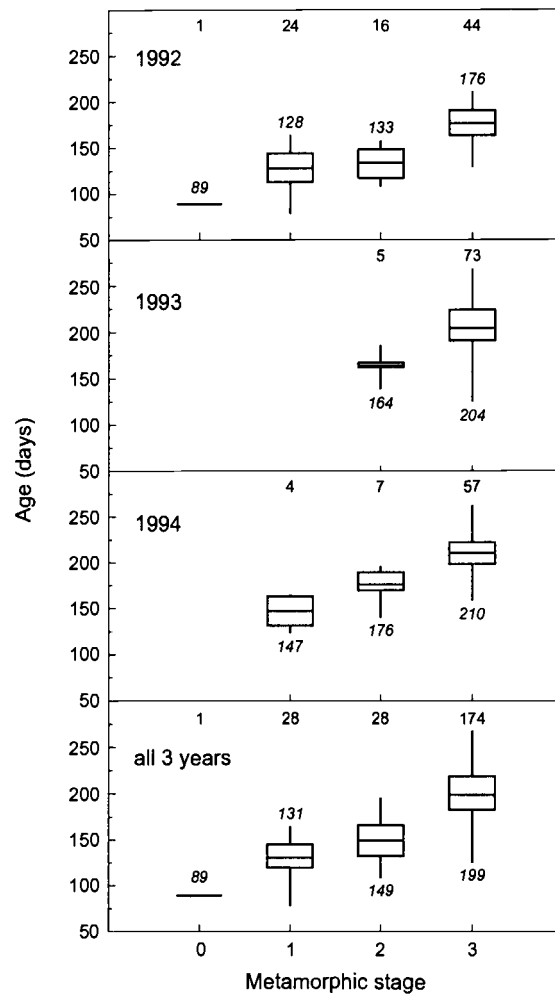


Figure 2.2. Age distribution of benthic Pacific sanddab (*Citharichthys sordidus*) collected in March 1992, 1993, and 1994 and pelagic fish collected off central California in May 1994 by metamorphic stage. Horizontal lines are the mean, boxes enclose 50% of observations, and vertical lines are the range. Means and numbers of fish are shown.

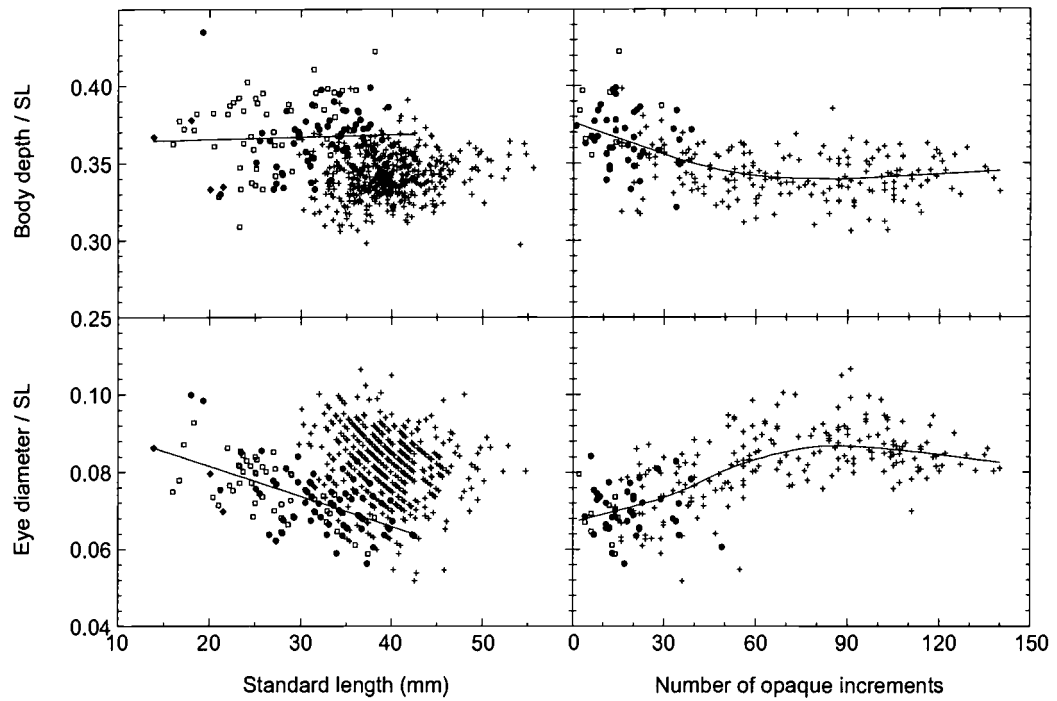


Figure 2.3. Relationships between relative body depth and relative eye diameter, and length and number of opaque sagittal increments for Pacific sanddab (*Citharichthys sordidus*). left: Lines are regressions for stages 0-2. right: Lines are locally weighted smooth. Symbols indicate metamorphic stage: ◆ = 0, □ = 1, ● = 2, + = 3.

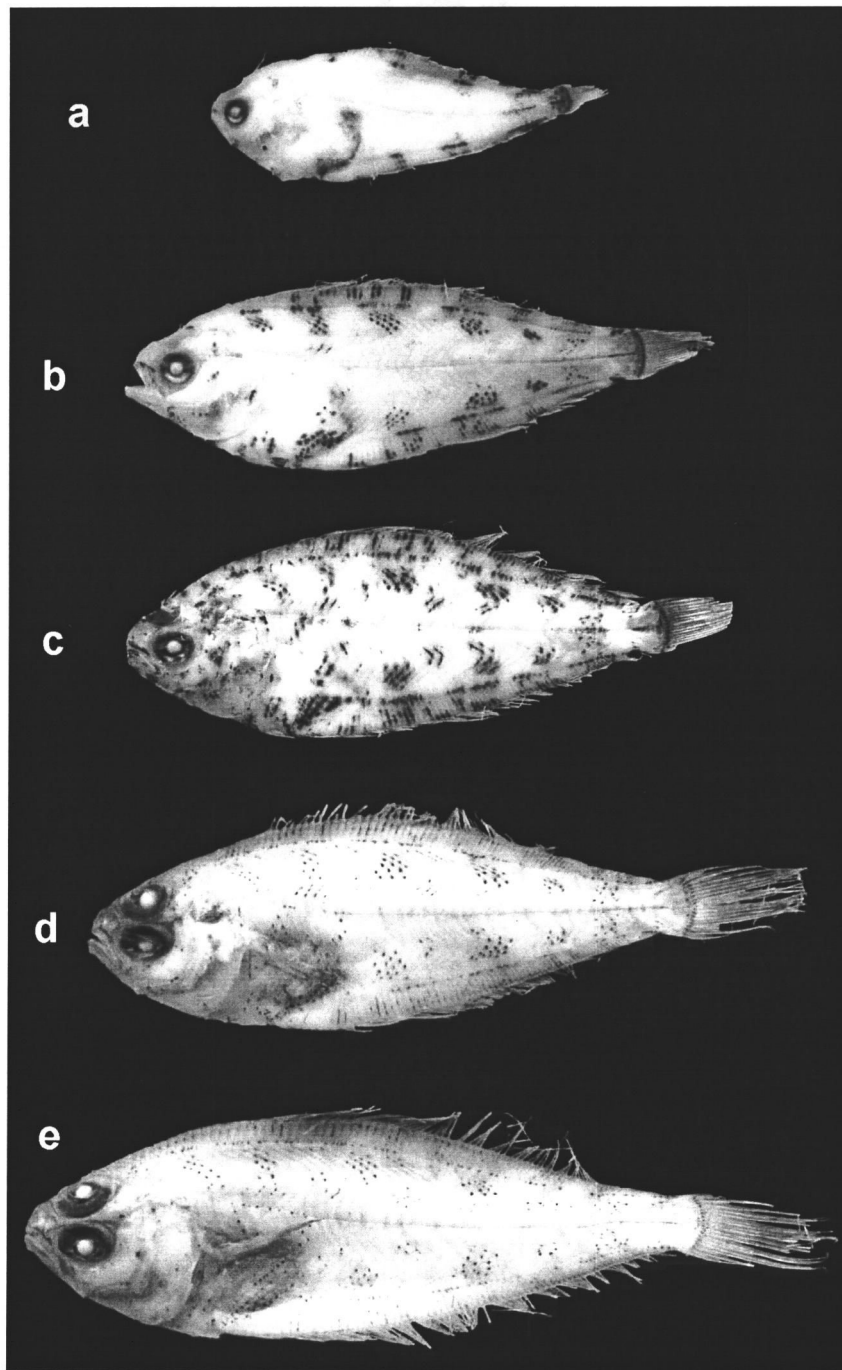


Figure 2.4. Development of larval (a-c) and juvenile (d-e) pigmentation in Pacific sanddab (*Citharichthys sordidus*). a) 24.8 mm SL stage 1, b) 34.0 mm SL stage 1, c) 36.3 mm SL stage 2, d) 40.3 mm SL stage 3, e) 44.7 mm SL stage 3.

pectoral fins, development of pectoral fin rays, and initiation of scale formation along the lateral line. An endpoint for metamorphosis proper is difficult to define. However, plots of body depth and eye diameter versus number of opaque sagittal increments (Figure 2.3) suggest that these features reached the juvenile state between 60 and 90 d after the opaque region formed or 1-2 months after CEM.

Otolith microstructure and relationship to metamorphosis

Sagitta

Clear central region

Three regions were visible in sagittae of large juvenile Pacific sanddab; a clear central region, a middle high density (HD) opaque region, and an outer low density (LD) opaque region. The innermost region of the sagitta was translucent (clear), with all growth originating from a single central primordium (Figure 2.5). The first increment formed at a radius of 1.3-13.4 μm (mean=5.3, $n=25$). Increment width gradually increased from 1.2-4.0 μm (mean=1.7, $n=25$) near the core to 1.8-6.1 μm (mean=3.6, $n=23$) near the edge of the clear central area. A notch was present in the anterior portion of the clear region in most sagittae of larger fish.. This notch was absent in sagittae of stage 0-2 larvae 18.0-32.0 mm SL ($n=17$) and present in stage 0-2 larvae 20.1-29.8 mm SL ($n=13$), suggesting the notch formed during metamorphic stages 0-2. Right and left sagittae were not symmetrical. Left sagittae initially grew at a similar rate in all directions, but right sagittae grew more rapidly in the anterior field, resulting in a core that appears slightly off center of the clear central area (Figure 2.5). The number of clear increments ranged from 77-184 (mean=124, $cv=0.171$, $n=241$) in sagittae in which the HD opaque region had formed.

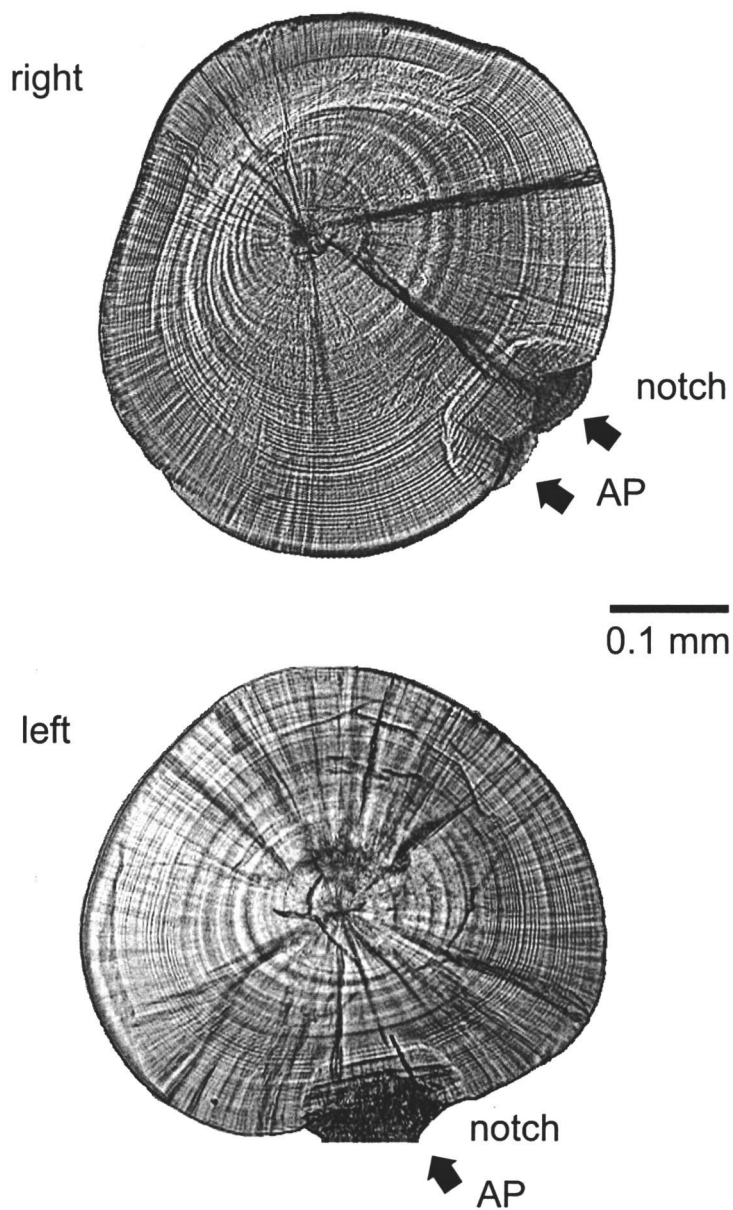


Figure 2.5. Photographs of polished left and right sagittae from a 28.0 mm SL stage 1 Pacific sanddab (*Citharichthys sordidus*) showing asymmetry in locations of the central primordia, notches in the anterior field, and the first few accessory primordia (AP).

High density opaque region

Numerous secondary growth centers or accessory primordia (AP) formed along the periphery of the clear region during metamorphosis. The first (most proximal) AP usually formed in the notch in the anterior field (Figure 2.5). Growth from AP was very dense and opaque. About the time the first AP formed, growth from the central primordium shifted abruptly from clear to opaque (Figure 2.6). This transition from clear to opaque increments occurred at a sagitta length of 0.42-0.61 mm (mean=0.52, cv=0.088, $n=47$). Opaque increments from the central primordium became enclosed by opaque growth from numerous AP and together formed the continuous HD opaque region. The number of HD opaque increments ranged from 18 to 75 (mean=43, $n=60$) in a subsample of sagittae in which the LD opaque region had formed.

Sagitta growth rate increased markedly about the time the first AP and HD opaque region formed. Width of increments from the central primordium increased from an average of 3.6 μm at the edge of the clear region to 7.8 μm in the opaque region. Increments within AP were generally wider, averaging 11.2 μm (range=6-17 μm). Sagitta growth rate remained high for an average of 40-50 d after the opaque region formed, then declined sharply (Figure 2.7). A plot of sagitta length versus number of opaque increments shows a strong inflection at a sagitta length of ~1.5 mm and ~45 opaque increments. Slopes of regressions fit to the two segments indicate a mean increment width of 11.7 μm in fish with <45 opaque increments and 2.2 μm in fish with ≥ 45 opaque increments.

The HD opaque region formed during eye migration. Opaque increments were absent in pre-metamorphic larvae (stage 0), present in 31% of stage 1, 72% of stage 2, and 100% of stage 3 fish. Thus the HD opaque region formed when the migrating eye was either to the right or on the midline. Stage 3 fish had a minimum of 14 opaque increments and stage 2 larvae had

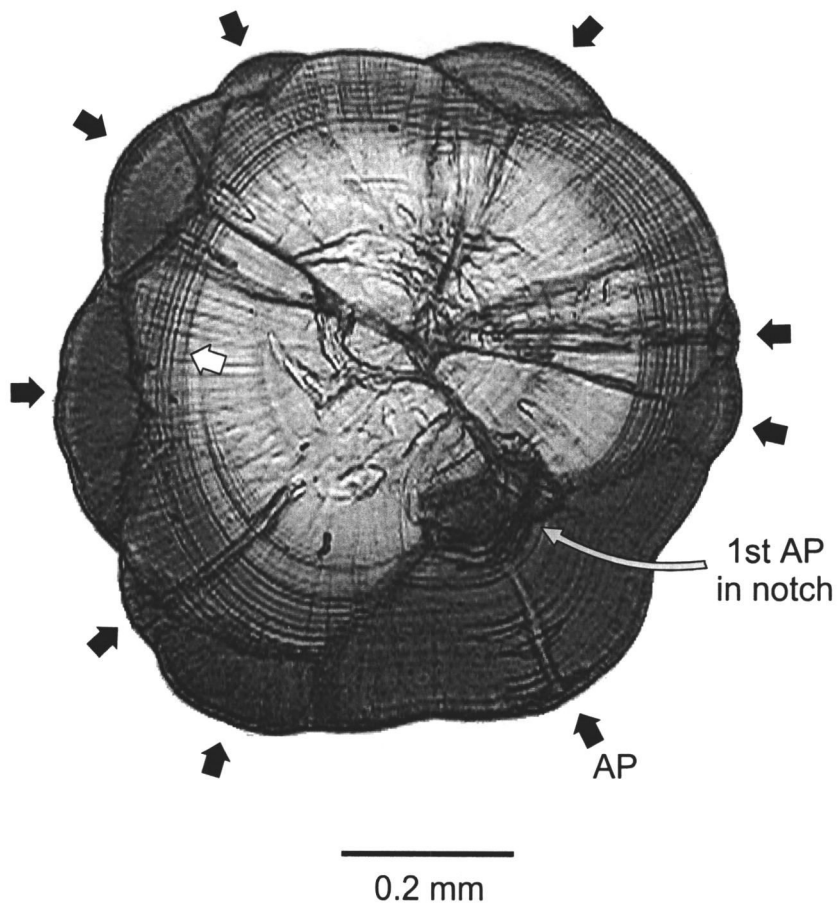


Figure 2.6. Photograph of a polished sagitta from a 37.6 mm SL stage 2 Pacific sanddab (*Citharichthys sordidus*) using transmitted light which shows the transition from the clear central region to the opaque outer region (white arrow) and accessory primordia (black arrows).

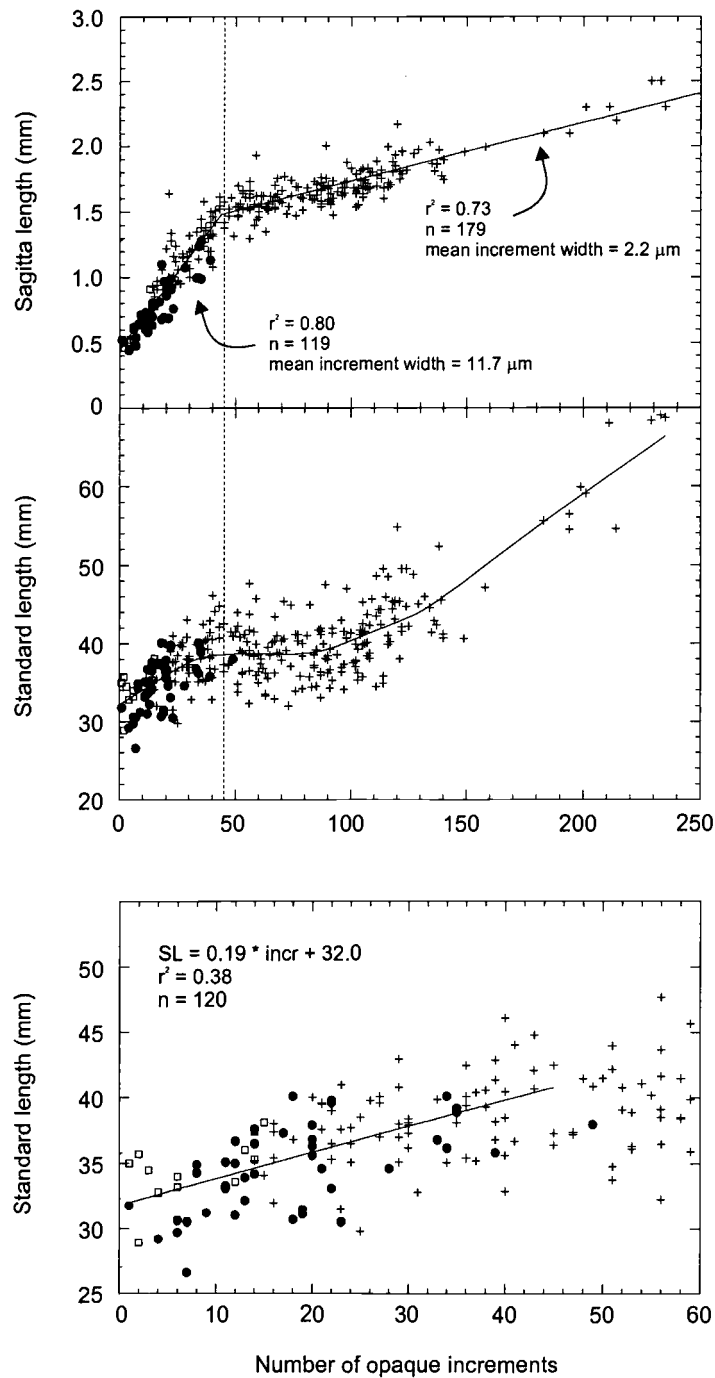


Figure 2.7. Relationship between sagitta length, standard length, and number of opaque sagittal increments for Pacific sanddab (*Citharichthys sordidus*). Symbols indicate metamorphic stage: \square = 1, \bullet = 2, $+$ = 3. top: regressions for otoliths with <45 and ≥ 45 opaque increments are shown. middle: smoothed fit (locally weighted average). bottom: detail, regression is for individuals with 1-45 opaque increments.

up to 49 opaque increments, indicating that the HD opaque region formed 2-7 weeks before CEM.

Formation of the first AP and HD opaque region also depended on body size. Lengths of stage 1 and stage 2 larvae indicate the right eye reached the midline at 21.2-38.1 mm SL, a range of 16.9 mm SL. However the first AP formed over a more narrow range, from 25.0 to 32.0 mm SL. Likewise, the HD opaque region was absent in all larvae <26.6 mm SL and present in all >34.6 mm SL, a range of only 8 mm SL. This pattern suggests formation of the first AP and the HD opaque region are more closely related to standard length than to the exact position of the migrating eye. Mean length at opaque formation was estimated for larvae with 1-25 opaque increments using the equation $SL_{opaque} = SL - (G * I_{opq})$, where G is the individual growth rate and I_{opq} is the number of opaque increments. Mean length at formation of the opaque region was 32.2 mm SL (range 27.2-36.0, $cv=0.070$, $n=45$).

Low density opaque region

Otolith density and otolith growth rate both decreased as sagittae grew. The decrease in density was gradual in some sagittae, but in many there was a rapid transition from HD to LD opaque regions (Figure 2.8). This transition was accentuated by a distinct translucent band in some but not all sagittae. The band was distinct in 36%, indistinct (faint, partial, or discontinuous) in 46%, and absent in 18% of large juveniles ($n=111$). The diameter of this band indicates it formed at a sagitta length of 0.91-1.69 mm (mean=1.35, $n=50$). Overlap among stage 2 and stage 3 fish shows that sagitta length at CEM ranged from 0.81 to 1.64 mm. Furthermore, the LD opaque region was only present in sagitta of stage 3 fish, indicating the transition from HD to LD occurred at or shortly after CEM. Mean sagitta growth rate also decreased from 11.7 to 2.2 $\mu m/d$ at a mean sagitta length of 1.5 mm (Figure 2.7).

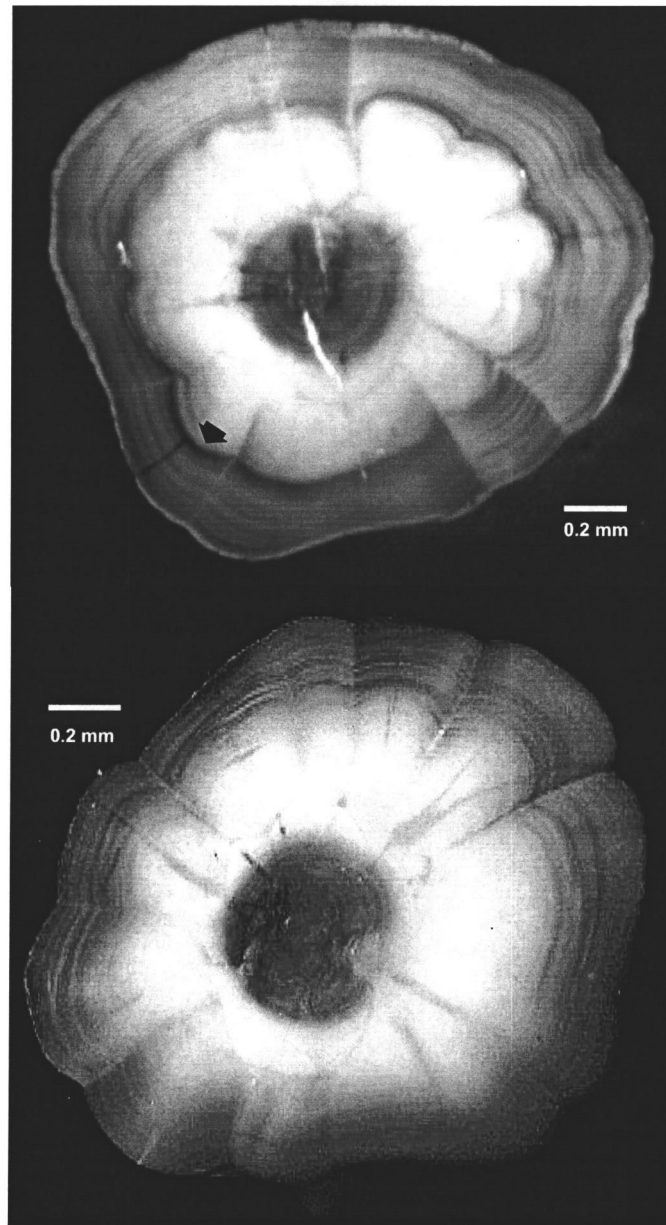


Figure 2.8. Photographs of polished sagittae from 42.1 mm SL (top) and 41.7 mm SL (bottom) stage 3 Pacific sanddab (*Citharichthys sordidus*) under reflected light. The inner clear region is surrounded by the high density and low density opaque regions. The transition can be distinct and accentuated by a translucent band (top, marked by arrow) or gradual (bottom).

Sagittae of pelagic fish

Sagittae of pelagic Pacific sanddab, 20.1-48.0 mm SL, did not appear to differ from those of benthic fish. AP and opaque regions were present in all fish ≥ 29.7 mm SL. Low density opaque increments and translucent bands were present in sagittae of some large juveniles, which would seem to suggest that these features are not induced by settlement. However sand was present in the stomachs of 17 of 38 (45%) stage 3 fish, indicating that some individuals had settled and then re-entered the water column.

Asteriscus

Growth of the asteriscus was less complex than the sagitta (Figure 2.9). The core was irregular and larger than in the sagitta with a radius of 2.4-48.1 μm (mean=20.4, cv=0.385, $n=179$). Asteriscus increments were translucent and all growth was from the central primordium. AP did not form and increments did not become opaque during metamorphosis. However, contrast of increments decreased sharply in some but not all asterisci at a radius of 0.17-0.28 mm (mean=0.21, cv=0.144, $n=36$, Figure 2.9). Overlap in asteriscus radius of stage 2 and stage 3 fish shows that CEM occurred at a radius of 0.18-0.26 mm. For comparison, an asteriscus radius of 0.20-0.34 mm (mean=0.26) corresponds to the range at which the translucent band formed in the sagitta. As in the sagitta, asteriscus increment widths temporarily increased during metamorphosis. Although the pattern differed among fish, mean increment width increased from 1.5 μm at a radius of 0.05 mm to a maximum of 3.0 μm at a radius of 0.18 mm, and decreased to 1.7 μm at 0.35 mm ($n=191$).

The number of asteriscus increments was regressed on the number of sagitta increments to compare growth of the two otoliths (Figure 2.10). The slope of the GM regression was 0.98, indicating that increments formed at the same rate in both pairs of otoliths. The intercept of the regression showed that the first asteriscus increment formed an average of 46 d after the first sagitta increment.

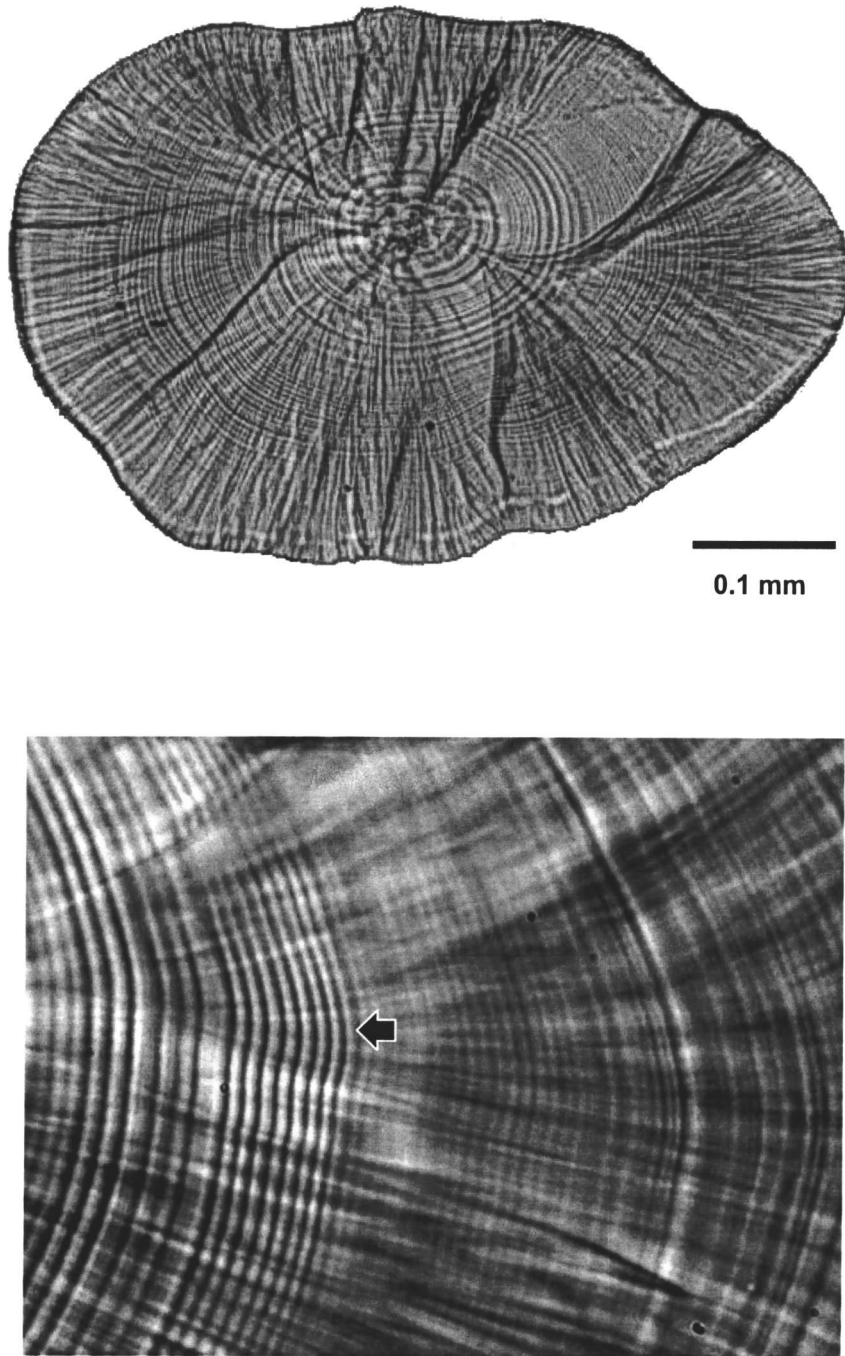


Figure 2.9. Photographs of polished asterisci from Pacific sanddab (*Citharichthys sordidus*). top: whole otolith, 43.7 mm SL stage 3. bottom: transition from high to low contrast increments, 39.2 mm SL stage 3.

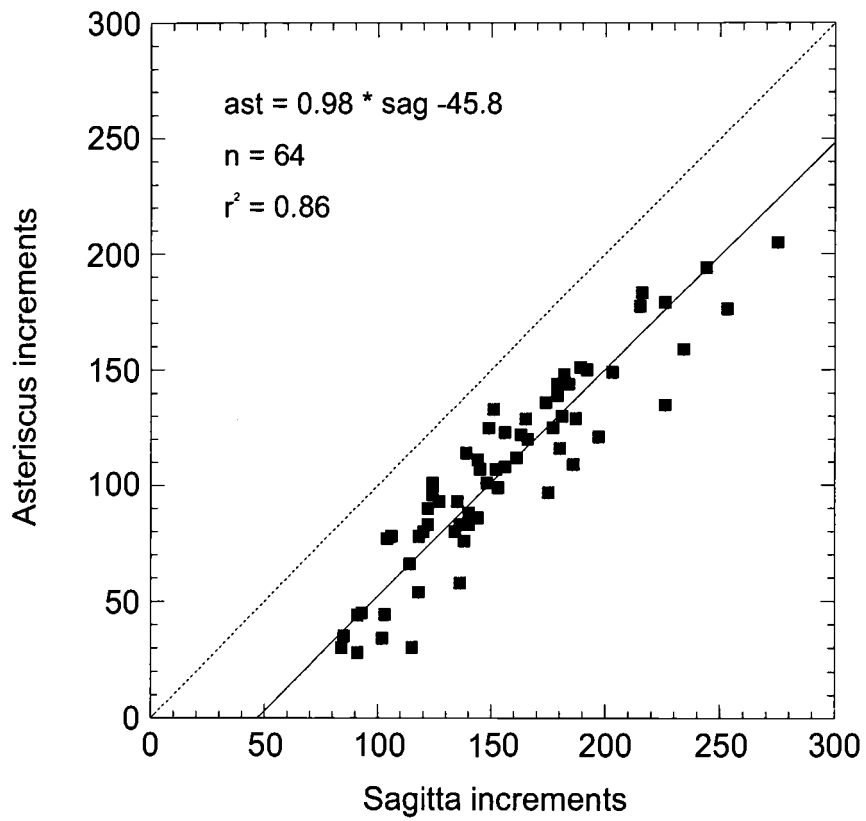


Figure 2.10. Relationship between counts of increments in the sagitta and asteriscus. The results of the GM regression and the 1:1 line are shown.

Relationships between otolith size and somatic length

Temporary increases in otolith growth rates resulted in complex relationships between otolith size and standard length. The relationships shifted twice during metamorphosis and were best described by a three segment regression model (Table 2.1). Sagitta growth rate dramatically increased relative to somatic growth at sagitta length of ~0.6 mm and standard lengths of 27-35 mm. This first shift occurred during eye migration (stages 1 and 2) and roughly coincided with the formation of the HD opaque region (Figure 2.11). Sagittae 0.6-1.4 mm long had 6-63 opaque increments (mean=25, $n=95$). Relative sagitta growth rate slowed markedly at a sagitta length of ~1.7 mm, after CEM and during metamorphosis proper (Figure 2.11). Sagitta growth slowed slightly relative to somatic growth in larger juveniles and adults. This relationship was best described by a power function. The association between standard length and sagitta length was strong in small and large fish (segments 1 and 3), but was weak during the period of rapid otolith growth ($r^2=0.16$, $n=384$, Table 2.1).

Similar though less dramatic shifts occurred in the asteriscus (Figure 2.11, Table 2.1). Asteriscus growth also increased relative to somatic growth at 27-35 mm SL and an asteriscus length of ~0.3 mm. Relative asteriscus growth rate slowed at an asteriscus length of ~0.6 mm, again after CEM and during metamorphosis proper (Figure 2.11). Asteriscus growth also slowed relative to somatic growth in larger juveniles and adults. The association between standard length and otolith length during the period of rapid otolith growth (segment 2) was stronger in the asteriscus than in the sagitta, but still relatively weak ($r^2=0.28$, $n=240$, Table 2.1).

Somatic growth

Somatic growth rates were estimated for the periods corresponding to the clear, HD opaque, and LD opaque regions of the sagitta. Individual growth rates of larvae without an

Table 2.1. Results of regressions of standard length (mm) on sagitta and asteriscus length (mm) for Pacific sanddab (*Citharichthys sordidus*). The general form of the model for each segment was $SL = a + b(OL - c_i)^d$ where c_i is the otolith length of the inflection point at the start of the segment. Simple linear regression ($d=1$) was used for segments 1 and 2.

segment	a	b	c	d	n	r^2
sagitta						
1	9.54	42.27	0	-	63	0.79
2	34.98	3.91	0.60	-	384	0.16
3	39.25	31.28	1.69	1.082	1188	0.97
asteriscus						
1	13.78	62.12	0	-	52	0.77
2	33.03	25.14	0.31	-	240	0.28
3	40.33	132.79	0.60	1.429	290	0.96

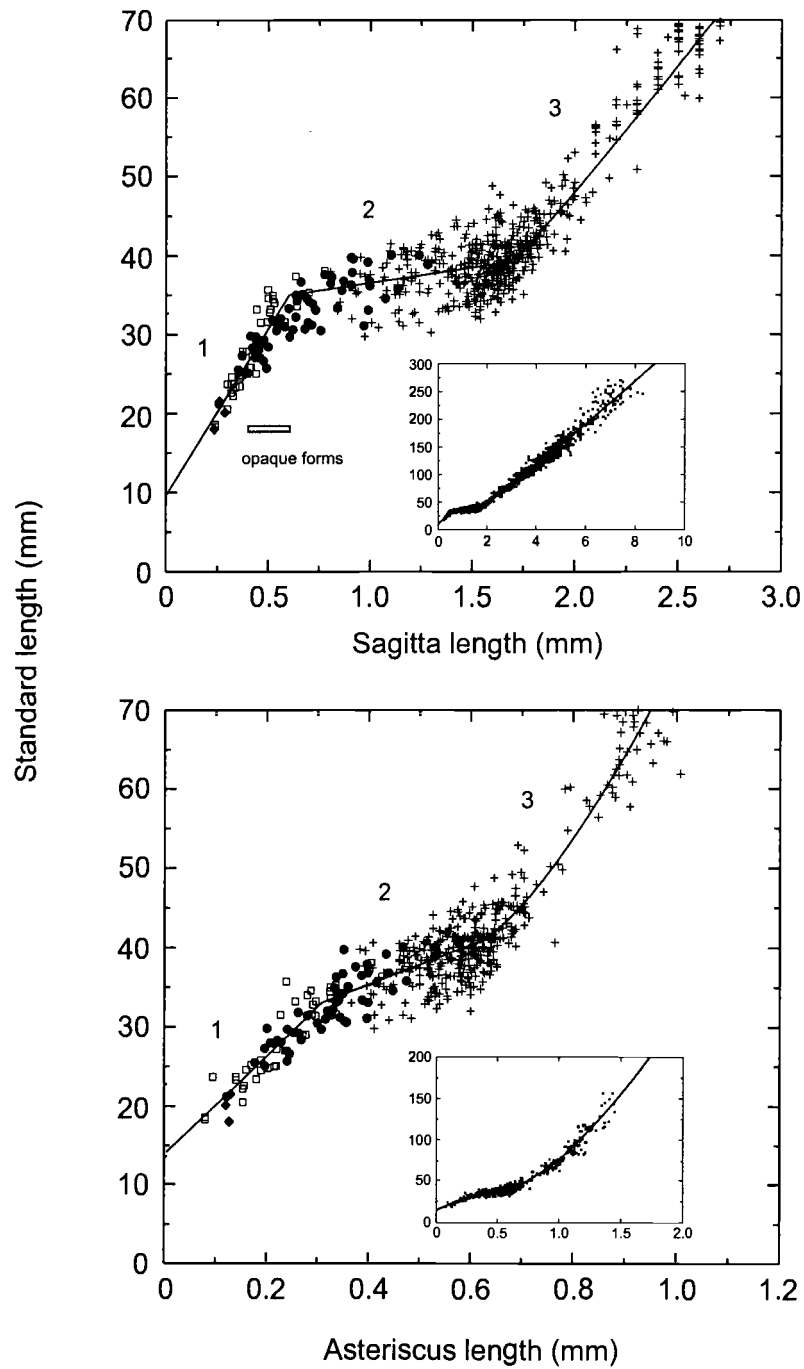


Figure 2.11. Relationship between standard length and sagitta and asteriscus length in Pacific sanddab (*Citharichthys sordidus*). Regression parameters for the three segments are shown in Table 2.1. Symbols indicate metamorphic stage: ◆ = 0, □ = 1, ● = 2, + = 3. Insets show relationships over a larger size range. Sagitta length at formation of the high density opaque region is also shown.

opaque region in the sagitta ranged from 0.14 to 0.32 mm/d (mean=0.20, cv=0.188, $n=33$). Growth rates of individuals with 1-45 opaque increments also ranged from 0.14 to 0.32 (mean=0.21, cv=0.157, $n=121$) and a regression of standard length on number of opaque increments yielded an estimated growth rate of 0.19 mm SL/d ($r^2=0.38$, $n=120$, $P<0.001$, Figure 2.7). Thus somatic growth did not appear to slow during the period of rapid otolith growth. In contrast, regression showed that standard length did not increase among individuals with 50-100 opaque increments ($r^2<0.01$, $n=98$, $P=0.98$), suggesting that somatic growth temporarily halted after the period of rapid otolith growth (Figure 2.7). This period of no somatic growth occurs after CEM and roughly coincides with metamorphosis proper (Figure 2.3). Length increased in individuals with >100 opaque increments at 0.20 mm SL/d ($r^2=0.74$, $n=77$, $P<0.001$). Overall, length increased at approximately 0.13 mm/d in individuals with >50 opaque increments ($r^2=0.57$, $n=175$, $P<0.001$).

DISCUSSION

Metamorphosis

In Pacific sanddab, eye migration begins at 16-22 mm SL and is completed at 30-42 mm SL. Fish grow 8-26 mm SL during the process, which takes 36-118 d. Other metamorphic changes (reduction in body depth (Figure 2.3), enlargement of the eye, reduction in length of the 2nd and 3rd dorsal fin rays, elongation of pectoral fins, development of pectoral fin rays, initiation of scale formation along the lateral line, and development of asymmetrical juvenile coloration) occur after eye migration is completed, in stage 3 at 30-42 mm SL. Our results show a total transformation time in Pacific sanddab of 4-5 months; eye migration takes about 3 months and other metamorphic changes take about 1-2 months.

Variation in length and age at metamorphosis was small. The coefficient of variation (CV) for length at CEM in Pacific sanddab was 0.081. The average CV for length at metamorphosis for lab-reared winter flounder was 0.051 (mean SL =8 mm), for lab-reared

starry flounder, *Platichthys stellatus*, - 0.056 (mean SL = 7 mm), and for lab-reared yellowtail flounder, *Pleuronectes ferrugineus*, - 0.128 (mean SL = 17 mm) (Policansky, 1982; Chambers and Leggett, 1987; Benoît and Pepin, 1999). Thus, variation in length at metamorphosis in Pacific sanddab was similar or less than flatfishes that metamorphose at smaller sizes.

Variation in age at metamorphosis is also remarkably similar among flatfishes; Pacific sanddab - CV=0.122, winter flounder - CV= 0.123, starry flounder - CV= 0.132, and yellowtail flounder - CV= 0.130 (Chambers and Leggett, 1987; Benoît and Pepin, 1999). Similar variation among these flatfishes is consistent with the hypothesis that variation in size and age at metamorphosis in marine fishes is generated by a common mechanism (Benoît and Pepin, 1999). Length at CEM was also less variable than age at CEM in Pacific sanddab, consistent with the hypothesis that flatfishes metamorphose when they reach a target length rather than a specific age (Chambers et al., 1988).

Pacific sanddab fit a pattern in which the duration of flatfish metamorphosis is related to size at metamorphosis. Metamorphosis takes 6 d in starry flounder which transform at 5-9 mm SL (Policansky, 1982), 1 week in winter flounder which transform at 8 mm SL (Chambers and Leggett, 1987), 15-50 d in Japanese flounder, *Paralichthys olivaceus*, which complete eye migration at 10-17 mm SL (Fukahara, 1986; Seikai et al., 1986), 30-90 d in summer flounder, *Paralichthys dentatus*, which complete eye migration at 14-21 mm SL (Keefe and Able, 1993), and 9 months to >1 year (excluding eye migration) in Dover sole, which begin metamorphosis proper at 41-58 mm SL (Markle et al., 1992; Butler et al., 1996). Pacific sanddab approach Dover sole in their size at the beginning of metamorphosis proper, 30-52 mm SL, but not in duration. Metamorphosis may take longer in Dover sole because it requires greater morphological restructuring, including a two-fold reduction in body depth and the development of an intestinal loop (Markle et al., 1992).

Because eye migration in Pacific sanddab is interrupted, the right eye is partially migrated, and larvae are asymmetrical, for an average of 3 months, about half the larval period.

Most species of flatfish metamorphose at 10-25 mm and an age of 1-2 months (Ahlstrom et al., 1984; Miller et al., 1991), a size range assumed to be pleisomorphic for the group (Hensley and Ahlstrom, 1984). In Pacific sanddab, eye migration begins within this size range (16-22 mm SL), but halts while larvae continue to grow for several months to 30-52 mm SL before completing eye migration. This pattern suggests that large size at metamorphosis in Pacific sanddab was achieved by interrupting eye migration rather than delaying its onset. A similar developmental pattern occurs in Dover sole where eye migration begins at 9-13 mm SL, halts while larvae continue to grow to 41-58 mm SL before eye migration is completed (Markle et al., 1992). In contrast, eye migration in rex sole begins at 35-50 mm SL and large size at completion of eye migration, 49-89 mm SL, (Pearcy et al., 1977) is apparently due to delay. Published figures show that the start of eye migration in some bothids that transform at large sizes (e.g. *Laeops* and *Chascanopsetta*) is also apparently delayed until larvae reach large sizes (Amaoka, 1979). Because transitional forms are often assumed to be maladapted, large size at metamorphosis would be expected to be achieved through delay rather than through interrupted eye migration. The long period of asymmetry in Pacific sanddab and Dover sole represents one way to achieve large size at metamorphosis if initiation of eye migration is unchanged from the ancestral state. The similarity in development pattern between species in different families (Pacific sanddab and Dover sole) and differences within the pleuronectids support the view that large size at metamorphosis must have evolved independently in several lines of flatfishes (Hensley and Ahlstrom, 1984).

Earlier studies report 'length at metamorphosis' in Pacific sanddab to range from 20 to >39 mm SL (Matarese et al., 1989) and 25 to 40 mm SL (Moser, 1996). These ranges appear to refer to larvae with the migrating eye on the midline, an inappropriate metric of variation given the metamorphic process described herein. Although CEM does not mark the end of metamorphosis, it is a convenient landmark. Pacific sanddab caught in our study completed eye migration at 30 to 46 mm SL, and transforming larvae up to 52 mm SL (equivalent to stage 2)

have been collected off central California (Sakuma and Larson, 1995). Thus, the length at CEM in Pacific sanddab ranges from 30 to >52 mm SL.

Counts of sagittal increments suggest that Pacific sanddab are 125-224 d or 4-7 months old at CEM. Because metamorphosis proper takes an additional 1-2 months, we estimate Pacific sanddab are approximately 5-9 months old at the start of the juvenile period. Sakuma and Larson (1995) reported that pelagic Pacific sanddab were up to 271 d old, but their sample may have included individuals well past CEM. Our estimates of age at CEM for Pacific sanddab are similar to those for speckled sanddab, *Citharichthys stigmaeus*, which also settle off Oregon and California and metamorphose at a similar length. Age at settlement in speckled sanddab, which appears to coincide with CEM, ranged from 104 to 324 d with a mode at 180-200 d (Kendall, 1993). Both *Citharichthys* studies are unvalidated, but several lines of evidence support the assumption that increment formation is daily. First, our results, based on counts of sagittal increments, show that Pacific sanddab grew an average of 0.13 mm/d after CEM. Seasonal increases in mean length also show that settled juveniles grew at 0.11 to 0.13 mm/d (Donohoe and Markle, MS [Ch. 3]). Second, spawn dates backcalculated from counts of sagittal increments agree with estimates of spawning season based on adult condition (Donohoe and Markle, MS [Ch. 3]). The general agreement of these estimates suggests increment formation in the sagitta was approximately daily. Further studies are needed to validate daily increment formation and the age at first increment formation for Pacific sanddab.

Relationship between otolith microstructure and metamorphosis

Our results show that sagitta of Pacific sanddab have 3 regions: a clear central region, AP and an associated HD opaque region, and a LD opaque region. Several species with mesopelagic early life history stages also show this pattern, including myctophids (Ozawa and Peñaflo, 1990; Gartner, 1991; Linkowski, 1991) and Dover sole (Toole et al., 1993).

Clear central region

The clear central region of the sagitta represents the early larval period. By stages, 100% of stage 0, 69% of stage 1, 28% of stage 2, and 0% of stage 3 only have a clear central region. The first AP formed at 25-32 mm SL and the HD opaque region formed at 27-35 mm SL, but eye migration began at lengths of 16-22 mm SL, well before the changes in the sagitta. Thus we detected no consistent microstructural mark associated with initiation of eye migration.

AP and associated high density opaque region

The first AP and HD opaque region formed after initiation and 2-7 weeks before completion of eye migration in Pacific sanddab sagittae. AP form in otoliths of flatfishes and several other groups of fishes during the larva to juvenile transition (Brothers, 1984). AP form as the migrating eye crosses the midline in winter flounder (Sogard, 1991) and plaice *Pleuronectes platessa* (Modin et al., 1996), and just after completion of eye migration in Dover sole (Toole et al., 1993). Flatfish AP may therefore form before, during, or after the migrating eye crosses the midline. In winter flounder and plaice, metamorphosis is rapid and completed shortly after eye migration. As a result, AP serve as valuable landmarks for the start of the juvenile period (Sogard, 1991) and can be used to backcalculate timing of metamorphosis and settlement (Alhossaini et al., 1989). In Pacific sanddab and Dover sole, metamorphosis is slower and not completed until 2-12 months after the first AP forms (Markle et al., 1992; Toole et al., 1993) suggesting that AP formation is not a universal proxy for the start of the juvenile period in flatfishes, especially those with a protracted metamorphosis.

AP formation has been attributed to either a shift in habitat (Campana, 1984b; Gartner, 1991) or to physiological changes associated with metamorphosis such as the shift in allometry in bluefish, *Pomatomus saltatrix* (Hare and Cowen, 1994). In Pacific sanddab, AP formation coincided with an increase in relative otolith growth rate (Figure 2.11). Increments within AP were much wider than increments from the central primordium. Increments within AP are also

wider than those from the central primordium in other flatfishes, (Campana, 1984b; Toole et al., 1993) and relative otolith growth rate increases at AP formation in many but not all myctophids (Ozawa and Peñaflor, 1990; Linkowski, 1991). In Pacific sanddab, growth from the central primordium also increased relative to earlier increments at AP formation and otolith growth rate also increased in the asteriscus, which lack AP. These observations suggest that sagittal AP form coincident with a general increase in overall otolith growth rate. The abrupt shift from clear to opaque increments within the central field also suggests a change in surrounding endolymph composition at AP formation. Thus AP may form because conditions that promote rapid otolith growth may also favor nucleation at new sites.

Low density opaque region

The formation of the LD opaque region and the translucent band occurred after CEM and was associated with a reduction in mean increment width from 11.7 to 2.2 μm (Figure 2.7). These features may be valuable landmarks for the start of metamorphosis proper but the transition was gradual in some specimens and the translucent band was not always present. Although otolith density was not directly compared to increment widths, the decrease in otolith density appears to reflect slowing of otolith growth. Likewise, the narrow translucent band may form in response to the temporary cessation of somatic growth and other changes in physiology associated with restructuring during metamorphosis proper. These hypotheses are consistent with the general observation that less dense or translucent regions of otoliths generally form during periods of slow growth. Conversely, the translucent band may form in response to a decrease in temperature at settlement. Many Pacific sanddab appear to settle to the middle continental shelf around CEM and start of metamorphosis proper (Donohoe and Markle, MS [Ch. 3]). Discriminating among these two hypotheses is difficult. Comparing otoliths of benthic and pelagic fish was not informative because Pacific sanddab appear to alternate between habitats during settlement. Arora (1951) noted this translucent band in Pacific sanddab

sagitta and concluded that all growth inside the band represented the pre-metamorphic period. A similar translucent band is present in sagittae of speckled sanddab *Citharichthys stigmaeus* (Kendall, 1993). The band was absent from pelagic larvae and present in recently settled juveniles and thus was interpreted as a reliable settlement mark. We suspect the translucent band is a marker for initiation of metamorphosis proper. If settlement involves a period of alternation between habitats rather than a discrete event, and if initiation of metamorphosis proper coincides with the beginning of this period, the translucent band would indeed be a useful marker.

However, the translucent band is not universally present in sagitta of Pacific sanddab. Translucent or hyaline bands are also found in sagitta of flounder, *Platichthys flesus*, and some plaice, *Pleuronectes platessa*, but are absent from most sole, *Solea solea* (Berghahn, 2000). Translucent bands in these flatfishes appear to be a stress response caused by extreme environmental conditions in intertidal portions of coastal nurseries (Berghahn, 2000). It is not clear if translucent bands in Pacific sanddab are also a response to extreme environmental conditions during settlement on middle continental shelf nurseries. But, variability in the presence or absence of the band in metamorphic, settled fish suggests that the band may not be a reliable marker of either metamorphosis or settlement. As is the case with all otolith microstructures, it is important to determine if the band is induced by internal (metamorphosis) or external (settlement) events and to determine the degree of coincidence between events.

Asteriscus

The transition from high to low contrast increments in the asteriscus occurred over the same range in otolith radius as CEM and the start of metamorphosis proper. This suggests the decrease in contrast is a response to physiological changes associated with metamorphosis proper. Abrupt decreases in increment contrast have been observed in otoliths of other fishes at time of metamorphosis and settlement (Victor, 1983; May and Jenkins, 1992; Wilson and

McCormick, 1997, 1999). These regions of low or poor contrast may be due to poor growth or stress during metamorphosis proper. Conversely, the shift from high to low contrast may represent settlement. Diel variation in temperature, such as that experienced by vertically migrating fish, has been shown to enhance increment contrast in some species (Campana, 1984a). The sharp decrease in contrast is a potentially valuable marker of metamorphosis proper or settlement. But because it was not visible in all asterisci of large juveniles, this mark is also not a reliable landmark of either event.

Relationships between otolith and somatic growth

Strong correlations between otolith size and standard length before and after metamorphosis (segments 1 and 3, Figure 2.11) indicate that it is possible to backcalculate length at age from otoliths. However nonlinear models must be used to compensate for the large shifts in the otolith-somatic relationships during metamorphosis (Laidig et al., 1991). Poor correlations during the period of rapid otolith growth (segment 2) indicate low precision for backcalculated estimates of length around the time of metamorphosis. Preliminary data suggests that some of the observed variation is due to interannual differences in the otolith-somatic relationships. It may be possible to improve precision by constructing separate relationships for each year.

Otolith growth appears to be a conservative process in Pacific sanddab. Somatic growth appeared to halt for about 50 d during metamorphosis proper. Sagitta growth slowed during this period but did not appear to halt (Figure 2.7), suggesting that sagitta and somatic growth rates are temporarily uncoupled during metamorphosis proper. Otolith growth has been shown to continue even if somatic growth has ceased (Secor and Dean, 1992). Somatic growth also ceases for ~ 60 d during metamorphosis in English sole (Rosenberg and Laroche, 1982).

The asteriscus offers few advantages and several disadvantages over the sagittae as a record of somatic growth and age. Because growth of the asteriscus is less complex than in the

sagitta, shifts in the otolith-somatic relationship were less dramatic, and the correlation during rapid otolith growth was slightly higher, the asteriscus should provide a better history of somatic growth than the sagitta. Unfortunately the first asteriscus increment does not form until well after hatching, and thus the asteriscus is not suitable for aging in Pacific sanddab.

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CHAPTER 3

Settlement, Distribution, and Abundance of Age-0 Pacific Sanddab (*Citharichthys sordidus*) on the Oregon Continental Shelf

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ABSTRACT

Depth stratified benthic surveys were conducted on the continental shelf and upper slope off central Oregon bimonthly in 1989 and in March 1990-1994 to determine patterns of settlement and depth distribution of Pacific sanddab (*Citharichthys sordidus*). Cross-shelf patterns suggest settlement was not a singular event, but a gradual transition from pelagic to benthic life. In March, larvae that had not completed eye migration occurred primarily on the upper slope and outer shelf, while more advanced stages were most abundant at depths of 80-119 m. Individuals on the middle shelf were an average of 50-60 d older than those on the upper slope, suggesting gradual inshore movement. Settled fish migrated further inshore in summer to depths of 50-99 m. The depth distribution of young-of-the-year was similar to older conspecifics, indicating there is no separate nursery area for Pacific sanddab. In 1989, settlement was highest in late fall and winter prior to the onset of upwelling, but some settlement occurred throughout the year. Recently settled Pacific sanddab captured in March were spawned from July to December and completed eye migration from December to March, supporting the conclusion of late fall and winter settlement. Abundance of recently settled fish in March was highest in 1992, due to presence of a large fall-spawned cohort absent in other years. Abundance on the upper slope and outer shelf in March was strongly correlated to onshore Ekman transport during the preceding 30 d ($r=0.91$, $P=0.013$, $n=6$) and to sea surface temperature during March surveys ($r=0.82$, $P=0.05$, $n=6$). These results suggest onshore Ekman transport can be important for fishes that do not settle nearshore or in estuaries but have nurseries on the middle shelf.

INTRODUCTION

Recruitment of most marine fishes is variable and dependent upon survival of early life history stages. Although research has focused on the early larval stage, survival of late larval and early juvenile stages may be critical determinants of year class success (Sissenwine, 1984; Peterman et al., 1988; Bradford, 1992). Survival of these early stages can be affected by numerous processes, including wind-driven surface transport of larvae. Offshore Ekman transport during the early larval period may reduce survival by carrying larvae away from nursery areas over the continental shelf (Bailey, 1981). Onshore Ekman transport appears responsible for moving late-stage larvae from offshore to nearshore and estuarine nursery areas (Nelson et al., 1977; Boehlert and Mundy, 1987). Recruitment of Dover sole, which settle to nurseries on the mid-continental shelf, has been correlated to offshore convergence of surface waters caused by unequal wind stress (Hayman and Tyler, 1980) although Toole et al. (1997) found no such relationship.

The early life history strategies of flatfishes are quite variable (Moser, 1981). Most flatfishes metamorphose at relatively small sizes of 10-25 mm SL, have short pelagic periods on the order of 1-3 months, and settle to shallow nearshore and estuarine nursery areas (Ahlstrom et al., 1984; Miller et al., 1991; Chambers and Leggett, 1992). Research on recruitment of flatfishes has focused on species with this life history strategy, and is particularly well documented for temperate flatfishes in the North Atlantic (Lockwood, 1980; Van der Veer, 1986; Bergman et al., 1988; Van der Veer et al., 1990; Beverton and Iles, 1992; Leggett and Frank, 1997). A smaller number of flatfishes transform at large sizes, have long pelagic durations, and settle to nursery areas on the mid-continental shelf (Pearcy et al., 1977; Miller et al., 1991; Markle et al., 1992; Minami and Tanaka, 1992; Toole et al., 1997). The early life history of these species, including the processes which affect settlement and recruitment to deep nurseries, are not well understood.

Pacific sanddab, *Citharichthys sordidus*, occur along the western coast of North America from Baja California to the Bering Sea (Miller and Lea, 1972). Adults inhabit the continental shelf in areas with sand substrates and are most abundant at depths of 35 to 90 m where they prey primarily on pelagic crustaceans (Demory, 1971; Pearcy and Hancock, 1978). Adults attain a maximum size of 400 mm TL and age of 10+ years (Arora, 1951; Miller and Lea, 1972) and support small but important commercial fisheries off Oregon and central California.

Adults are reported to spawn off central California from July to September with a peak in August and in Puget Sound from March to May (Smith, 1936; Arora, 1951), but small larvae are present in the plankton all year (Moser et al., 1993). Spawning occurs on the continental shelf and is centered off northern Oregon (Urena, 1989; Doyle, 1992). Eggs occur near the surface and early larvae are found deeper in the water column and are extensively dispersed offshore (Doyle, 1992). Compared to many other flatfishes, Pacific sanddab metamorphose at a large size and have a long larval period. Recent studies show that larvae complete metamorphosis at a length of 30-52 mm SL and age of 4-7 months (Sakuma and Larson, 1995; Donohoe and Markle, MS [Ch. 2]). Because the pelagic period is long, larvae are potentially advected long distances by strong alongshore currents (Strub et al., 1987).

The process of settlement in Pacific sanddab is poorly understood. Early metamorphic-staged larvae are offshore in the upper portion of the water column and appear to be vulnerable to transport, while more advanced stages occur closer to shore and deeper in the water column, perhaps in preparation for settlement (Sakuma and Larson, 1995; Sakuma and Ralston, 1995). Individuals that have completed eye migration also occur in the water column which suggests that settlement may not coincide with metamorphosis (Sakuma and Larson, 1995). The primary nursery appears to be on the continental shelf, but the depth distribution of benthic young-of-the-year has not been reported. Juveniles <120 mm SL are most abundant at 37-91 m (Demory, 1971) and individuals <70 mm SL have been collected from depths of 74-102 m (Pearcy, 1978).

Young-of-the-year Pacific sanddab generally have not been reported from bays or close to shore (Pearcy and Myers, 1974; Kramer, 1991; Yoklavich et al., 1991), but see Rogers (1985). The season of settlement has also not been determined.

Our study examines the process of settlement in Pacific sanddab. In particular, we describe the timing of spawning and settlement, cross-shelf patterns in size, age, and metamorphic stage during settlement, and the seasonal depth distribution of young-of-the-year and older conspecifics. We compare abundance of settlers during a season of transitional oceanographic conditions (March) to onshore transport to explain annual variation. From this information we describe the process of settlement in Pacific sanddab.

METHODS

Survey design

Pacific sanddab were collected from the continental shelf and upper slope off central Oregon during surveys originally designed to capture larval and juvenile Dover sole, *Microstomus pacificus* (Toole et al., 1997). Benthic fish were collected with a 27.4 m headrope, 28.5 m footrope commercial shrimp trawl composed of 34.9 mm mesh (stretched) and lined with 6.4 mm mesh in the cod end. Stratified random surveys were conducted in three transects; a northern transect off Netarts Bay, a central transect off Cape Foulweather, and southern transect off Heceta Head (Figure 3.1). Each transect was 18.5 km (10 nm) wide and oriented perpendicular to shelf isobaths. Transects were divided into 6 depth strata bounded by the 50, 80, 100, 120, 160, 220, 400 m isobaths. Benthic tows were made at randomly selected depths and locations within each stratum for five minutes along the selected isobath after paying out the pre-determined length of cable for the given depth. Because the area swept by each tow could not be estimated accurately, abundance is reported as number caught per tow. The approximate area swept by each tow was 0.005 km² (Toole et al., 1997). Rocky areas were not sampled.

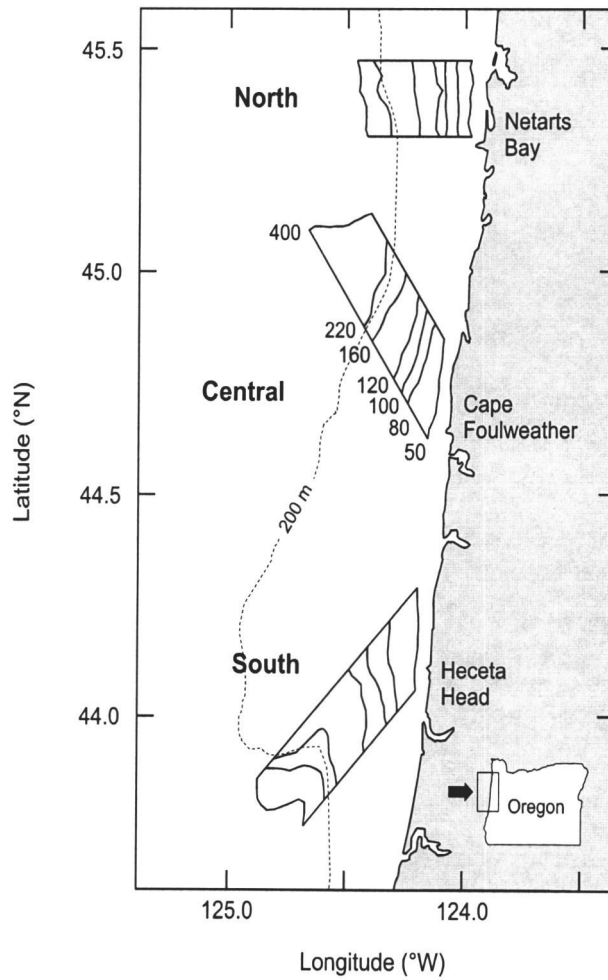


Figure 3.1. Locations of the trawl transects off the central Oregon coast. Contours are boundaries of depth strata (m).

Sampling frequency and effort differed among years. In 1989, surveys were made in January, March, May, July, September, and November in all three transects. A minimum of 3 tows was attempted in each transect and depth stratum, although the number of successful tows varied from 0 to 13 (Table 3.1). From 1990-1994, surveys were conducted primarily in March in the central transect. Additional surveys were conducted in September 1991 and February 1993 to increase seasonal and geographic coverage (Table 3.1). Sampling effort was not proportional to stratum area but was greater in the narrow midshelf strata (80-159 m) to increase the catch of recently settled flatfish. A seventh depth stratum (25-49 m) was added in 1992.

Sample processing

During the first 3 years (1989-1991), Pacific sanddab were measured at sea to the nearest centimeter total length (TL) and then discarded. Large catches were subsampled. Beginning in September 1991, all young-of-the-year and subsamples of larger, older Pacific sanddab were measured at sea and then frozen. In the laboratory, fish were thawed, standard length (SL) was measured to 0.1 mm and metamorphic stage was recorded. Fish were classified into four metamorphic stages based on the position of the right (migrating) eye: stage 0 - eyes symmetrical, stage 1 - eye beginning to migrate but right of midline, stage 2 - eye intersecting the midline, and stage 3 - eye migration complete. Individuals classified as stage 3 have not necessarily completed metamorphosis (Donohoe and Markle, MS [Ch. 2]).

Otolith preparation and analysis

We examined otoliths of benthic Pacific sanddab collected in March 1992, 1993, and 1994. In addition, we examined otoliths of 57 pelagic Pacific sanddab obtained from the annual juvenile rockfish survey conducted by NMFS scientists off central California in May 1994 using a 26 x 26 m modified Cobb midwater trawl (cruise number DSJ-9406). These pelagic fish were preserved in ethanol, but lengths were not corrected for potential shrinkage, which prior experience suggested would be small.

Table 3.1. Number of benthic tows made in each survey by transect (north, central, and south) and depth stratum

date	transect	depth stratum (m)							total
		25-49	50-79	80-99	100-119	120-159	160-219	220-400	
1989									
Jan	N		0	0	3	4	1	0	8
	C		3	2	3	13	3	1	25
	S		1	3	4	7	2	0	17
Mar	N		2	3	3	5	3	2	18
	C		2	3	3	5	3	3	19
	S		3	3	3	3	4	2	18
May	N		3	3	3	3	3	3	18
	C		3	3	3	3	3	2	17
	S		2	3	2	3	3	3	16
July	N		3	3	3	4	3	1	17
	C		3	3	4	4	3	3	20
	S		3	3	3	3	3	0	15
Sep	N		3	3	3	3	3	3	18
	C		3	3	3	3	3	3	18
	S		3	3	3	5	3	1	18
Nov	N		3	3	3	3	3	2	17
	C		3	3	3	3	3	3	18
	S		3	2	4	3	3	2	17
			46	49	56	77	52	34	314
March									
1990	C		4	4	7	5	3	5	28
1991	C		6	5	6	9	3	3	32
1992	C	6	6	7	7	3	3	3	35
1993	C	4	4	7	8	6	4	4	37
1994	C	1	5	8	11	5	5	4	39
		11	25	31	39	28	18	19	171
other									
Feb 1993	C	2	7	6	6	7	3	3	34
Sep 1991	C	5	6	7	8	3	3	3	35
	S	4	5	7	8	4	3	3	34

Sagittae were removed, cleaned of adhering tissue, and mounted in thermoplastic resin. Whole otoliths were ground in the sagittal plane on both faces to the level of the central primordium (core) to expose increments. Otoliths were ground on silica sandpaper and polished with 0.05 μm alumina powder. Increments were counted under a light microscope at 100-1000x magnification. Separate counts were made in the clear central region and the opaque outer region, but only the opaque increments were counted for pelagic fish. Increments in each sagitta were counted two times on different dates without knowledge of the size of the fish and the counts were averaged. If the counts differed by more than 15%, the otolith was read a third time and the two most similar counts were averaged. We assumed the first sagittal increment formed at yolk absorption which we estimated to be 5 days after hatching based on the development of English sole, *Pleuronectes vetulus* (Laroche et al., 1982). Age was therefore estimated by adding 5 to the total number of increments. Spawn dates were calculated by subtracting age and an additional 5 day incubation period from the date of capture. Pacific sanddab eggs are 0.78-0.84 mm in diameter (Moser, 1996). Fish eggs of this size generally hatch in 4-6 d at 8-12 °C (Pauly and Pullin, 1988).

Eye migration in Pacific sanddab is completed and metamorphosis proper begins 14-49 d after the first opaque increment forms in the sagitta (Donohoe and Markle, MS [Ch. 2]). Metamorphosis was therefore estimated to occur 30 d after the first opaque increment formed. Individual growth rates were estimated by subtracting length at hatching (2.5 mm, Moser, 1996) from length and dividing by age.

Estimates of CPUE and abundance

Individuals were assigned to either the 0 or ≥ 1 age class based on analysis of the length frequency distribution for each survey. The first size mode was generally distinct (see results). If the first size mode overlapped the second mode, individuals in the common length interval were divided equally among the two age classes. Length frequency analysis was also used to

corroborate otolith-based daily age estimates for the 1992-1994 year classes. Total lengths were converted to standard length using the equation $SL = 0.848 * TL - 1.093 \text{ mm}$ ($r^2=0.999$, $n=2911$).

The distributions of catch per unit effort (CPUE) for age 0 and age ≥ 1 Pacific sanddab were not normal. Typical of trawl data, a large proportion of the data consisted of zero catches. The distributions of the nonzero catches did not differ from lognormal for most depth strata and surveys (Kolmogorov Smirnov test, $P>0.05$). Catch data were therefore transformed by $CPUE = \ln(\text{number per tow} + 1)$. Because the distribution of log-transformed catch data also differed from normal (due to the large proportion of zero catches), means and 95% confidence intervals (CI) for the log-transformed data were estimated using the bootstrap method (Efron and Tibshirani, 1993). Although the means of log-transformed data can be biased, the mean is less sensitive to the occasional large catch. The bootstrap is a resampling method that allows estimation of a mean and CI for nonsmooth distributions of data. Parameters are estimated by drawing a random sample of size m with replacement from the original n observations. The mean is calculated for the m values and the process is repeated a large number of times (B). The sample mean and CI are then calculated in the usual manner for the resulting B bootstrap replicates. In this study, resampling for each estimate was repeated 1000 times.

Within-stratum mean CPUE was estimated using a resample size of $m=n$. Transect means (across-strata) were estimated using an extension of the bootstrap to stratified survey designs (Rao and Wu, 1988; Smith, 1997). This procedure used a resample size of $m_h = n_h - 1$ (rescaled bootstrap) to reduce bias of the variance estimate. Transect mean CPUE was estimated as the sum of the stratum mean CPUE weighted by the relative area and proportion of tows in each stratum (Cochran, 1953; Smith, 1997). Transect mean CPUE is proportional to abundance of fish within the entire transect and was used as an index of abundance. Confidence limits for within- and across-strata means were estimated using the bias corrected and accelerated (BC_a) method (Efron and Tibshirani, 1993). The bootstrap was also used to

calculate confidence limits for the average difference between two means (e.g. between depths, months, years). The two means were considered to be significantly different if the 95% confidence interval of the average difference (percentile method) did not include zero.

Statistical tests

The index of abundance of age 0 Pacific sanddab in the central transect during March 1989-94 was compared to the average daily onshore component of Ekman transport at 45 °N and 125 °W during the 30 and 90 d preceding each March survey (Bakun and Parrish, 1980). Ekman transport was calculated by U.S. Navy Fleet Numerical Meteorological and Oceanographic Center, Monterey, California and was obtained from the Pacific Fisheries Environmental Laboratory of the National Marine Fisheries Service.

Kruskal-Wallis non-parametric ANOVA was used to test for significant differences among group means for non-abundance data. Post-hoc pairwise comparison α levels were adjusted using the Bonferroni inequality. Annual means of size, age, and spawn date were weighted by stratum abundance (i.e. not sampling effort).

RESULTS

Distribution and abundance

General

The distribution of age 0 Pacific sanddab in the study area was patchy. Age 0 fish were caught in 187 of 485 tows (39%) made in 1989 and March 1990-94. The catch rate varied from 0 to 55 per tow (mean=3.1). For nonzero tows, the mean catch rate was 8.0 per tow ($n=187$). Lloyd's index of patchiness (Lloyd, 1967), ($P = 1 + (\sigma^2 - \bar{x}) / \bar{x}^2$) was 6.6 for all depth strata and 4.3 for the two strata in which settled fish were most abundant. Values of $P > 1$ indicate an aggregated distribution. Consequently, the variances associated with estimates of mean catch rates were high.

Depth distribution

Age 0

Mean CPUE of age 0 Pacific sanddab in the 3 transects in 1989 differed among depth strata in all 6 months (Kruskal-Wallis, $P=0.04$ to <0.001). Mean CPUE was highest in the 50-79 m, 80-99 m, and 100-119 m depth strata in most months, but the distribution appeared to shift with season (Figure 3.2). Age 0 fish were present in the 3 deepest strata (120-159 m, 160-219 m, and 220-400 m) in March and May. The distribution shifted inshore to depths of 50-99 m in July, then increased at depths of 100-159 m in September, suggesting some fish returned offshore.

Depths of 25-49 m were not sampled in 1989, but age 0 fish were absent from this stratum in September 1991.

Mean CPUE of age 0 Pacific sanddab in the central transect in March 1989-1994 also differed among depth strata (Figure 3.3). Differences were significant when data from all 6 years was pooled (Kruskal-Wallis, $P<0.001$). Mean CPUEs for the 6 years were highest in the 80-99 m and 100-119 m strata, lowest in the 25-49 m strata, and intermediate in remaining strata (bootstrap paired comparisons, $P<0.05$). Mean CPUE on the middle shelf was similar among years, but was more variable on the outer shelf and upper slope (Figure 3.3). Age 0 fish were absent or rare in the 160-219 m and 220-400 m strata in three years (1989, 1991, and 1993). Mean CPUE was moderate in two years (1990 and 1994), and highest in 1992, resulting in a bimodal distribution in these years.

Age ≥ 1

Depth distributions of age ≥ 1 Pacific sanddab in the 3 transects in 1989 were similar to those of age 0 fish (Figure 3.2). Mean CPUE of age ≥ 1 fish was highest in the 50-79 m, 80-99 m, 100-119 m, and 120-159 m depth strata. Age ≥ 1 fish were rare in the 2 deepest strata. It appears that age ≥ 1 fish in the 100-119 m and 120-159 m strata migrated inshore to 50-79 m

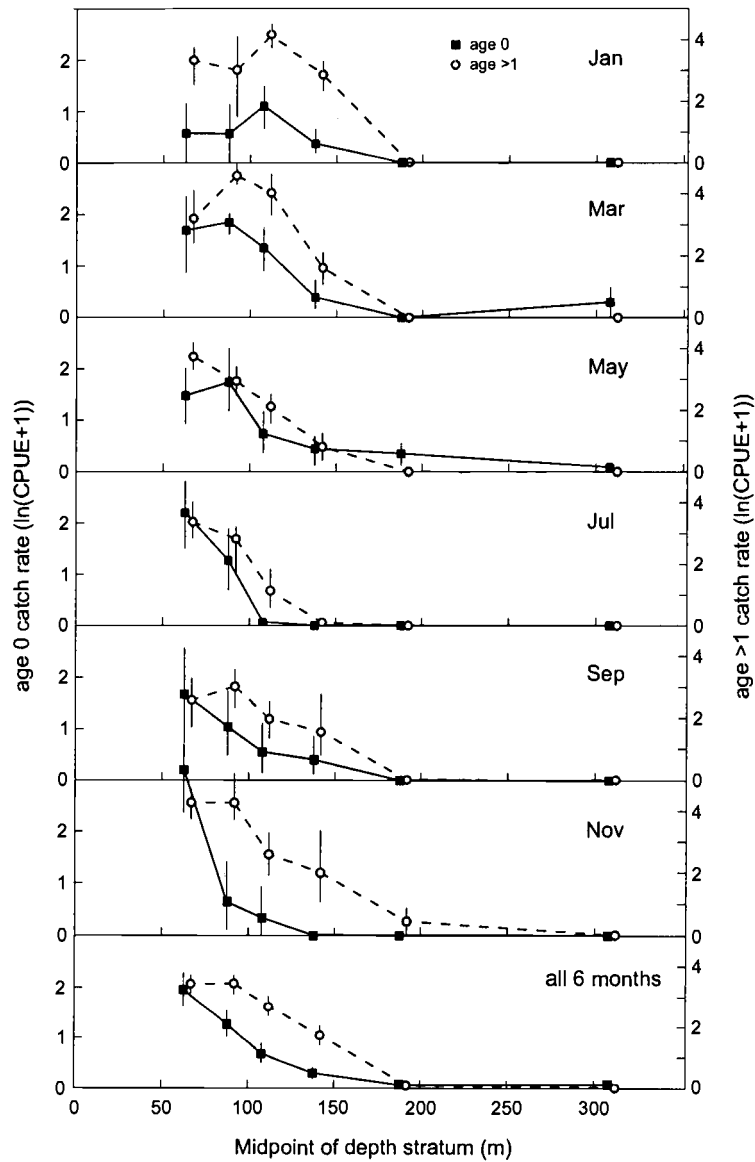


Figure 3.2. Seasonal changes in depth distribution of age 0 and age ≥ 1 Pacific sanddab (*Citharichthys sordidus*) in the 3 transects during 1989. Symbols are means and vertical lines are 95% confidence intervals.

and 80-99 m strata during the spring and summer then returned offshore in late summer and fall (Figure 3.2).

Depth distributions of age ≥ 1 Pacific sanddab in the central transect in March 1989-1994 were also similar to those of age 0 fish (Figure 3.3). Mean CPUE of age ≥ 1 fish for all 6 years (pooled) was highest in the 80-99 m and 100-119 m strata, intermediate in the two adjacent strata (50-79 m and 120-159 m) and lowest in remaining strata (bootstrap paired comparisons, $P < 0.05$). The depth distribution was slightly broader in 1993 and 1994 than in other years.

Seasonal and annual abundance

Age 0

Abundance of age 0 Pacific sanddab in the 3 transects during 1989 varied with season (Figure 3.4). Mean abundance (mean of stratum CPUEs weighted by stratum area) increased from January to a peak in March, and remained high to November. A few small fish, most likely members of the next year class, were also caught in November 1989. This pattern suggests that most Pacific sanddab settled during late fall and winter. In 1993, abundance in the central transect was low in February and significantly higher in March (Figure 3.4). Only 10 age 0 fish were caught in 34 tows in February compared to 174 fish in 37 tows in March. The low February catch suggests that most age 0 fish caught in March 1993 settled to the survey area within the previous 38 days.

Abundance of age 0 Pacific sanddab in the central transect in March differed among years (Figure 3.5). March abundance was significantly higher in 1992 than in the other 5 survey years (bootstrapped paired comparisons, $P < 0.05$). Abundance of age 0 fish was lowest in 1991, higher in 1989 and 1994, and intermediate in 1990 and 1993. High abundance in 1992 was due to higher abundance of fish on the outer shelf and upper slope (Figure 3.5). Abundance was less variable on the middle shelf.

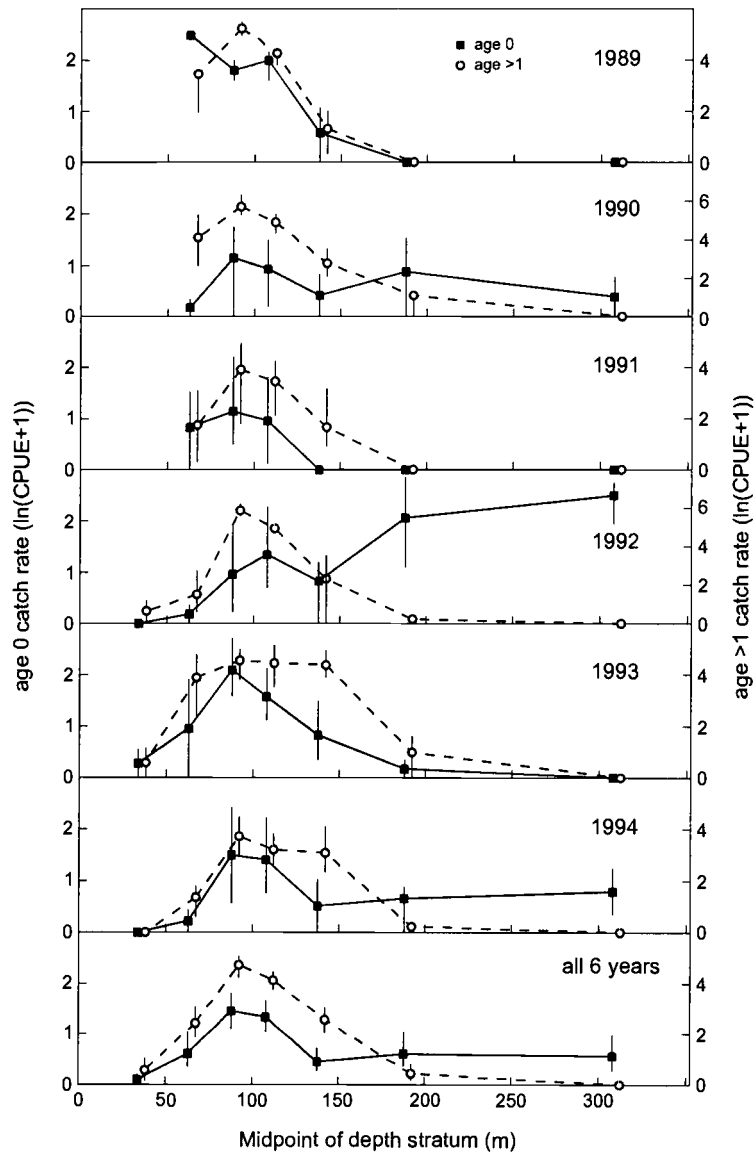


Figure 3.3. Depth distribution of age 0 and age 1 Pacific sanddab (*Citharichthys sordidus*) in the central transect in March 1989-1994. Symbols are means and vertical bars are 95% confidence intervals.

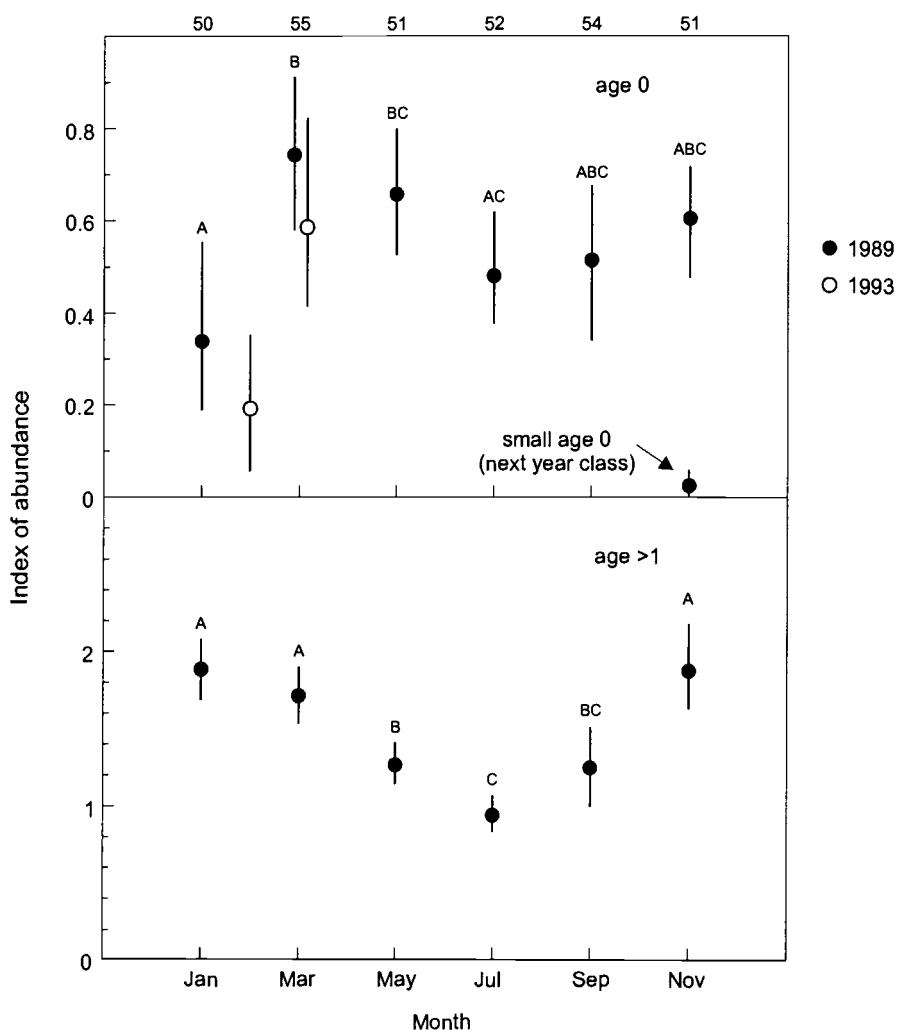


Figure 3.4. Seasonal changes in mean abundance (stratum-weighted) of age 0 and age 1 Pacific sanddab (*Citharichthys sordidus*) in the 3 transects during 1989 and in the central transect in February and March 1993. Symbols are means and vertical bars are 95% confidence intervals. Means with the same letter do not differ. Numbers of tows in 1989 are shown at top of figure.

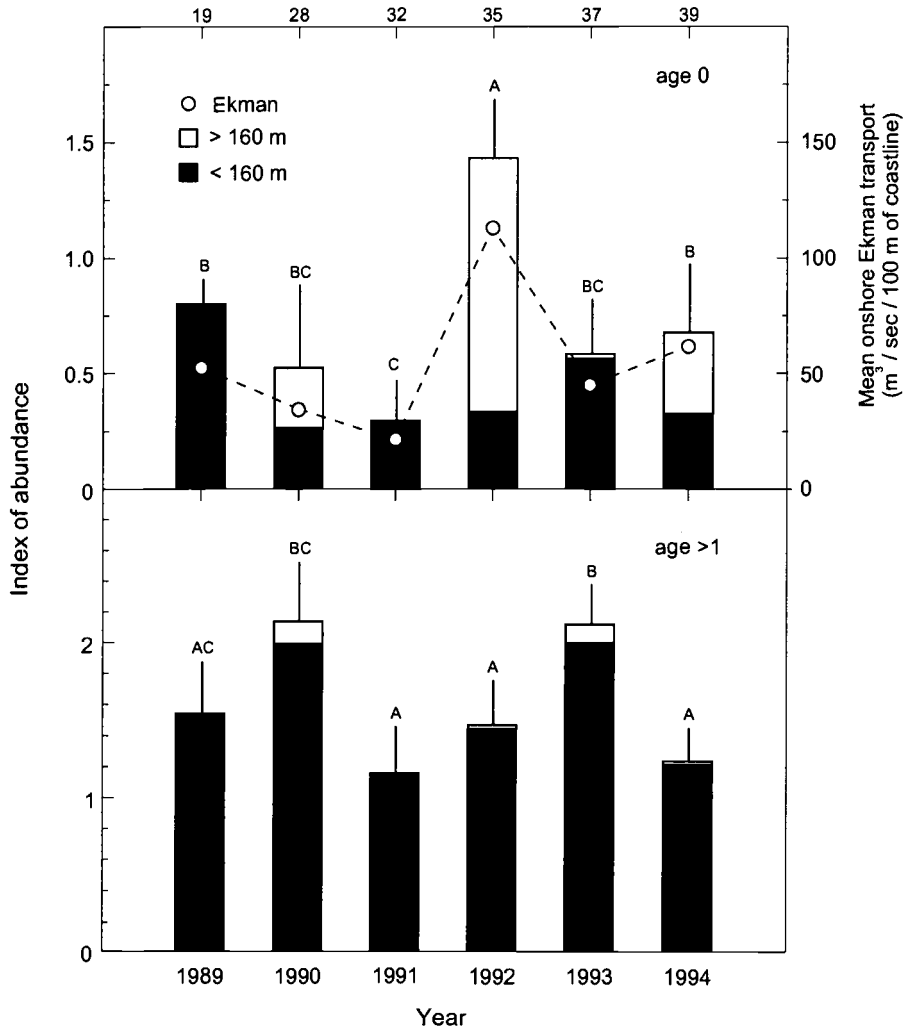


Figure 3.5. Relative abundance of age 0 and age 1 Pacific sanddab (*Citharichthys sordidus*) within middle continental shelf strata (<160 m) and outer shelf and upper slope strata (≥160 m) in the central transect in March 1989-1994. Vertical bars are 95% confidence intervals. Means with the same letter do not differ. Numbers of tows are shown. Mean onshore Ekman transport during the 30 d preceding each survey is also shown.

Age ≥ 1

Abundance of age ≥ 1 Pacific sanddab within the survey area also varied with season in 1989. Mean abundance in the 3 transects was high in January and March, decreased to a low in July, and then increased in September and November (Figure 3.4). The decline occurred in summer as the distribution of these fish shifted inshore (Figure 3.2) and may be the result of some age ≥ 1 fish moving inshore of the survey area.

March abundance of age ≥ 1 fish during 1989-1994 also differed among years. Mean abundance in the central transect was high in 1990 and 1993, lower in 1991, 1992, and 1994, and intermediate in 1989 (Figure 3.5). The high abundance of age ≥ 1 in 1993 followed the high abundance of age 0 fish in the previous year.

Relationship between abundance and environmental variables

March abundance in 1989-1994 was compared post-hoc to environmental variables in an attempt to explain annual variation. Seasonal variation in abundance (Figure 3.4) suggests that Pacific sanddab settle primarily in late fall and winter, during the 3 months prior to March surveys. Abundance of age 0 fish within the entire central transect in March was not significantly correlated with mean onshore Ekman transport at 45 °N during the 90 d prior to the survey ($r=0.68$, $P=0.13$, $n=6$, transport data not shown). However abundance on the upper slope and outer shelf (160-400 m) in March was significantly correlated to mean onshore Ekman transport during the 30 d prior to the March survey ($r=0.91$, $P=0.013$, Figure 3.5) and to mean surface temperature over the upper slope and outer shelf during March surveys ($r=0.82$, $P=0.047$, $n=6$). The relationship was driven by the high abundance on the slope in 1992. Slope abundance was also negatively correlated to survey date ($r=-0.95$, $P=0.004$, $n=6$). The 1992 survey was conducted about 1 week earlier than the 1994 survey and 2 weeks earlier than surveys in the other 4 years.

Length and age

Length frequency (at sea measurements 1989-1994)

Length of Pacific sanddab caught during all surveys ranged from 1 to 34 cm TL. The first size mode was distinct for most months (Figure 3.6 and Figure 3.7). The seasonal progression and alignment of the first size mode in 1989 clearly showed that this mode represented the first age class and suggests that spawning and/or recruitment was strongly seasonal. Modal length of age 0 fish in the 3 transects increased from January to November in 1989, but a few individuals as small as 4 cm TL (<37 mm SL) were caught in all months (Figure 3.6, Table 3.2). Mean length increased from 4.3 cm TL in January to 8.1 cm TL in November. This increase represents a linear growth rate of 0.013 cm TL/d or 0.11 mm SL/d during the first year ($r^2=0.98$, $n=6$, $P<0.001$). In 1991, mean length of age 0 fish increased from 4.6 cm TL in March to 7.4 cm TL in September, equal to a linear growth rate of 0.015 cm TL/d or 0.13 mm SL/d. Mean length of age 0 fish in March 1989-1994 ranged from 3.8 to 5.0 cm TL or 31 to 42 mm SL (Figure 3.7, Table 3.2).

Age 0 fish were often much less abundant in our collections than larger size classes suggesting that the efficiency of the trawl for age 0 fish was low (Figure 3.6 and Figure 3.7). Variation in the relative heights of the age 1 and age 2 size modes among years indicates that local recruitment was high for the 1988, 1990, and 1992 year classes (Figure 3.7).

Length, stage, and age of settling fish (March 1992-1994)

Cross-shelf pattern

Length, age, and metamorphic stage of age 0 fish showed a distinct cross-shelf pattern in all 3 years. On average, fish on the middle continental shelf were larger, further through metamorphosis, and older than fish on the outer shelf and upper slope, suggesting inshore movement of settling fish. Length of age 0 fish caught in all 3 years ranged from 13.9 to 54.8 mm SL. Fish on the outer shelf and upper slope (>160 m) ranged from 13.9 to 42.3 mm SL

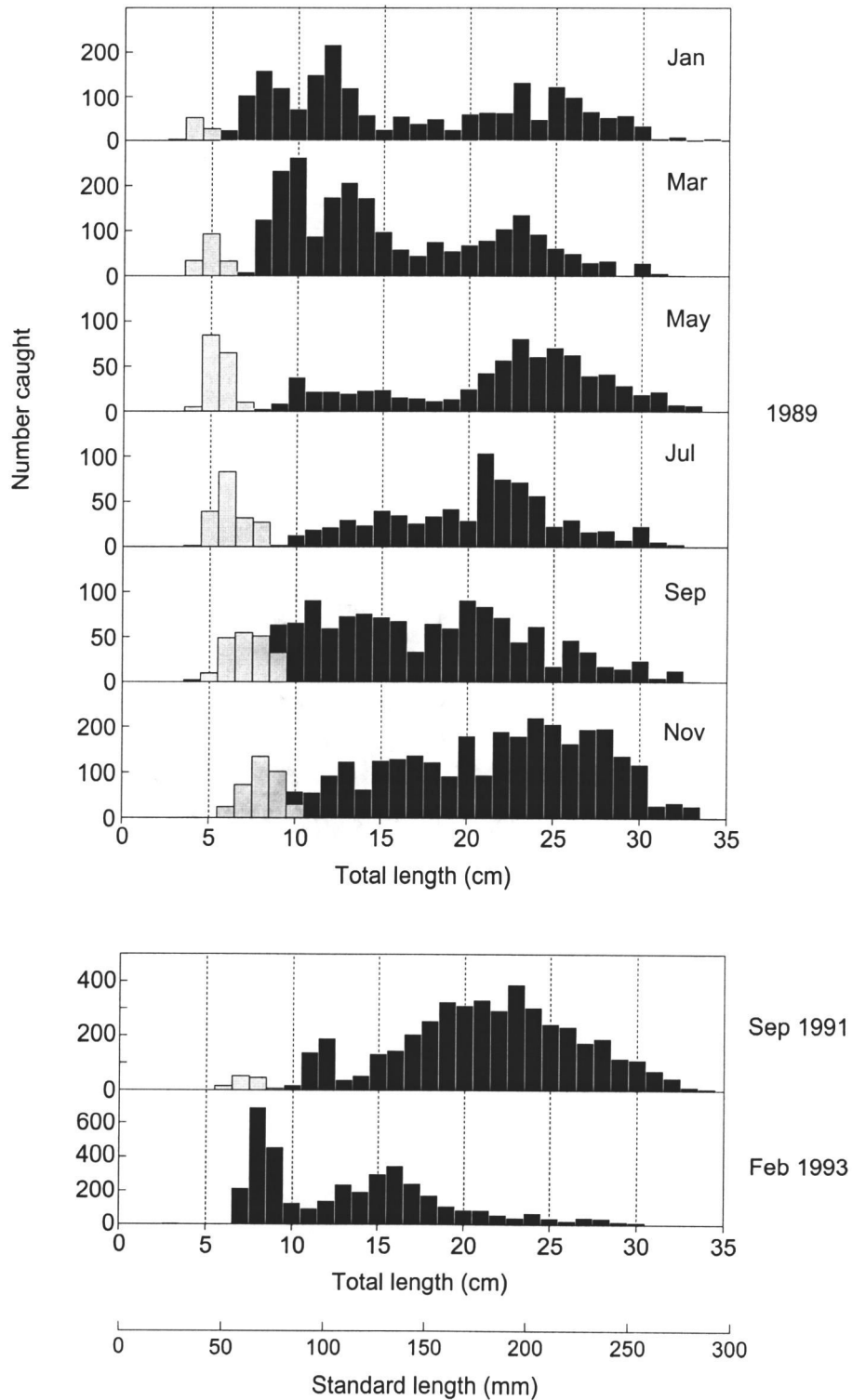


Figure 3.6. Length frequency distribution of Pacific sanddab (*Citharichthys sordidus*) caught in January to November 1989 (all 3 transects), September 1991 (central and south transects), and February 1993 (central transect). Age 0 = gray bars, age ≥ 1 = black bars. Sampling effort was not proportional to stratum area.

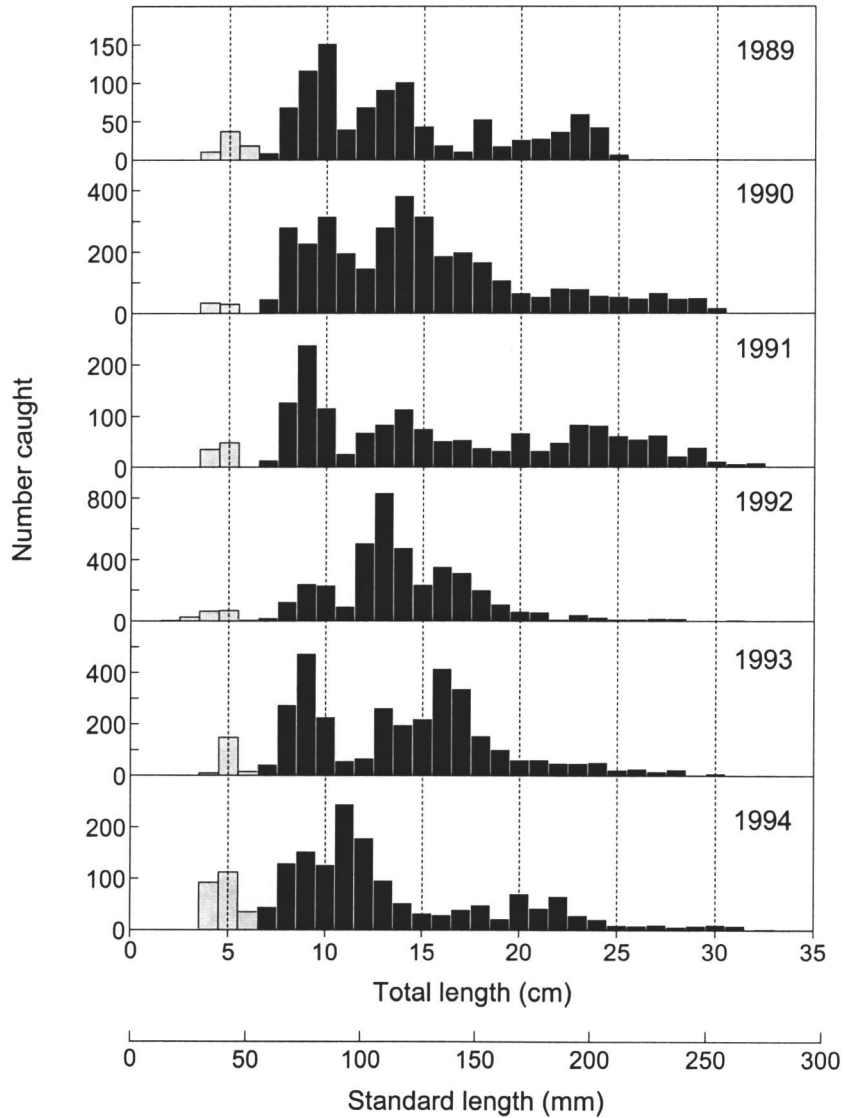


Figure 3.7. Length frequency distribution of Pacific sanddab (*Citharichthys sordidus*) caught in the central transect in March (1989-1994). Age 0 = gray bars, age ≥ 1 = black bars. Sampling effort was not proportional to stratum area.

Table 3.2. Length frequency distributions of age 0 Pacific sanddab (*Citharichthys sordidus*) based on measurements at sea for A) January to November 1989 in the 3 transects, and B) March 1989 to 1994 in the central transect. Mean lengths were weighted by stratum area.

TL (cm)	1989					
	Jan	Mar	May	Jul	Sep	Nov
3	2					
4	52	34	5	1	3	2
5	26	93	85	39	10	
6		33	65	83	49	24
7			10	32	55	73
8				27	51	135
9					32	102
10						29
mean TL (cm)	4.3	4.9	5.5	6.3	7.2	8.1
mean SL (mm)	35	41	45	52	60	67
n	80	160	165	182	200	365

TL (cm)	March					
	1989	1990	1991	1992	1993	1994
2				8		
3				24		2
4	10	34	35	65	9	92
5	37	30	48	68	149	112
6	18	2		10	16	35
mean TL (cm)	5.0	4.6	4.6	3.8	5.0	4.7
mean SL (mm)	42	38	38	31	42	39
n	65	66	83	175	174	241

(mean=30.3, $n=85$) and those on the middle continental shelf (<120 m) ranged from 30.3 to 52.9 mm SL (mean=39.5, $n=426$). Mean length differed among depth strata in all 3 years, but differences were small in 1993 and 1994 (Kruskal-Wallis, $P<0.01$, Figure 3.8). In 1992, fish on the middle shelf were an average of 9.8 mm larger than those from >160 m (Kruskal-Wallis, $P<0.001$).

Fish on the middle shelf tended to be older than those in deeper water (Figure 3.9). Age of settling fish on the outer shelf and upper slope ranged from 78 to 196 d (mean=138, $n=51$) and those on the middle shelf ranged from 125 to 268 d (mean=200, $n=167$). Mean age progressively increased from deep to shallow strata in all 3 years. Fish caught in the shallowest stratum were an average of 63, 59, and 48 d older than those from the deepest stratum (Kruskal-Wallis, $P<0.05$).

Fish on the middle shelf were also further through metamorphosis (Table 3.3). Over 97% of settling fish on the middle shelf had completed eye migration (stage 3). In contrast, over 90% of settling fish on outer shelf and upper slope were stage 0 to stage 2. It should be noted that most of the stage 0 - stage 2 larvae were caught in one year, 1992. Differences in otolith microstructure also show that fish on the middle shelf were further through metamorphosis. Opaque regions were present in sagittae of all fish on the middle shelf, but only 48% of fish on the outer shelf and upper slope. In addition, the mean number of opaque increments in the sagitta increased from deep to shallow strata in all 3 years (Kruskal-Wallis, $P<0.001$, Figure 3.10). Means increased from 5 to 63 increments in 1992, from 22 to 103 increments in 1993, and from 16 to 80 increments in 1994.

Annual variation

Mean length, metamorphic stage, mean age, and mean growth rate of settling fish differed among years. On average, age 0 Pacific sanddab caught in 1992 were smaller, less advanced, and younger than those caught in 1993 and 1994. These differences were mainly due

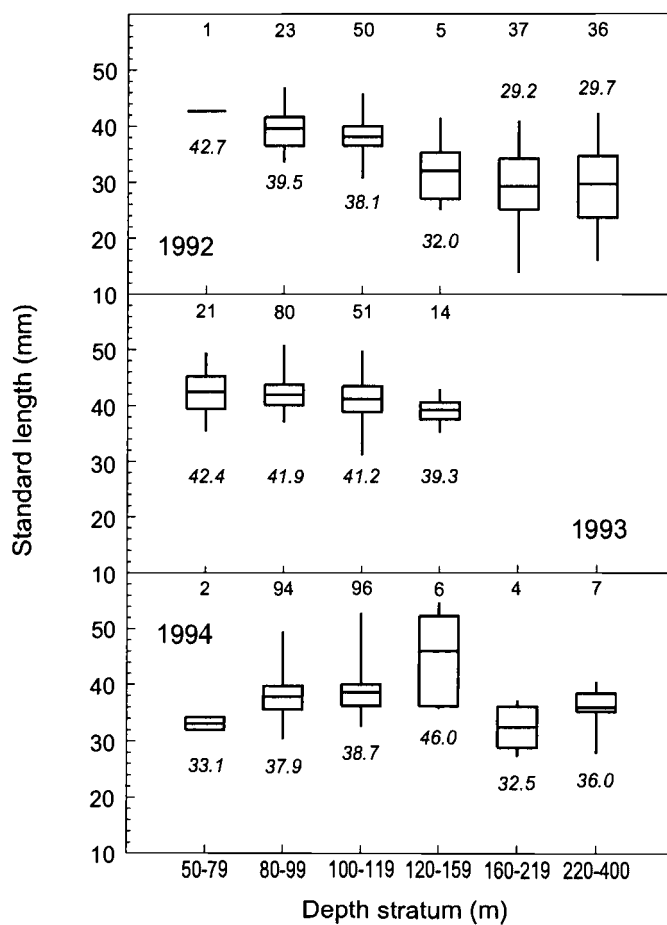


Figure 3.8. Length distribution of age 0 benthic Pacific sanddab (*Citharichthys sordidus*) in the central transect in March 1992, 1993, and 1994 by depth stratum. Horizontal lines are the mean, boxes enclose 50% of observations, vertical bars are the range. Means and numbers of fish at each depth are shown.

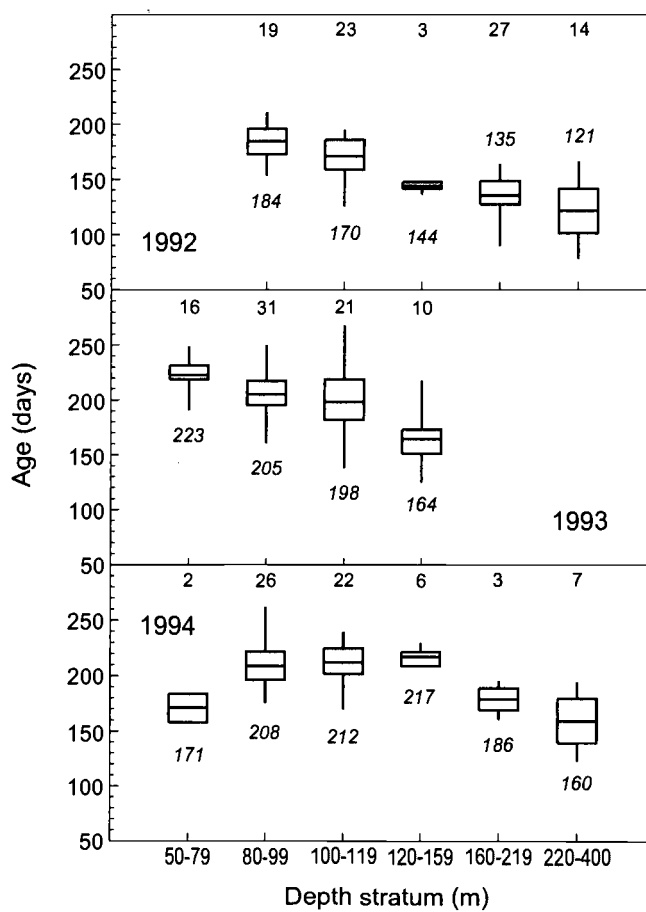


Figure 3.9. Age distribution of benthic Pacific sanddab (*Citharichthys sordidus*) in the central transect in March 1992, 1993, and 1994 by depth stratum. Horizontal lines are the mean, boxes enclose 50% of observations, vertical bars are the range. Means and numbers of fish at each depth are shown.

Table 3.3. Percentage of age 0 Pacific sanddab that had completed eye migration by depth stratum for surveys in March 1992, 1993, and 1994. Number of fish in each stratum is shown in parentheses.

year	depth stratum (m)							n
	25-49	50-79	80-99	100-119	120-159	160-219	220-400	
1992			100 (19)	96 (48)	20 (5)	8 (37)	9 (34)	143
1993	100 (1)	100 (20)	99 (80)	94 (51)	86 (14)	0 (1)		167
1994		100 (2)	99 (98)	100 (93)	100 (6)	0 (4)	14 (7)	199
all 3 years	100	100	99	97	76	7	10	520

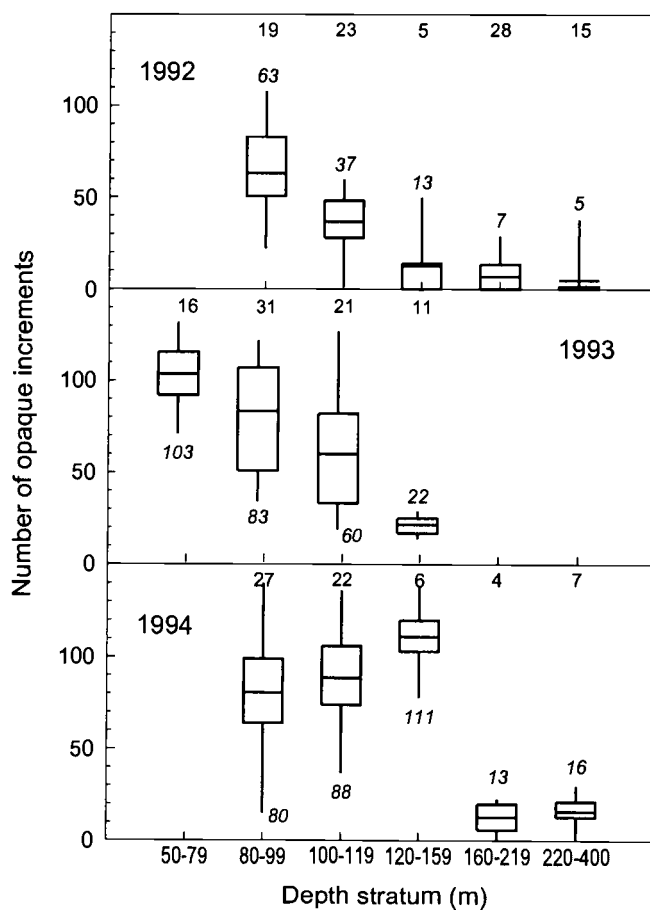


Figure 3.10. Number of opaque increments in sagittae of benthic Pacific sanddab (*Citharichthys sordidus*) in the central transect in March 1992, 1993, and 1994 by depth stratum. Horizontal lines are the mean, boxes enclose 50% of observations, vertical bars are the range. Means and numbers of fish at each depth are shown.

to the presence of small, young fish on the upper slope and outer shelf in 1992 (Figure 3.11 and Figure 3.12). Catch data showed that age 0 fish were abundant on the slope in March 1992 but not in other years, with only one caught on the slope in 1993 (Figure 3.5). Interannual differences in length of fish on the middle shelf (<160 m) were smaller. Mean length of fish on the middle shelf in the three years was 38.2, 41.5, and 38.5 mm SL. Fish were significantly larger in 1993 than in 1992 and 1994 (Kruskal-Wallis, $P < 0.001$). Mean length of fish on the outer shelf and upper slope in 1992 was 29.5 mm SL, about 9-12 mm SL less than those on the middle shelf (Figure 3.11). Mean age of fish on the middle shelf in the three years was 174, 202, and 211 d (Figure 3.12). Therefore fish on the middle shelf in 1993 and 1994 were an average of one month older than in 1992 (Kruskal-Wallis, $P < 0.001$). Mean age of fish on the outer shelf and upper slope in 1992 was 130 d or an average of 44-81 d less than those on the middle shelf. Mean growth rate of Pacific sanddab with fewer than 50 opaque increments from all depths did not differ between 1992 and 1993 but was lower in 1994 (Kruskal-Wallis, $P = 0.004$). Mean growth rates in the three years were 0.214 ($n = 67$), 0.213 ($n = 28$), and 0.184 mm/d ($n = 18$).

Spawn dates

Counts of sagittal increments show that age 0 Pacific sanddab caught in March 1992-1994 were spawned over a 6 month period, from June to December (Figure 3.13). Mean spawn date for fish from all depth strata (weighted by stratum abundance) differed among all 3 years (Kruskal-Wallis, $P < 0.001$). The weighted mean spawn dates for the 3 years were 9 October 1992, 24 August 1993, and 11 August 1994, or about 6 and 8 weeks later in 1992 than in 1993 and 1994. Mean spawn date was later in 1992 due to the presence of a large group of fall-spawned fish on the outer shelf and upper slope (Figure 3.13). Mean spawn dates for fish on the middle shelf (<160 m) differed by 4 weeks, ranging from 4 August to 4 September (Kruskal-Wallis, $P < 0.001$). In contrast, fish on the outer shelf and upper slope in 1992 were spawned an

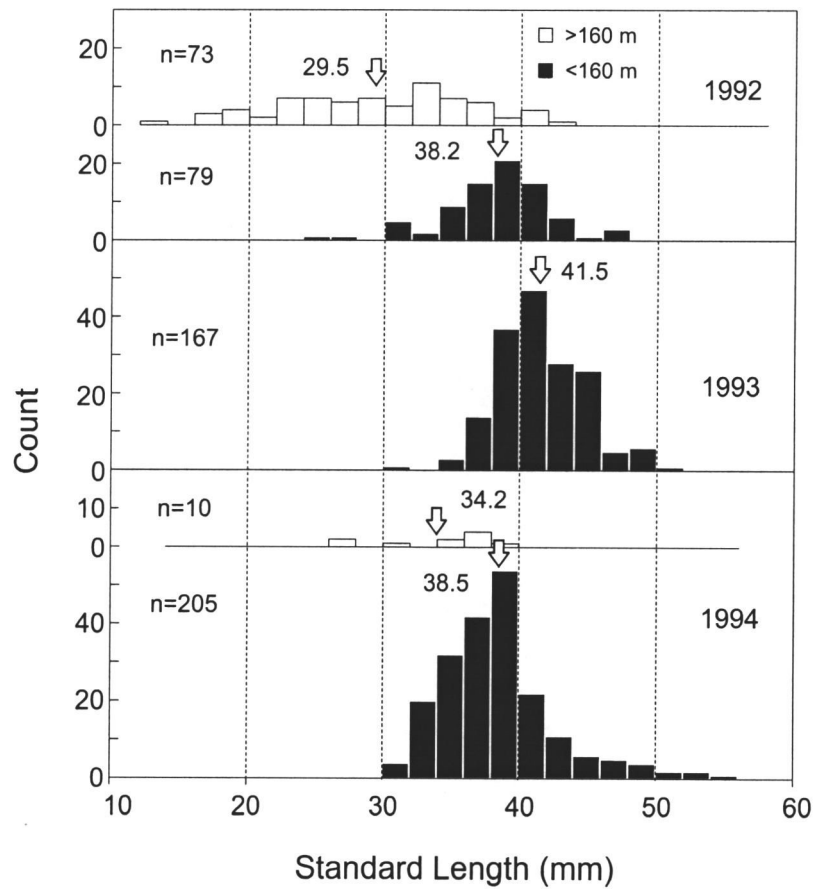


Figure 3.11. Length-frequency distributions of age 0 Pacific sanddab (*Citharichthys sordidus*) caught on the middle continental shelf (<160 m) and the outer shelf and upper slope (>160 m) in the central transect in March 1992-1994. Mean lengths are shown.

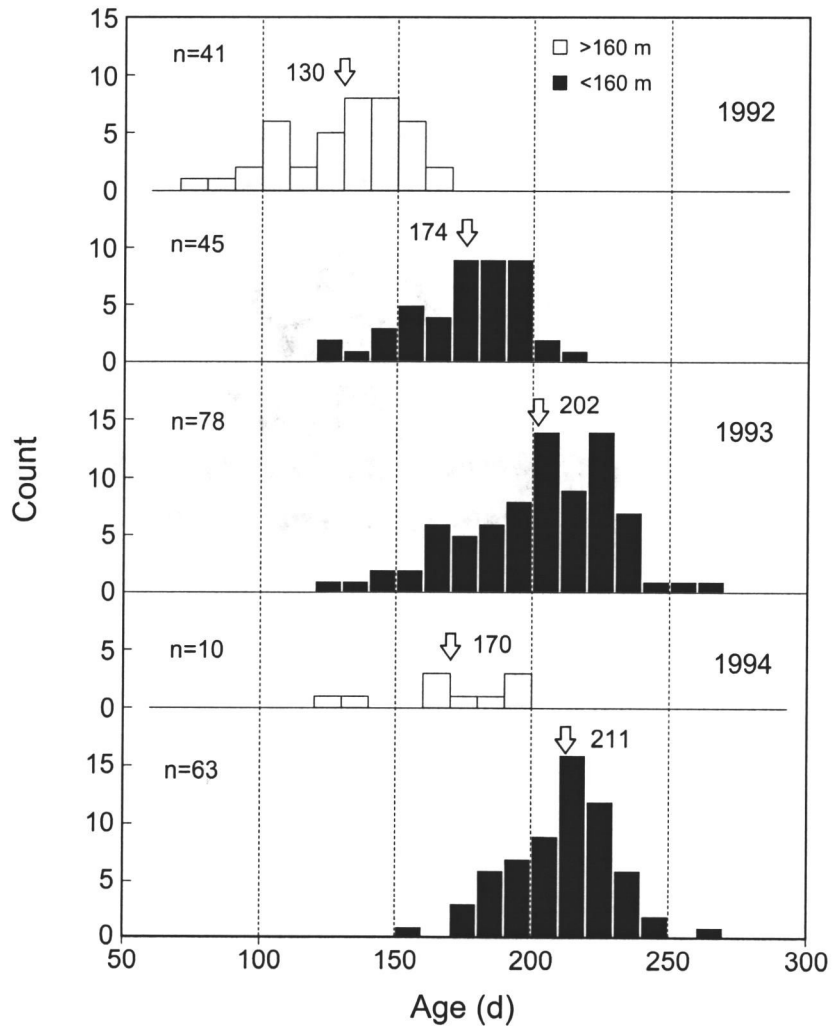


Figure 3.12. Age distributions of age 0 Pacific sanddab (*Citharichthys sordidus*) caught on the middle continental shelf (<160 m) and outer shelf and upper slope (>160 m) in the central transect in March 1992-1994. Mean ages are shown.

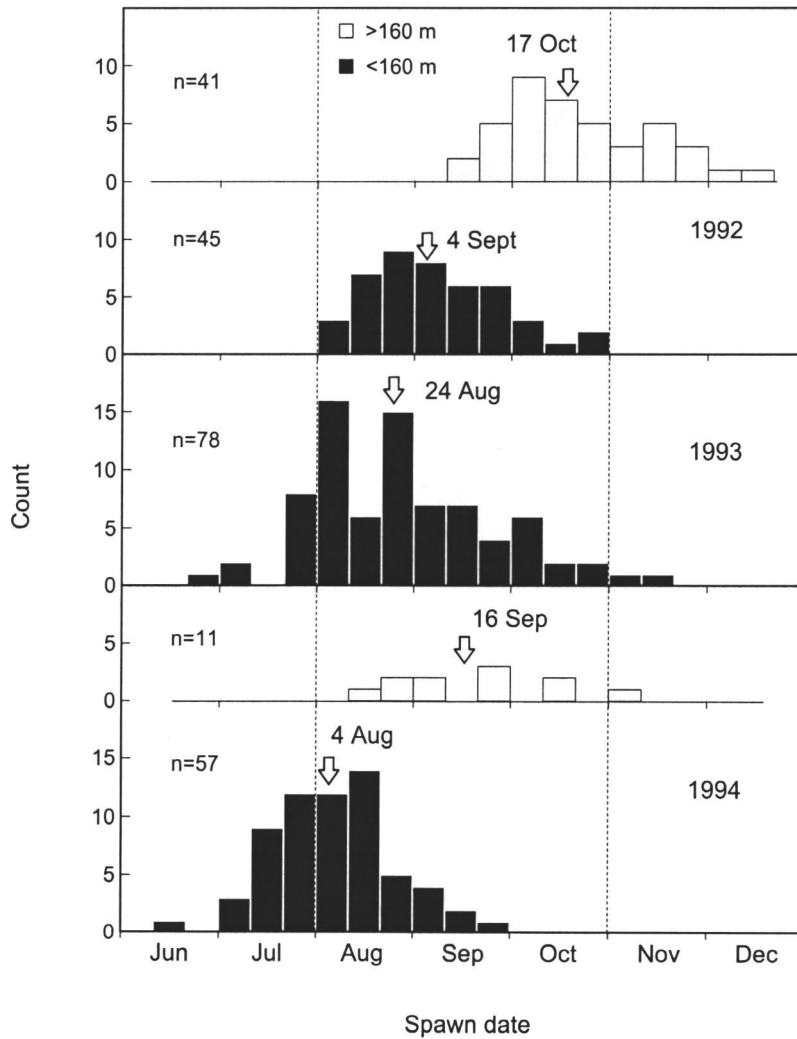


Figure 3.13. Spawn date distributions for age 0 Pacific sanddab (*Citharichthys sordidus*) caught on the middle continental shelf (<160 m) and the outer shelf and upper slope (>160 m) in March 1992-1994. Arrows indicate mean spawn date.

average of 6, 8, and 10 weeks later than those on the middle shelf in 1992, 1993, and 1994 (Figure 3.13). Mean spawn date for the small group of fish on the upper slope in 1994 was about 2, 3, and 6 weeks later than those on the shelf.

Date of metamorphosis

Metamorphosis (completion of eye migration) was estimated to begin 30 d after the first opaque increment formed in the sagitta. The approximate date of metamorphosis ranged from November to after April for Pacific sanddab caught in March 1992-1994 off central Oregon (Figure 3.14). Metamorphosis occurred later in 1992 than in 1993 and 1994. In 1992, metamorphosis occurred primarily from February to April, but the opaque region had not yet formed in half of settling fish. In 1993 and 1994, the distribution of dates was bimodal with peaks in December-January and March. The date of metamorphosis was later in pelagic Pacific sanddab collected in May and June 1994 off central California. In these fish, metamorphosis occurred from March to July, but the opaque region had not yet formed in a third of the sampled fish.

DISCUSSION

Spawning season

Recently settled Pacific sanddab caught in March off central Oregon were spawned from July to December, a wider range than suggested by spawning condition of adults. Arora (1951) examined adult Pacific sanddab off California and concluded spawning occurs from July to September with a peak in August. More recent studies of larval abundance off Washington, Oregon, and California indicate that Pacific sanddab spawn all year (Urena, 1989; Moser et al., 1993; Sakuma and Ralston, 1995; Moser, 1996). Our data and the literature indicate protracted, seasonally-biased spawning. Because our surveys were conducted in March and the larval period lasts 4-7 months, fish spawned after September would be under-represented in our benthic samples. However, the distinct size modes we observed for age 0 and age 1 Pacific

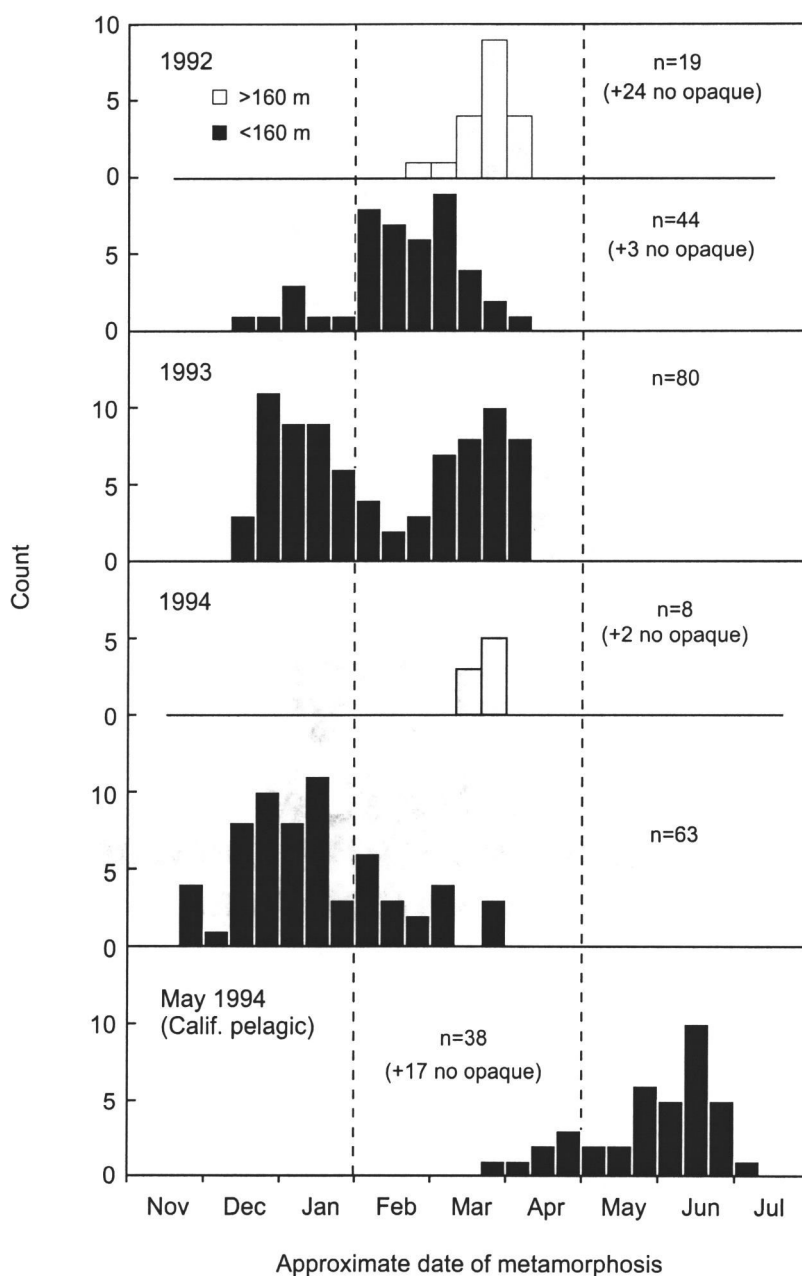


Figure 3.14. Approximate date of metamorphosis for Pacific sanddab (*Citharichthys sordidus*) taken in benthic collections off central Oregon in March 1992, 1993, and 1994 and pelagic collections off central California in May-June 1994. Metamorphosis was estimated to occur 30 d after the first opaque increment formed in the sagitta. The opaque region had not yet formed in a significant proportion of fish caught in March 1992 and May-June 1994.

sanddab in most years (Figure 3.6 and Figure 3.7) suggest that successful recruits were produced by seasonal spawners with a peak in late summer.

Settlement season

Seasonal increases in abundance from before January to March 1989 suggest that most Pacific sanddab settle off Oregon during winter (Figure 3.4). The large increase in abundance from February to March 1993 also suggests peak settlement in winter. Most age 0 Pacific sanddab caught in March 1992-1994 completed eye migration from December to March (Figure 3.14). If settlement coincides with metamorphosis (see below), then the timing of metamorphosis supports the conclusion of late fall and winter settlement. Because Pacific sanddab move inshore after initially landing on the upper slope, the presence of age 0 fish in the 220-400 m stratum in May 1989 (Figure 3.2) and of small individuals (4 cm TL or 29-37 mm SL) from July to November 1989 (Table 3.2), suggest limited settlement off Oregon during summer and fall. Seasonal peaks in abundance of pelagic larvae of Pacific sanddab also suggest a smaller settlement peak in late spring. Abundance of early larvae off northern California and Oregon is highest in late fall with a smaller peak in mid-spring (Urena, 1989). Early larval Pacific sanddab are present in the plankton off California and Baja California in all months, with a seasonal peak in abundance from August to October and a smaller peak in January and February (Moser et al., 1993). Our age data show Pacific sanddab are about 6 months old at settlement (Figure 3.9). If the pelagic larvae in the above studies are about 1 month old, settlement would peak from January to March with a smaller peak from June to July. Our results and the literature from pelagic surveys of Pacific sanddab suggest that settlement, like spawning, is protracted and seasonally-biased. Peak settlement is in winter with lower settlement in spring and summer and minor settlement in summer and fall. Latitudinal and annual variation in timing of settlement probably occur.

Depth of the nursery

Our surveys show that age 0 Pacific sanddab are most abundant between 80-119 m in March and between 50-99 m in summer and fall. Because our surveys did not extend inshore of 50 m, age 0 fish may be abundant further inshore during summer and fall. No previous study has specifically examined the depth distribution of age 0 Pacific sanddab. However, juvenile Pacific sanddab <120 mm SL were concentrated at 37-110 m in February and moved inshore to 18-73 m in May (Demory, 1971).

Age 0 Pacific sanddab migrated inshore between May and July, as did older age classes of Pacific sanddab (Figure 3.2) and other flatfishes. Recently settled Dover sole move inshore from 100-159 m in March to 50-79 m between May and July and older Dover sole move inshore between March and May (Demory, 1971; Pearcy, 1978; Toole et al., 1997). Small and large size classes of butter sole (*Pleuronectes isolepis*), slender sole (*Eopsetta exilis*), rex sole (*Errex zachirus*), and English sole (*Pleuronectes vetulus*) also migrate inshore in late spring (Demory, 1971). Demory's data show that all these species moved about 20 fa (37 m) shallower even though the center of their depth distributions ranged from 65 to 160 m. Toole et al. (1997) hypothesized that recently settled Dover sole move inshore to avoid predators such as Pacific hake and sablefish or to move into more productive inshore waters. Hayman and Tyler (1980) suggested the outer shelf provided better feeding and environmental conditions for recently settled Dover sole and these fish move inshore as their requirements changed. The widespread nature of the spring migration suggests fish move inshore in response to a common variable, one that affects several species, size classes, and a broad range of depths. Inshore migrations coincided with spring decreases in bottom temperature during seasonal upwelling, but differences in temperature among isobaths on the middle shelf appear to be small (Huyer, 1977).

Process of settlement

Movement from upper slope to middle shelf

Increases in size, metamorphic stage, and age from deep to shallow strata suggest that Pacific sanddab land on the upper slope and outer shelf and then move further inshore and settle to the middle shelf (Figure 3.8 -Figure 3.10, and Table 3.3). Overall, these cross-shelf patterns suggest that the process of settlement in Pacific sanddab is not a singular event, but a gradual transition from pelagic to benthic life.

Stage 0 to stage 2 larvae occurred almost exclusively on the outer shelf and upper slope while stage 3 fish were caught primarily on the middle shelf (Table 3.3). Stomachs of several larvae from the outer shelf contained sand and shelled gastropods, evidence these fish had been on the bottom. In addition, sagittae of most Pacific sanddab on the outer shelf and upper slope had <30 opaque increments while most on the middle shelf had >30 (Figure 3.10). Because completion of eye migration occurs about 14-49 d after the opaque region forms (Donohoe and Markle, MS [Ch. 2]), these patterns suggest that Pacific sanddab land on the upper slope prior to completion of eye migration then move inshore and settle to the middle shelf at about the time they complete eye migration. However, settlement to the middle shelf may not always coincide with metamorphosis. The low abundance of Pacific sanddab in the February 1993 survey (Figure 3.4) suggests that nearly all age 0 fish captured in March 1993 had settled within the previous 38 d. The fact that many of these fish appear to have completed eye migration in December and January (Figure 3.14) suggests that some Pacific sanddab delay settlement and remain in the water column for a few months after completing eye migration. Alternatively, fish caught in March 1993 may have settled outside of our survey area in December and January and migrated into it after February. Unfortunately, we cannot differentiate between these two possibilities. If settlement does not always coincide with completion of eye migration, the first opaque increment in the sagitta may not be a reliable proxy for settlement.

Progressive increases in mean age from deep to shallow strata suggest that settling Pacific sanddab take an average of 50-60 d to move from the upper slope to the middle shelf. Similar cross-shelf transit times have been reported in other fishes. Larval gulf menhaden *Brevoortia patronus* take 40-74 d and sand seatrout *Cynoscion arenarius* take 30-94 d to cross the shelf to estuarine nurseries in the Gulf of Mexico (Shaw et al., 1988).

Pacific sanddab may move from the upper slope to middle shelf either along the bottom or by re-entering the water column. Our surveys show that Pacific sanddab ranging from 14 to 55 mm SL occurred on the bottom, with stage 0 - stage 2 larvae on the slope and outer shelf and stage 3 fish on the middle shelf. Pacific sanddab in this same size range and stage of development also occur in the upper 30 m of the water column, with more advanced stages occurring closer to shore (Sakuma and Larson, 1995). This broad overlap in sizes combined with the offshore-onshore pattern in metamorphic stages suggest that Pacific sanddab alternate among habitats as they move inshore to the middle shelf. Sand was present in the stomachs of many large pelagic Pacific sanddab (Donohoe and Markle, MS [Ch. 2]) which confirms that some fish re-enter the water column after settling. Food habits indicate that small Pacific sanddab continue to enter the water column long after reaching the middle shelf. Juveniles 50-100 mm SL feed on pelagic crustaceans (Percy and Hancock, 1978) and adults feed on pelagic fishes (Kravitz et al., 1976).

Settling Dover sole also alternate between the pelagic and benthic habitats as they move across the upper slope to a nursery on the middle shelf (Markle et al., 1992; Toole et al., 1997). Markle et al. (1992) suggested the upper slope functions as a 'landing zone' for settling Dover sole on their way to the nursery on the middle shelf. The upper slope appears to serve the same function for settling Pacific sanddab. Settling Pacific sanddab may descend in the water column to test the bottom for the nursery and ascend to take advantage of onshore currents in the upper water column. Unlike fishes that settle nearshore or in estuaries, fishes with nurseries on the

middle shelf must periodically descend as they move toward shore to avoid overshooting the nursery.

Movement from offshore to continental shelf

Prior to settlement, early stage Pacific sanddab larvae occur offshore beyond the continental shelf (Doyle, 1992; Sakuma and Ralston, 1995). Metamorphic-staged larvae occur in the upper 110 m of the water column at night, but are most abundant in the upper 30 m (Sakuma and Larson, 1995), placing them in or near the surface Ekman layer. Our results show that abundance of age 0 Pacific sanddab on the upper slope and outer shelf in March 1989-1994 was correlated with onshore Ekman transport during the previous 30 d (Figure 3.5). A period of 30 d is an appropriate temporal window because larvae do not appear to accumulate on the upper slope, but continue inshore. This correlation suggests that movement of Pacific sanddab larvae from offshore to the continental shelf is facilitated by surface Ekman transport. Previous studies have shown that onshore Ekman transport is important for fishes settling to inshore and estuarine nursery areas. Recruitment of Atlantic menhaden, *Brevoortia tyrannus*, was correlated to onshore Ekman transport during the larval period (Nelson et al., 1977). The abundance of English sole, *Pleuronectes vetulus*, settling to Yaquina Bay, Oregon was also related to onshore Ekman transport (Boehlert and Mundy, 1987). In contrast, Myers and Drinkwater (1989) found no relationship between Ekman transport and recruitment in 8 stocks in the Northwest Atlantic. Our results suggest that onshore Ekman transport can be important for fishes that do not settle nearshore or in estuaries but have nurseries on the middle shelf.

Settling Pacific sanddab may use multiple mechanisms to move inshore. Although Pacific sanddab settling off Oregon in winter appear to use surface Ekman transport to move inshore, late larvae are present and presumably settle in areas and at times when surface Ekman transport is reduced or predominantly offshore. Surface Ekman transport during fall and winter is predominantly onshore off Oregon and Washington, but it is weak or offshore off California

(Parrish et al., 1981). Late larval Pacific sanddab are common off central California in May and June during the upwelling season when surface Ekman transport is predominantly offshore.

These fish may use one or more alternate mechanisms to move inshore. During the upwelling season, there are periods when alongshore winds weaken, allowing surface waters to relax and move onshore. These relaxation events appear to transport invertebrate larvae to the intertidal zone (Farrell et al., 1991), and may transport Pacific sanddab larvae inshore as well.

Alternately, settling Pacific sanddab may move shoreward in the weaker subsurface onshore return flow that occurs during active upwelling (Smith, 1981; Sakuma and Ralston, 1995).

Peterson et al. (1979) proposed that certain species of copepods use this subsurface return flow to maintain the population within the upwelling region. Some pelagic juvenile rockfishes also move deeper in the water column during upwelling, presumably to avoid offshore advection in the surface layer (Lenarz et al., 1991). In addition, swimming may be an important mode of onshore movement for settling Pacific sanddab. Early juvenile bluefish, *Pomatomus saltatrix*, swim over 100 km across the shelf to estuarine nurseries (Hare and Cowen, 1996). Late pelagic stages of reef fishes are also capable of sustained swimming (Stobutzki and Bellwood, 1997).

Late larval Pacific sanddab are large and probably capable of sustained swimming. We suspect that Pacific sanddab larvae swim and exploit both surface and subsurface transport. Further studies needed to determine the importance of these mechanisms for fishes settling to nurseries on the continental shelf.

Our results and the literature suggest that shoreward movement of Pacific sanddab is initiated by a change in vertical migration behavior of late stage larvae. Stage 0 to stage 2 larvae make small vertical migrations, moving up in the water column at night and deeper during the day (Sakuma et al., 1999). Diel vertical migration has been observed in many species of flatfishes including yellowtail flounder, *Limanda ferruginea* (Smith et al., 1978), sand sole, *Psettichthys melanostictus* (Boehlert et al., 1985) and stone flounder, *Kareius bicoloratus* (Yamashita et al., 1996). Vertical migrations of larvae typically become more

extensive as fish grow and develop (Smith et al., 1978; Neilson and Perry, 1990; Brodeur and Rugen, 1994). We propose that Pacific sanddab make larger vertical migrations during late stage 2, moving both higher and deeper in the water column. Such an increase in the amplitude of vertical migrations by Pacific sanddab would result in an increase in mean depth with metamorphic stage, consistent with the observed pattern (Sakuma and Larson, 1995). A few stage 1 or stage 2 larvae have been captured in midwater at depths of 200 to >500 m (W.G. Pearcy, unpublished data). Migrations to depths of >400 m would explain the presence of late larvae on the upper slope as they move inshore.

Slope abundance was also correlated with surface temperature in the study area during March and with survey date. Higher temperatures can affect abundance by increasing larval growth rate and reducing stage duration and mortality (Houde, 1987). However mean growth rates were the same in 1992 and 1993 suggesting that the high abundance in 1992 was not due to a shorter larval period. We suspect that the direct influence of temperature was small and that the observed correlation merely reflects the transport of warm offshore water onto the shelf and upper slope. The high age 0 abundance in 1992 does not appear directly related to the 1992-93 El Niño because these conditions did not develop off northern California and Oregon until March (Lenarz et al., 1995). High abundance in March 1992 is also not an artifact of earlier sampling because the high abundance persisted and resulted in a large year class (Figure 3.7).

Early life history strategy of Pacific sanddab

Although in different families, the early life history strategy of Pacific sanddab is remarkably similar to two pleuronectids that occur off Oregon and transform at a large size. Spawning in Pacific sanddab peaks in summer to early fall, fish are pelagic for 4-7 months, complete metamorphosis at 30-52 mm SL, and settle to depths of 80-119 m in late fall and winter prior to the onset of upwelling. Dover sole are spawned primarily in winter and spring

off Oregon, are pelagic for 9 months to 2 years, metamorphose at 49-79 mm SL, and settle to depths of 100-159 m on the shelf in winter (Markle et al., 1992; Butler et al., 1996; Toole et al., 1997). Rex sole (*Errex zachirus*) also spawn in winter and spring, metamorphose at 49-89 mm SL, are pelagic for about 1 year, and settle to depths of 150-200 m on the shelf off Oregon in winter (Hosie and Horton, 1977; Pearcy et al., 1977). Larvae of all 3 species are advected offshore. Although the season of spawning and length of the larval period differs, all three species settle off Oregon in winter during seasonal onshore transport. This pattern is consistent with the hypothesis that the life history strategies may be timed to use onshore Ekman transport to return to the shelf from further offshore (Parrish et al., 1981).

The large size at metamorphosis and long pelagic period in Pacific sanddab may be related to settlement in deep water. Flatfishes that settle to deep nurseries or live deep generally metamorphose at large size and have long pelagic periods (Minami and Tanaka, 1992). Moser (1981) noted that flatfishes with large larvae often have broader geographic ranges suggesting an adaptation to increase dispersal. Large size at metamorphosis is also advantageous if food abundance is low or if large predators occur in the nursery area (Minami and Tanaka, 1992). Moser (1981) also suggested that species with long pelagic phases may have a broader window for settlement and metamorphosis, increasing the probability of settlement success. The settlement process in these species appears to require coupling of a behavioral change with a seasonally predictable oceanographic process. Because the strength and duration of Ekman transport is variable, the strategy resembles the "lottery" strategy of tropical reef fishes (Sale, 1978), especially in Pacific sanddab where the strategy is coupled to protracted seasonally-biased spawning. The result of the spawning strategy is protracted seasonally-biased settlement with metamorphically competent Pacific sanddab available for settlement all year but the majority available when the probability of onshore Ekman transport is highest. Protracted, seasonally-biased spawning could result if timing of spawning was age related, such that younger fish spawning early or late in the season have a greater probability of producing

successful recruits. A better understanding of size, age, and season of reproduction in Pacific sanddab would facilitate understanding the impacts of a fishery on this unusual life history strategy.

Summary

In summary, settlement in Pacific sanddab is not a singular event but a gradual transition from pelagic to benthic life. Peak settlement off Oregon is in late fall and winter and coincides with onshore transport. Movement from offshore to the continental slope appears to be facilitated by onshore Ekman transport when it is available, but can occur when transport is absent or offshore, possibly by subsurface transport or swimming. The upper slope and outer shelf serve as a landing zone for Pacific sanddab as they move inshore to the nursery. Settlement to the middle shelf generally coincides with metamorphosis, but some fish may delay settlement. The nursery is located between 80-119 m in late winter and shifts inshore to <50-99 m in summer. Because age 0 Pacific sanddab occur at the same depths as older age classes, commercial fisheries that target adults may affect young-of-the-year.

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CHAPTER 4

Ontogenetic and Individual Variation in Otolith Microchemistry of Two Recently-Settled Flatfishes, Dover Sole (*Microstomus pacificus*) and Pacific Sanddab (*Citharichthys sordidus*)

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ABSTRACT

Concentrations of Ca, Sr, Cl, Na, K, and P in otoliths of settling Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*) were measured with a wavelength dispersive electron microprobe to determine if cross-otolith patterns represent an environmental record of settlement and inshore movement and to test for fixed differences that could be used to discriminate among settling cohorts. Transects across otoliths revealed strong, consistent trends in concentrations of Sr, K, and P in both species and of Ca in Dover sole. These trends explained an average of 74% of the variation in Sr, 46% of the variation in K, 59% of the variation in P, and 50% of the variation in Ca in individual fish. None of the 6 elements showed a consistent shift in concentration at settlement, although P increased in about half of Pacific sanddab at settlement. Cross-otolith patterns in Sr concentration did not correspond to thermal experience or to known patterns of otolith and somatic growth. Element concentrations at the margin were not related to depth or temperature at capture (<17% of observed variation explained), but concentrations of Cl (both species) and K (Dover sole) near the otolith margin were strongly correlated with levels near the core ($r=0.78$ to 0.87) which indicated an individual (perhaps genetic) effect present early in life. Margin concentrations of these elements differed among groups of fish caught as little as 5-8 km apart, potentially indicating meso-scale patchiness at settlement. If these patchy distributions resulted from patchy settlement, this implies that groups of fish (cohorts) tended to remain together during the pelagic period and settle together. This result is surprising given the 9 month to 2 year pelagic period of Dover sole.

INTRODUCTION

Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*) are commercially important flatfishes that occur along the western coast of North America from Baja California to the Bering Sea (Miller and Lea, 1972). Larvae are pelagic and occur offshore beyond the edge of the continental shelf (Pearcy et al., 1977; Doyle, 1992). Dover sole are pelagic for 9 months to 2 years (Markle et al., 1992; Butler et al., 1996) and Pacific sanddab for 4-7 months (Donohoe and Markle, MS [Ch. 3]). Patterns of larval drift have not been determined, but larvae are probably transported long distances by strong seasonal alongshore currents (Strub et al., 1987; Markle et al., 1992). Although the process of settlement is not fully known, larvae of both species appear to temporarily settle to the outer shelf and upper slope, then move shoreward to nursery areas on the mid-shelf (Markle et al., 1992; Toole et al., 1997; Donohoe and Markle, MS [Ch. 3]). Details of the settlement process have been difficult to infer from survey data because individuals settle over a wide size range and a period of several months (Markle et al., 1992; Toole et al., 1997). Otolith landmarks that serve as rough proxies for settlement have been identified (Toole et al., 1993; Donohoe and Markle, MS [Ch. 2]), but these have been insufficient tools for resolving the exact timing and depth of settlement and subsequent movements of individuals.

Otolith microchemistry may provide valuable information about the settlement process. Sagittal otoliths are composed primarily of calcium carbonate in the aragonite form (Degens et al., 1969), but numerous elements are also incorporated into the otolith matrix. Concentrations of these elements can be influenced by environmental conditions at the time of deposition (Radtke and Shafer, 1992). Because the otolith grows each day and otolith material is not resorbed or reworked after deposition (Campana and Neilson, 1985), the otolith may contain a detailed record of environmental experience.

Element concentrations in otoliths have been shown to vary with several environmental variables including temperature (Radtke, 1989; Townsend et al., 1995), salinity (Secor et al.,

1995), and water chemistry (Mugiya et al., 1991). Element concentrations in some soft tissues covary with concentrations in sediments (Hanson, 1997). Element concentrations in otoliths also vary with ontogenetic variables such as size or age (Edmonds et al., 1992; Hoff and Fuiman, 1993; Campana and Gagne, 1994) and growth rate (Kalish, 1989; Sadovy and Severin, 1992, 1994). In addition, genotype may influence element concentrations, as concentrations at the otolith core, which generally forms before hatching, can differ among fish from different geographic regions (Campana and Gagne, 1994; Thresher et al., 1994) and concentrations often vary greatly among individuals reared under identical conditions (Hoff and Fuiman, 1995). These studies suggest a first order model of element concentration:

$$C_{\text{concentration}} = E_{\text{environment}} + O_{\text{ontogeny}} + G_{\text{genotype}} + \epsilon_{\text{error}},$$

that is, the concentration of an element in the otolith is dependent upon the combined influences of environment, ontogeny, genotype, and random variation. The relative importance of these four factors and their interaction terms are likely to vary among elements and species.

Variation in otolith composition has been interpreted primarily in two ways. Cross-otolith variation has been used to infer the temperature histories of individual fish (Radtke, 1989; Townsend et al., 1989, 1995; Radtke et al., 1990) and the timing of migrations among habitats (Tzeng and Tsai, 1994; Radtke et al., 1996; Secor and Piccoli, 1996). Otolith Sr/Ca ratios in Dover sole vary during early life with a minimum around settlement (Toole et al., 1993). These studies suggest otolith composition of Dover sole and Pacific sanddab may vary in response to settlement. Because metamorphosis and settlement do not coincide in Dover sole (Markle et al., 1992), it may be possible to discriminate between the influence of these two events on otolith microchemistry. An elemental settlement mark, combined with otolith age information, would allow precise estimation of the timing of settlement for individual fish.

Differences in otolith composition or 'elemental fingerprints' among geographic groups of fish have been used to infer or confirm stock or population structure (Mulligan et al., 1987; Edmonds et al., 1989, 1992; Campana and Gagne, 1994; Campana et al., 1994). Although these

differences may be genetic or environmental, these studies suggest otolith composition may differ among cohorts and allow identification of geographic structure within a settling year class. The scale of this structure may allow inferences about the scale of the processes controlling settlement and recruitment.

In this study, we examined otolith composition of two species of flatfish during settlement. The specific goals were to 1) characterize elemental variation in the otoliths of Dover sole and Pacific sanddab, 2) determine if cross-otolith patterns in element concentrations represent an environmental record of settlement and inshore movement, 3) determine if there are inherent (fixed) differences in otolith composition among individuals, and if so to 4) use these inherent differences to determine if there is small-scale geographic structure within the settling year class. Our primary approach was to compare natural variation in element concentrations to life history events and environmental conditions at time of capture. A secondary approach was to evaluate the influence of sediments on element concentrations in a laboratory experiment.

MATERIALS AND METHODS

Collections

Settling Dover sole (47-70 mm SL) and Pacific sanddab (23-42 mm SL) were collected at 22 stations on the continental shelf and upper slope off central Oregon at depths of 88-357 m (Figure 4.1, Table 4.1). Most stations (A to Z) were located within a 700 km² area off Cape Foulweather, just north of Newport. Two stations (1 and 2) were located ~100 km to the south, off Heceta Head. At each station, a single benthic tow was made with a 27.4 m commercial shrimp trawl lined with 6.4 mm mesh in the cod end. Tow duration was short, so that fish in each haul were caught within 300 m of one another. Most fish were collected in March 1992 and frozen at sea. Live Dover sole and sediments were collected in February 1993 for a laboratory experiment (see below).

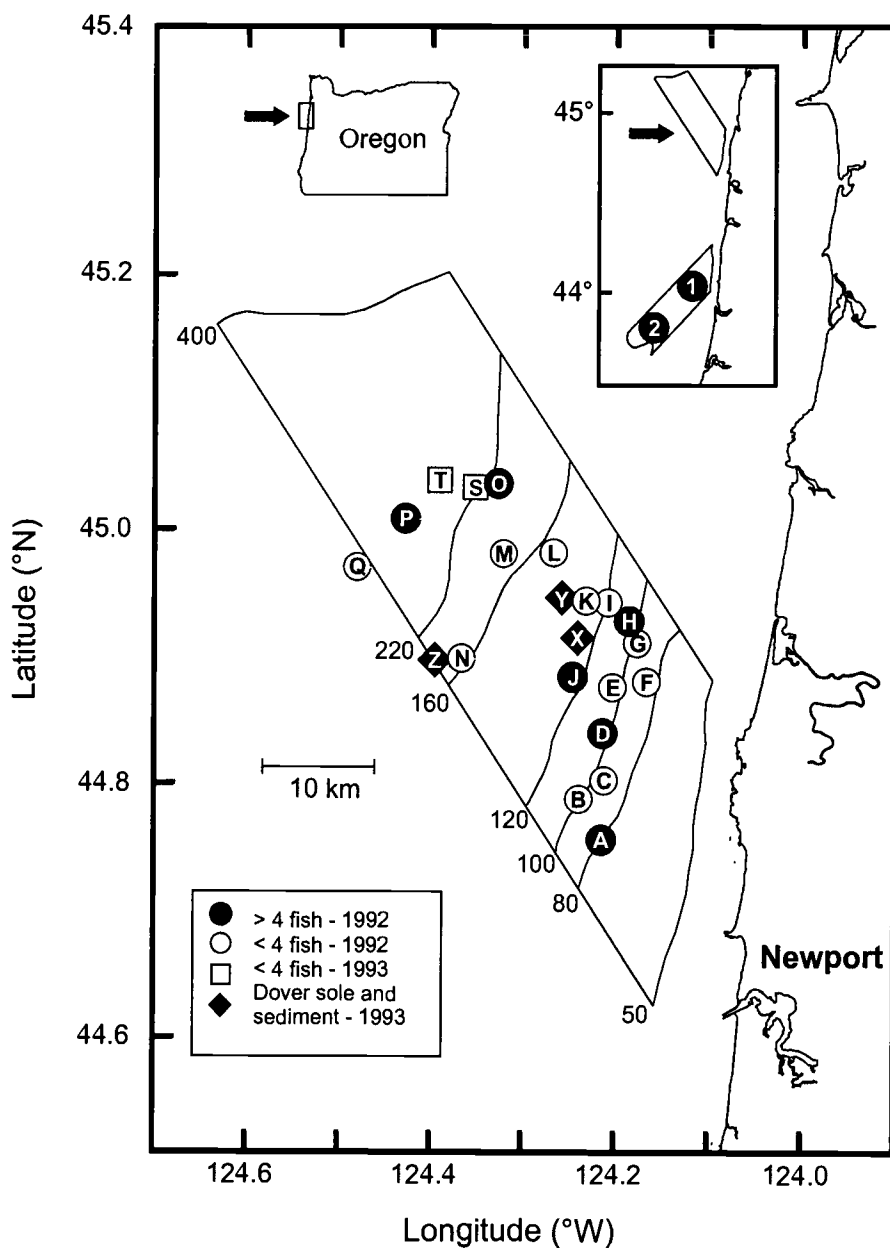


Figure 4.1. Map of the central Oregon coast showing locations where Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*) were collected. Stations A to Z were off Newport; stations 1 and 2 were ~100 km to the south off Heceta Head. Stations A to Q, 1, and 2 were sampled in March 1992. Stations S to Z were sampled in March 1993. Live Dover sole and sediments were collected at stations X, Y, and Z. Depth contours (m) are also shown.

Table 4.1. Number of Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*) otoliths that were analyzed along transects or near the otolith margin, listed by station, depth, and month of capture.

location - dates	station	depth (m)	number examined			
			transects		near margin	
			Dover sole	Pacific sanddab	Dover sole	Pacific sanddab
Newport						
<i>March 1992</i>	A	88			1	6
	B	108				1
	C	99			1	
	D	110	1	4	5	5
	E	110	1			
	F	95			1	
	G	104			1	
	H	108	3		4	
	I	119	6		1	
	J	132			5	
	K	132			1	2
	L	157	1		1	2
	M	176			1	2
	N	174				1
	O	207		3	1	6
	P	307	2	2	2	5
	Q	357	1	1	1	2
<i>March 1993</i>	S	230	2		3	
	T	276			2	
Heceta Head						
<i>March 1992</i>	1	90		4		8
	2	210			8	
totals			17	14	39	40

In the laboratory, fish were thawed, measured, and metamorphic stage was recorded. Dover sole stages were assigned using the criteria of Markle et al. (1992): stages 1 and 2 are pelagic larvae, stage 3 is a recently-settled larva, stage 4 is a late-metamorphic demersal larva, and stage 5 is a fully transformed juvenile. Pacific sanddab were classified into four metamorphic stages based on the position of the right (migrating) eye: stage 0 - eyes symmetrical, stage 1 - eye beginning to migrate but right of midline, stage 2 - eye intersecting the midline, and stage 3 - right eye migrated to left side. Individuals classified as stage 3 have not necessarily completed metamorphosis. Sagittae were removed, cleaned of adhering tissue, rinsed with water, and mounted in Crystalbond 509 thermoplastic resin. Whole otoliths were ground in the sagittal plane to the level of the central primordium (core) to expose increments from the core to margin. Sagittae were ground on silica sandpaper and polished with 0.05 μm alumina powder. Millipore-filtered distilled water was used to wet sandpaper and powder and to rinse otoliths. Polished sagittae were carbon coated just prior to elemental analysis.

Microprobe analyses

Concentrations of Ca, Sr, Cl, Na, K, P, and Mg in the sagitta were measured with a Cameca SX-50 wavelength dispersive electron microprobe. The incident electron beam had an accelerating voltage of 15 kV, a 30 nA current, and 15 μm defocused beam diameter which yielded a beam power density of 2.5 $\mu\text{W } \mu\text{m}^{-2}$. Resulting X-rays were counted for 20 secs on peak and 10 secs on background on the K α emission lines for all elements except Sr, which was counted on the L α line. X-rays emitted by Ca, Cl, K, and P were diffracted by a PET diffraction crystal, and those emitted by Sr, Na, and Mg by a TAP crystal.

Because microprobe analyses are based on counts of X-rays, it is possible to estimate the statistical or counting error and thus the detection limit for each measurement. The standard deviation of a single measurement was estimated by the method outlined by Williams (1987), and the 99% lower limit of detection (LLD) of a single measurement was estimated as 2.58

standard deviations above zero. The average minimum LLD for each element was calculated by regressing LLD on element concentration, and solving for the point at which the LLD equaled the measured concentration.

Elemental variation

Two distinct zones are visible in sagittae of both Dover sole and Pacific sanddab; a clear central region and an opaque outer region (Figure 4.2). In both species, the opaque region and numerous accessory primordia (AP) form around the start of a gradual metamorphosis (Toole et al., 1993; Donohoe and Markle, MS [Ch. 2]). In Pacific sanddab, metamorphosis and initial settlement appear to coincide, so that the transition between regions serves as a rough landmark for both events (Donohoe and Markle, MS [Ch. 2]). In contrast, settlement in Dover sole generally occurs several to many months after metamorphosis begins and roughly coincides with complete enclosure of the clear central area by growth from accessory primordia that form the opaque region (Toole et al., 1993). Thus there are separate landmarks for metamorphosis and settlement in Dover sole sagittae.

Transects

Sagittae of 17 Dover sole and 14 Pacific sanddab were analyzed with the microprobe at 9-19 points (mean=15) along a transect from the otolith core to the margin. Distance between point centers varied among fish and otolith regions, but averaged 48 μm in the clear central region and 36 μm in the outer opaque region. Radial distance from each point to the core was also recorded.

Cross-otolith trends

Cross-otolith trends in element concentration were assessed by regressing element concentration on distance from the otolith core for each individual. Linear models were fit to most elements, but a two-piece linear regression model was employed for Sr and P. Mean

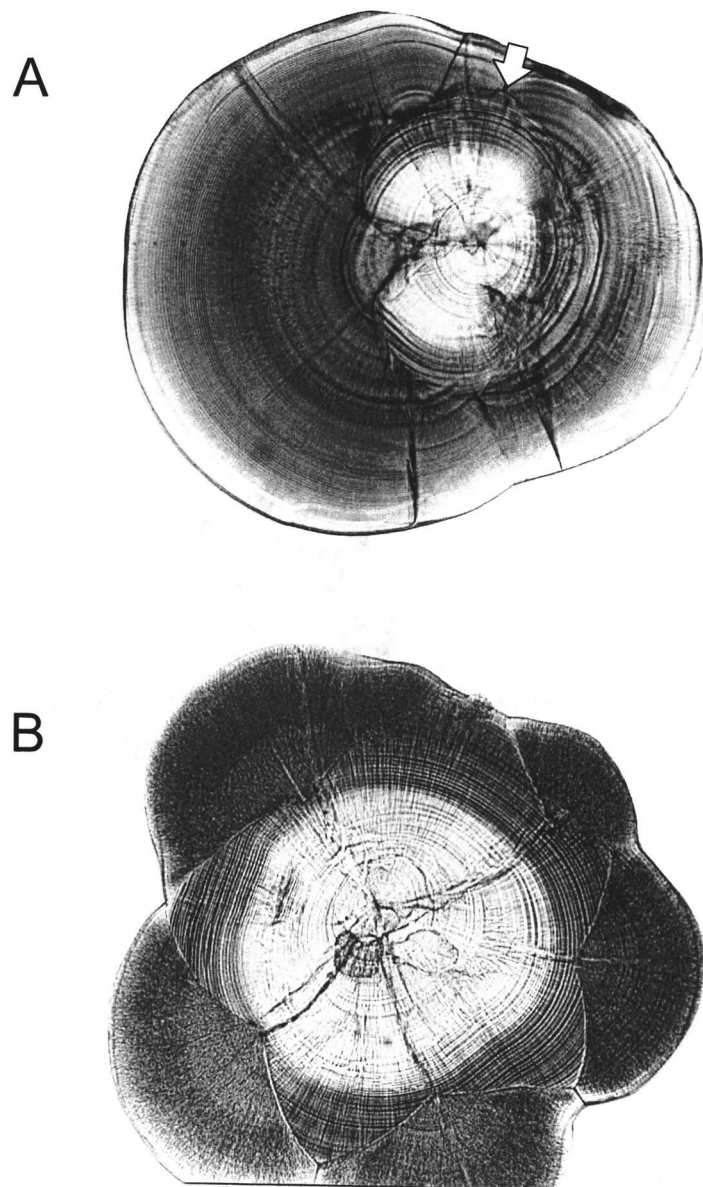


Figure 4.2. Sagittal sections of the right sagitta of A) a 53.1 mm stage 3 Dover sole (*Microstomus pacificus*) and B) a 23.3 mm stage 1 Pacific sanddab (*Citharichthys sordidus*) showing the clear central region, opaque outer region, and accessory primordia (AP). Enclosure of the clear central region by growth from accessory primordia on the Dover sole sagitta is indicated by the arrow.

cross-otolith trends for each species were estimated by fitting a single regression to pooled data obtained from transects across otoliths (17 Dover sole or 14 Pacific sanddab) and from analyses made at the otolith margin on an additional 33 Dover sole or 27 Pacific sanddab (see below). Regressions that explained $>10\%$ of the variation in an element were used to adjust margin concentrations to reduce size- or life history-related bias in later analyses. Deviations from these regressions (residuals) represent 'normalized' concentrations and are denoted by a prime (e.g. Ca', Sr', and K').

Changes at settlement and metamorphosis

Cross-otolith patterns in element concentration (elemental histories) were inspected to determine if changes in concentration coincided with otolith landmarks associated with settlement and metamorphosis. Elemental histories of fish settling to the same and different stations on the continental shelf and slope were also compared. If element concentrations reflect local environment, then elemental histories of fish which settled to the same station should converge after settlement, while the histories of fish settling to different stations should diverge.

Individual bias

The inherent or individual component of element variation was assessed by testing for correlations between the concentration near the margin and that near the core. Concentrations near the core were represented as the mean of transect points 2 and 3. Analyses of the core (point 1) were excluded because the estimated concentrations differed markedly from adjacent points in some elements, perhaps due to the presence of small cracks at the core.

Concentrations near the margin were represented by the mean of the two transect points nearest the margin. A significant correlation would indicate that differences in element concentrations among individuals tend to persist through early life.

Margins

Otolith margins of 39 Dover sole and 40 Pacific sanddab caught at depths of 88-357 m were analyzed to determine element concentrations at time of capture (Table 4.1).

Concentrations were measured at five points along the margin and then averaged. Otoliths from different stations were interspersed in the analysis sequence to reduce potential bias caused by instrument drift. Mean margin concentrations were normalized (adjusted) if necessary to reduce size-related bias and regressed on temperature and depth of capture to determine if these variables were related to elemental variation.

Sediment experiment

Live Dover sole (51-73 mm SL) and sediments were collected in February 1993 from three stations on the continental shelf off Newport. Pacific sanddab could not be kept alive for these experiments. The three stations (X, Y, and Z) were 10 km apart and located at depths of 126, 155, and 179 m (Figure 4.1). Sediments were collected by trailing a small section of pipe from the cod end of the trawl. Logistic problems prevented collection of both sediments and live fish from a broader range of depths.

Captured Dover sole were reared sequentially on two types of sediment. Dover sole were initially anesthetized with MS-222, injected with tetracycline to mark the otoliths, and then reared in replicate aquaria containing sediments collected from the station at which they were captured (native sediments). After 54 d, fish were anesthetized again and transferred onto sediments taken from a different station (foreign sediments). After an additional 16 d, fish were sacrificed. This design produced otoliths consisting of an inner region formed in the sea, a tetracycline mark, a middle region formed on native sediment, and an outer region formed on foreign sediment. Four combinations (treatments) of native-to-foreign sediment pairs were used: 1) 126 to 179 m; 2) 155 to 126 m; 3) 179 to 155 m; and 4) 126 m to no sediment.

Sagittae were prepared for analysis as described above. Element concentrations in each region were measured at five points and then averaged.

The influence of captivity on each element was estimated as the mean difference in concentration between the sea and native regions of an otolith, with $n=2$ to 6 fish per treatment. Absolute concentrations were not used because initial concentrations differed among individuals. The influence of sediment type was estimated as the mean difference between native and foreign regions of an otolith, and the combined influence of captivity and sediment type as the mean difference between the sea and foreign regions. Mean changes in element concentrations were considered statistically significant if the 95% confidence interval around the mean did not include zero.

Distributions of settling flatfish

Elements that showed strong individual bias (fixed differences) were used to evaluate patterns of settlement in Dover sole and Pacific sanddab. Univariate and multivariate analysis of variance (ANOVA and MANOVA) were used to determine if mean margin concentrations of one or more of these elements differed among stations located 5 to 122 km apart. Multivariate post-hoc contrasts or univariate post-hoc pairwise comparisons (Tukey's HSD) were also performed. Cluster analysis was used to determine if fish with similar otolith composition tended to occur at the same station. Individuals were clustered based on standardized element concentrations, euclidean distances, and average linkage.

RESULTS

Element variation

General

Ca, Sr, Na, and K were present in otoliths of Dover sole and Pacific sanddab at concentrations well above the average minimum LLD (Table 4.2). Concentrations of Cl were below detection limits in 20 and 22% of analyses, but data were not censored. Cl

Table 4.2. Average minimum lower limits of detection (LLD) for elements measured by the wavelength dispersive electron microprobe. The LLD of a single measurement is 2.58 standard deviations above zero. The average minimum LLD was estimated by regressing individual LLDs on element concentration and solving for the point at which LLD equaled element concentration. The percentage of measurements below the LLD is also shown.

element	average minimum LLD (ppm)	points below LLD (%)	
		Dover sole (<i>n</i> =513)	Pacific sanddab (<i>n</i> =383)
Ca	520	0	0
Sr	485	0	0
Cl	245	20	22
Na	260	0	0
K	170	0.2	0.3
P	245	64	14
Mg	170	88	56

concentrations were log-transformed prior to statistical analysis to produce more normal distributions. Measured concentrations of P in Dover sole and Mg in both species were below the average minimum LLD at $\geq 56\%$ of points and were therefore dropped from later statistical analyses. One Dover sole (specimen 601, station 2) was a statistical outlier and was dropped from all analyses because measured concentrations of five of seven elements were > 3.3 standard deviation units above the mean.

Transects

Cross-otolith trends

Transects revealed strong cross-otolith patterns in the concentration of most elements in individual Dover sole and Pacific sanddab (Figure 4.3 and Figure 4.4). In general, concentrations of K, Ca, and Na increased during the larval and early juvenile stages, but regression showed that significant linear trends were not present in all fish (Table 4.3). K concentrations increased with distance from the otolith core in 71% of fish in both species, with distance explaining an average of 43% and 49% of the individual variation (Table 4.3). Ca concentrations also increased in 76% of Dover sole and 50% of Pacific sanddab and Na concentrations increased in 47% and 43% of fish, with distance explaining an average of 27% to 50% of the individual variation. In contrast, concentrations of Sr were highest near the core, decreased with distance in the clear central region, reached minimum levels in the opaque outer region, and then remained low or increased slightly to the margin (Figure 4.3 and Figure 4.4). Two-piece regressions explained an average of 72% and 77% of the individual variation during early life. This cross-otolith pattern was observed in nearly all individuals, but significance levels were not available for the two-piece models. The cross-otolith pattern in P concentration was more complex and differed among the two species. In both species, concentrations of P were usually highest in the clear central region, either at the core or 50-200 μm from the core, and then decreased to low levels at the transition from clear to opaque regions. In the opaque

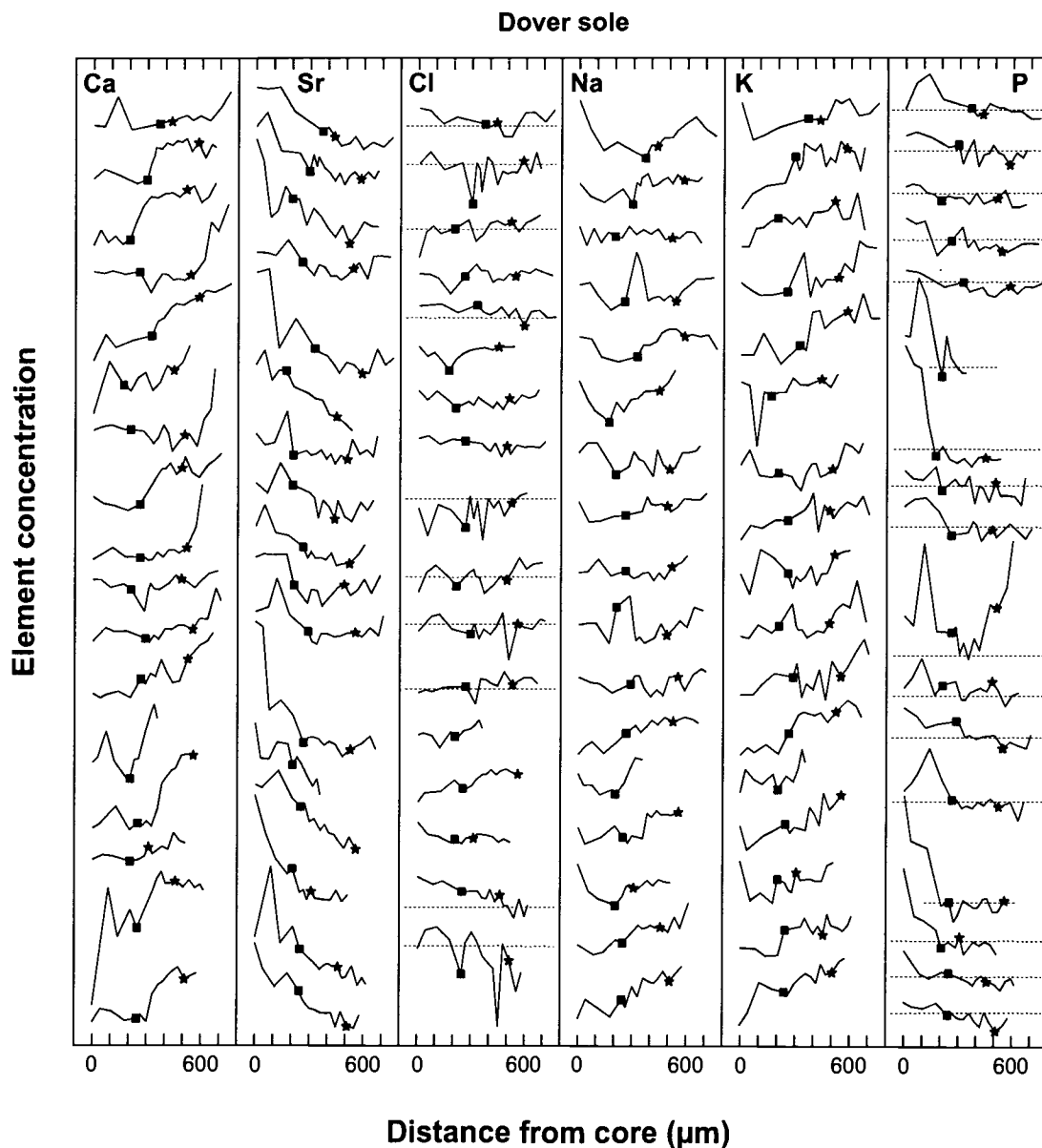


Figure 4.3. Cross-otolith patterns in element concentrations (by weight) for 17 Dover sole (*Microstomus pacificus*). Concentration scales differ among elements but are the same for individuals. Concentrations were measured at 12-19 points along a transect from the core to otolith margin. Squares indicate the transition from the clear to opaque region (early metamorphosis) and stars indicate enclosure of growth from the central primordium by growth from accessory primordium (predicted settlement). The average minimum 99% lower limit of detection (LLD) is shown as a dashed line for patterns that drop below the LLD.

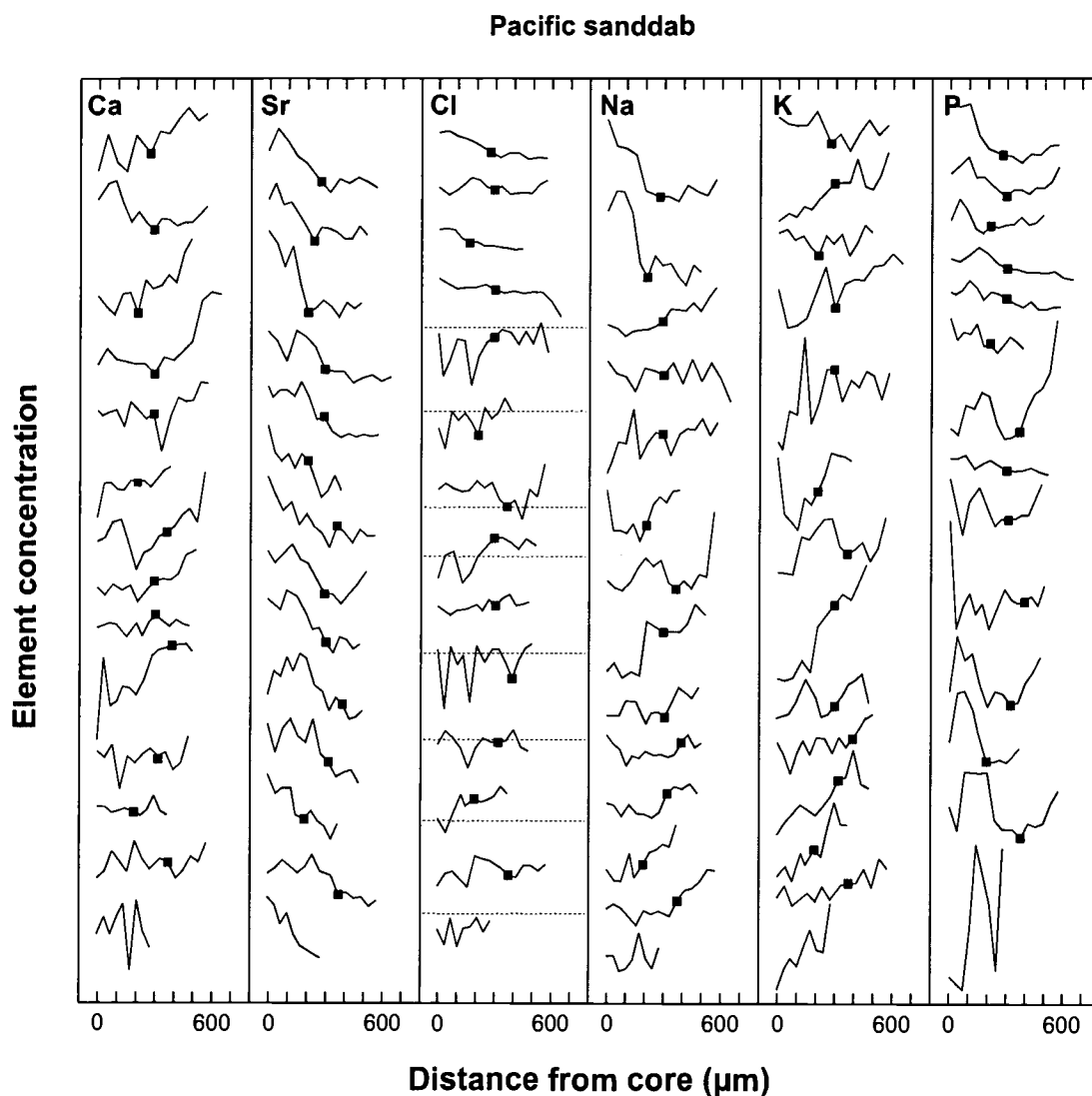


Figure 4.4. Cross-otolith patterns in element concentrations for 14 Pacific sanddab (*Citharichthys sordidus*). Concentration scales differ among elements but are the same for individuals. Concentrations were measured at 9-16 points along a transect from the core to otolith margin. Squares indicate the transition from the clear to opaque region (predicted settlement). The average minimum 99% lower limit of detection (LLD) is shown as a dashed line for patterns that drop below the LLD.

Table 4.3. Mean and range of coefficients of determination (r^2) for linear regressions of element concentration on distance of the analysis from the otolith core for each of 17 Dover sole and 14 Pacific sanddab. Concentrations were analyzed at 9 to 19 points (mean=15.0) along a transect from core to margin. Linear models were used for most elements, but two-piece linear models were used for Sr and P. The number of significant ($P<0.05$) positive and negative relationships are also shown. P -values were not available for Sr and P.

		r^2	frequency of significant relationships	
element	range	mean	#	%
Dover sole (<i>n</i>=17)				
Ca	0.08-0.93	0.50	13+	76
Sr	0.19-0.94	0.72	-	-
Cl ¹	0.00-0.83	0.28	2+, 4-	12, 24
Na	0.00-0.81	0.27	8+	47
K	0.12-0.80	0.43	12+	71
P	0.37-0.95	0.62	-	-
Pacific sanddab (<i>n</i>=14)				
Ca	0.01-0.68	0.34	7+, 1-	50, 7
Sr	0.55-0.93	0.77	-	-
Cl ¹	0.00-0.90	0.35	2+, 3-	14, 21
Na	0.03-0.80	0.36	6+, 2-	43, 14
K	0.00-0.93	0.49	10+	71
P	0.08-0.91	0.55	-	-

¹ Cl concentrations were below the lower limit of detection at more than two points in 8 of 17 Dover sole and 6 of 14 Pacific sanddab.

region, P concentrations remained below detection limits in most Dover sole but concentrations increased in many Pacific sanddab. Two-piece regressions explained an average of 62% and 55% of the individual variation. Concentrations of Cl were fairly stable during early life in most fish (Figure 4.3 and Figure 4.4). Significant cross-otolith trends in Cl were detected in ~35% of individuals but these trends had both positive and negative slopes.

Mean cross-otolith trends explained significant portions of the total variation in concentrations of K, Ca, Na, Sr, and P within and among Dover sole and Pacific sanddab (Figure 4.5). Distance from the otolith core explained 31% and 32% of the variation in K, 32% and 19% of the variation in Ca, and 9% and 5% of the variation in Na when data from individual transects and analyses near the margin were combined (Figure 4.5). Two-piece regressions explained 63% and 62% of the variation in Sr concentrations and 26% and 14% of the variation in P concentrations in Dover sole and Pacific sanddab. Mean concentrations of Cl did not covary with distance from core in either species ($r^2 \leq 0.05$).

changes at settlement

Concentrations of P, Sr, and Ca shifted near otolith landmarks associated with settlement, but these changes were not consistent, occurring in <60% of individuals in either species (Figure 4.3 and Figure 4.4). Concentrations of P were generally below detection limits after metamorphosis in Dover sole, but concentrations increased from minimum levels at settlement in 8 of 14 Pacific sanddab. Sr concentrations also increased from minimum levels around settlement in 6 of 17 Dover sole and in 5 of 14 Pacific sanddab, but these increases were small. Step-like increases in Ca occurred in 8 of 17 Dover sole (Figure 4.3), but increases coincided with the settlement landmark (enclosure) in three fish and coincided with the metamorphosis landmark (transition from clear to opaque) in the other five. Ca concentrations increased at settlement in only 1 or 2 Pacific sanddab. In both species, concentrations of Cl, Na,

Figure 4.5. Relationships between element concentration and distance of microprobe analysis from the central primordium (core) in sagittae of Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*). Concentrations (by weight) are in parts per million for all elements except Ca, which is a percentage. Symbol color indicates location of the analysis: white = clear central region, black = opaque region, gray = transition between regions. Symbol shape indicates type of data: square = single measurement from transect across otolith, diamond = mean of 5 measurements near margin. Linear and two-piece regression lines and associated r -squared values are shown. Significance of linear relationships are indicated by asterisks; *** < 0.001 . Dashed lines represent the average minimum 99% lower limit of detection.

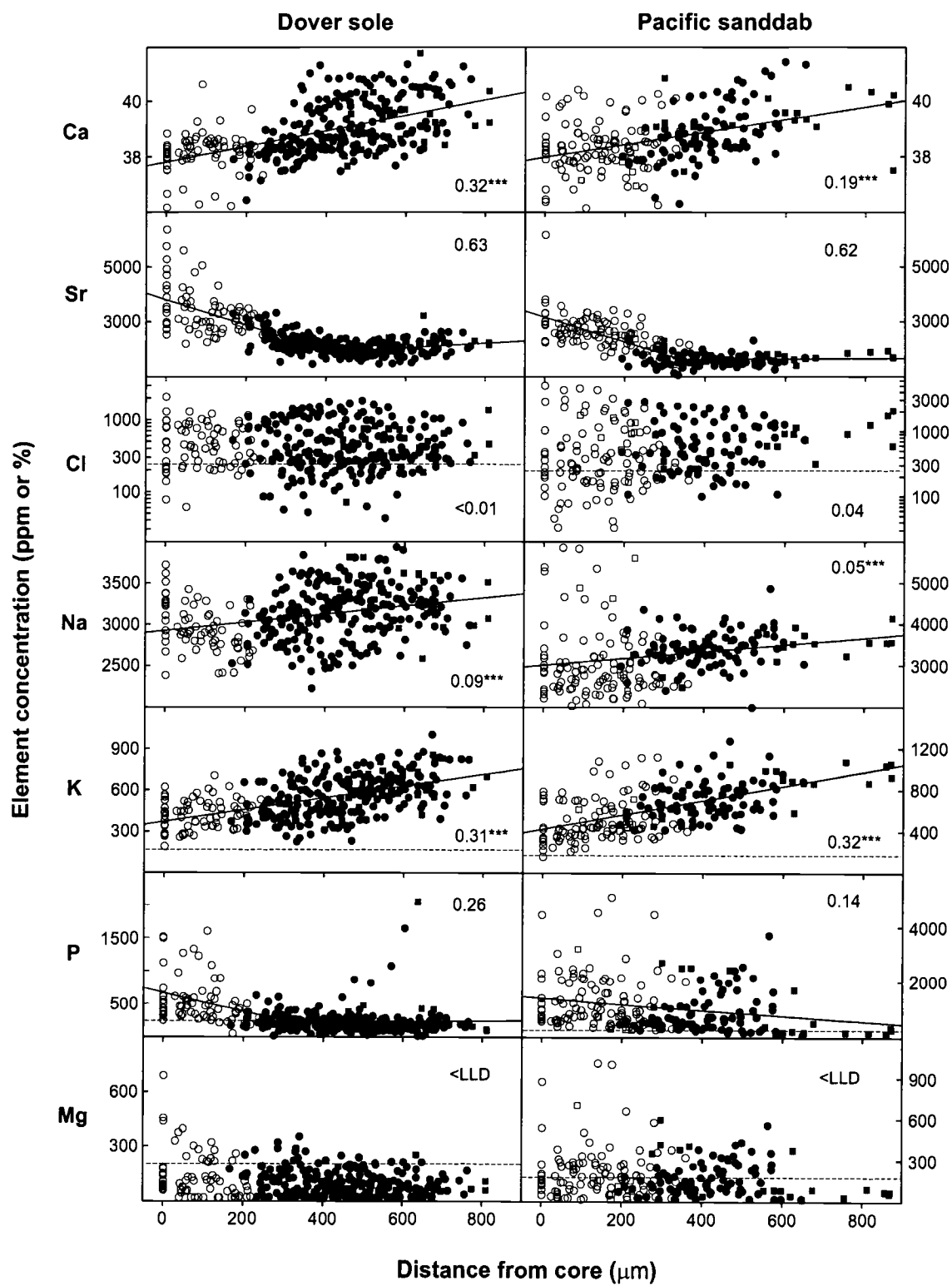


Figure 4.5

and K were either constant at settlement, or changed only gradually at settlement, reflecting long-term trends.

With one exception, element histories of fish caught at the same station did not appear to converge after settlement in either species as would be expected if concentrations were determined by the local environment (Figure 4.6 and Figure 4.7). Concentrations of several elements did appear to converge among Dover sole caught at station I. At station I, Ca concentrations first diverged after metamorphosis and then converged after settlement. Concentrations of Na and K also appear to converge slightly among fish at station I (Figure 4.6). Element histories also converged among fish caught at several other stations, but these convergences occurred well prior to predicted settlement. For example, Na histories of Pacific sanddab at stations I and D and Ca histories of Dover sole at station H converged prior to settlement (Figure 4.6).

Mean element histories for groups of fish caught at the same station did not diverge after settlement from mean histories for other stations (Figure 4.6 and Figure 4.7). Variation among mean element histories for each station also did not increase after settlement. Mean concentrations of Na in Dover sole appeared to diverge slightly among stations, but the divergence began well prior to predicted settlement.

Individual bias

Element concentrations near the core were compared to those at the margin to determine if early differences among larvae persisted later in life. Cl concentrations near the otolith core and margin were significantly correlated in Dover sole ($r=0.56$, $n=17$, $P=0.02$) and highly significantly correlated in Pacific sanddab ($r=0.87$, $n=14$, $P<0.001$; Figure 4.8). However, Cl concentrations were below the LLD at either the core or margin in 5 of 17 Dover sole and in 6 of 14 Pacific sanddab. Among fish with Cl concentrations above the LLD, Cl

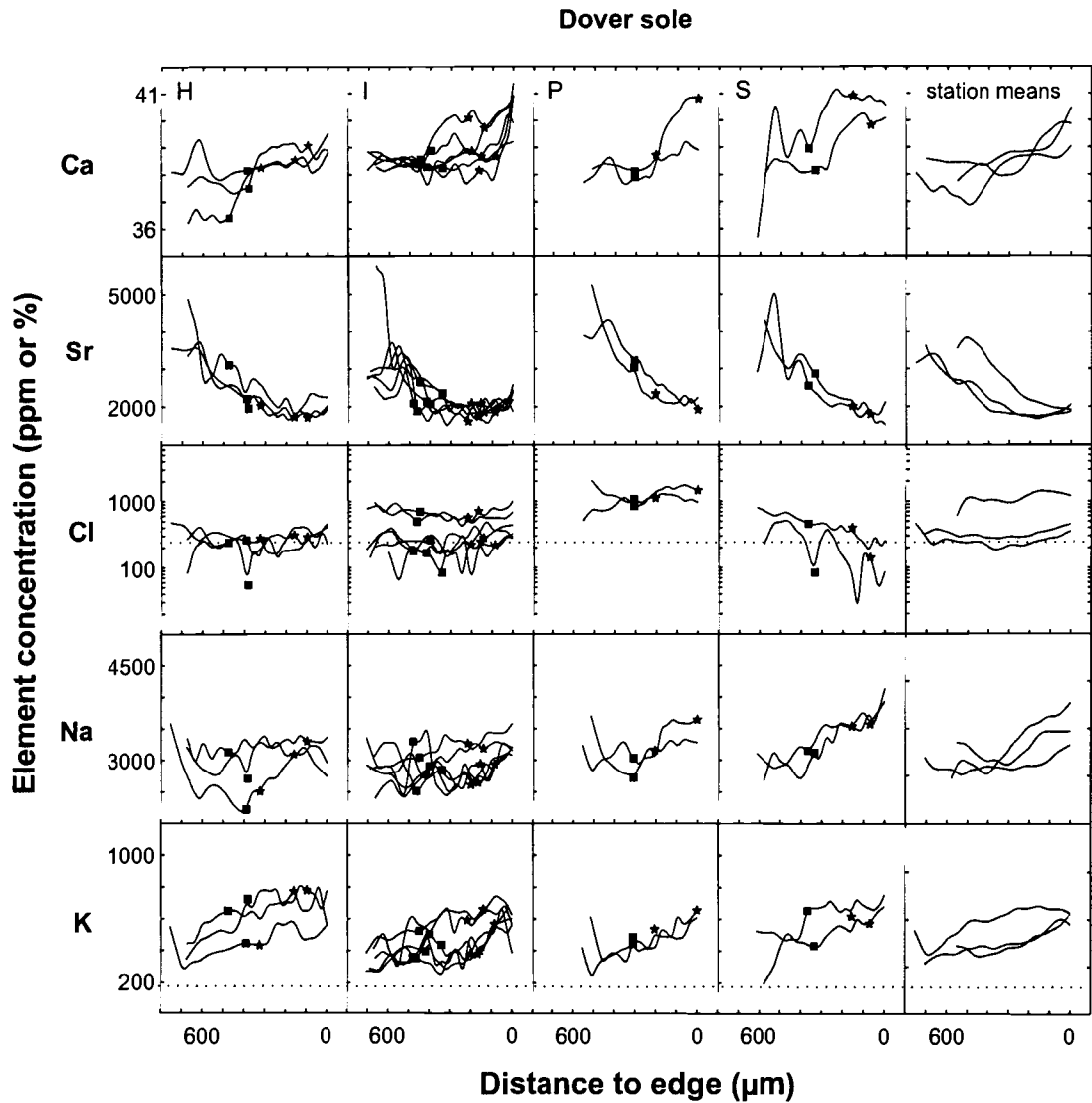


Figure 4.6. Individual and mean cross-otolith patterns in element concentrations for 13 Dover sole (*Microstomus pacificus*) collected at stations H, I, P, and S (mean pattern for station S not shown). Concentrations were measured at 12-19 points along a transect from the core to otolith margin. Series are aligned by distance to the otolith margin. Station patterns represent locally-weighted moving averages of several fish. Squares indicate the transition from the clear to opaque region (early metamorphosis) and stars indicate enclosure of growth from the central primordium by growth from accessory primordium (predicted settlement). Dashed lines represent the average minimum 99% lower limit of detection.

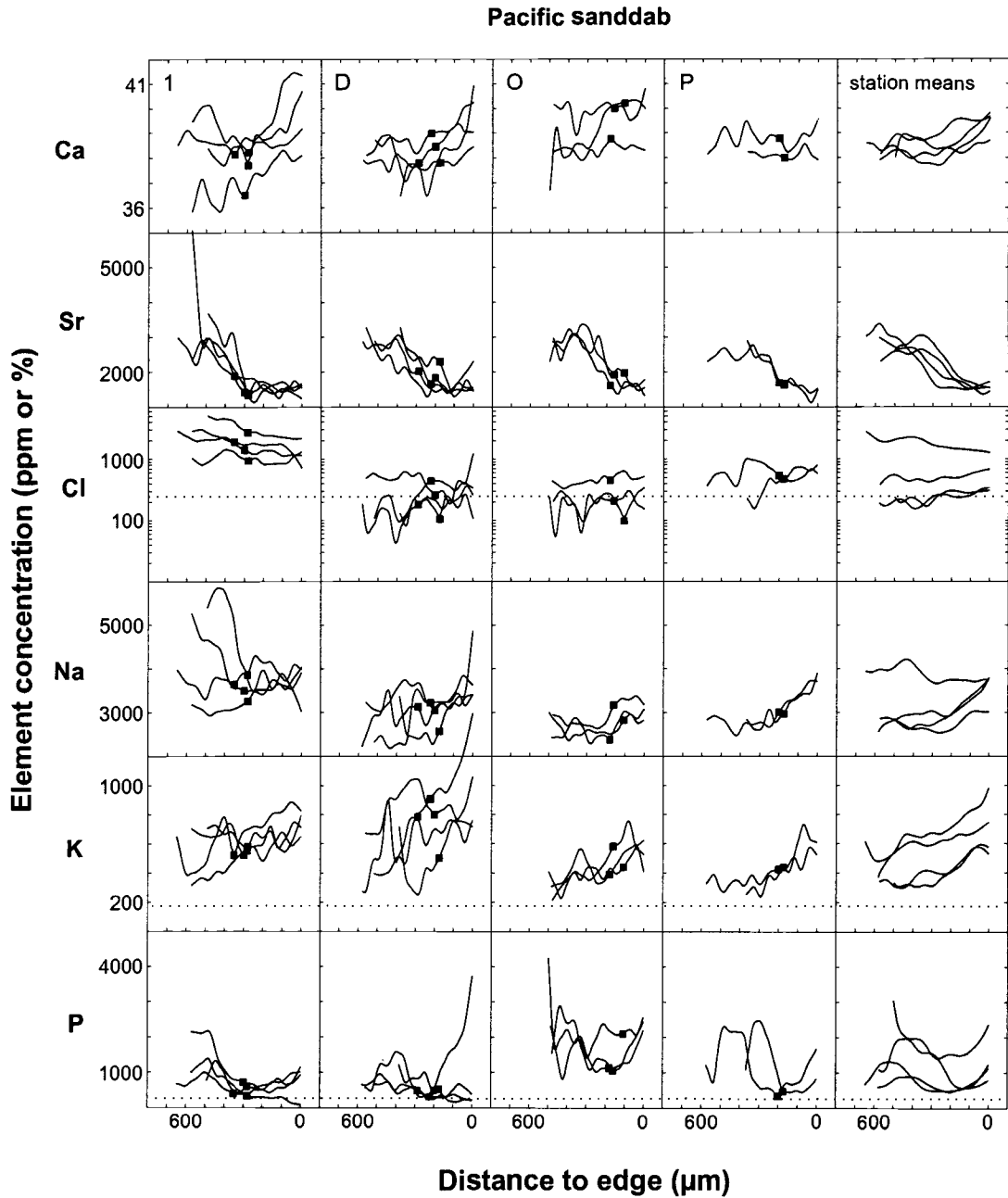


Figure 4.7. Individual and mean cross-otolith patterns in element concentrations for 13 Pacific sanddab (*Citharichthys sordidus*) collected at stations 1, D, O, and P. Concentrations were measured at 9-16 points along a transect from the core to otolith margin. Series are aligned by distance to the otolith margin. Station patterns represent locally-weighted moving averages of several fish. Squares indicate the transition from the clear to opaque region (predicted settlement). Dashed lines represent the average minimum 99% lower limit of detection.

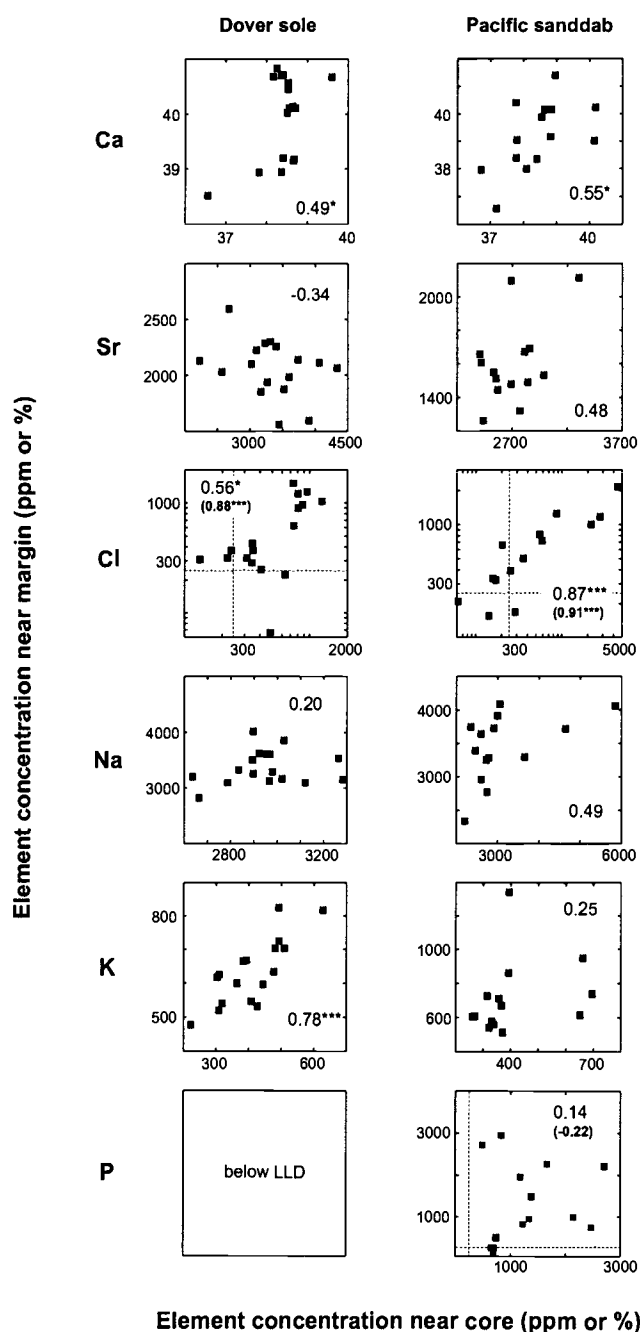


Figure 4.8. Relationships between element concentration near the core and near the margin in sagittae of 17 Dover sole (*Microstomus pacificus*) and 14 Pacific sanddab (*Citharichthys sordidus*). Core concentrations represent the mean of transect points 2 and 3 and margin concentrations are the mean of the two transect points closest to the margin. Pearson correlation coefficients (r) are shown; r -values in parentheses are based on values above the LLD. Significant correlations (Bartlett Chi-square) are indicated with asterisks; * ≤ 0.05 , ** ≤ 0.01 , *** ≤ 0.001 .

concentrations near the core and margin were significantly correlated in both Dover sole ($r=0.88$, $n=12$, $P<0.001$) and Pacific sanddab ($r=0.91$, $n=8$, $P<0.001$). K concentrations near the core and margin were also highly correlated in Dover sole ($r=0.78$, $n=17$, $P<0.001$). In addition, margin and core concentrations of Ca were correlated in both Dover sole ($r=0.49$, $n=17$, $P=0.04$) and Pacific sanddab ($r=0.55$, $n=14$, $P=0.04$). Correlations for the remaining elements were not statistically significant.

Margin concentrations

Analyses at the otolith margin confirmed that Sr concentrations are related to otolith size and metamorphic stage (Figure 4.9). Among Dover sole, regression showed that margin concentrations increased slightly with otolith radius ($n=37$, $r^2=0.14$, $P=0.02$, one outlier excluded). However, Sr concentrations were also higher in stage 4 fish (late metamorphosis) than in stage 3 fish, with metamorphic stage explaining a greater portion of the observed variation in Sr (ANOVA, $P<0.001$, $SS_{\text{stage}}/SS_{\text{total}}=0.42$). Even after removing the otolith size-related trend, metamorphic stage still explained a greater portion of the variation in residual Sr (ANOVA, $P<0.01$, $SS_{\text{stage}}/SS_{\text{total}}=0.21$). Among Pacific sanddab, margin concentrations of Sr varied with otolith radius ($n=40$, $r^2=0.82$, Figure 4.9). Sr concentrations decreased with otolith radius in fish that had not completed eye migration (stages 0-2) and increased with otolith radius in fish that had completed eye migration (stage 3).

Margin concentrations of several elements covaried with both depth and temperature at time of capture, but depth and temperature explained only 10-17% of the observed variation (Figure 4.10 and Figure 4.11). Concentrations of K, Sr, and Ca were adjusted prior to analysis to reduce size- or life history-related bias. Because water temperature was strongly correlated with depth ($n=49$, $r=-0.94$, $P<0.001$), element concentrations show nearly identical relationships with depth and temperature. In Dover sole, margin concentrations of Ca' and Na decreased slightly with temperature ($n=38$, $r^2=0.12$ and 0.10 , $P < 0.05$). In Pacific sanddab, margin

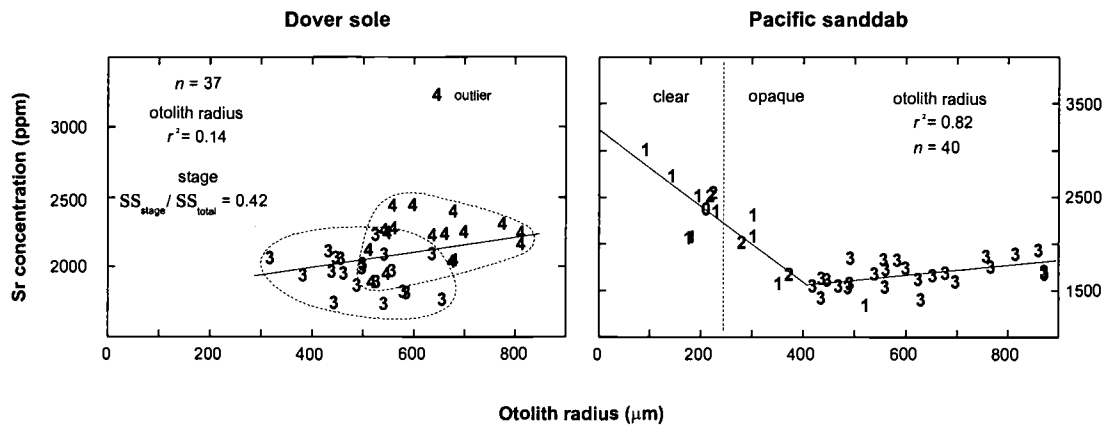


Figure 4.9. Relationships between Sr concentration at the otolith margin, distance of analyses from core (ca. otolith radius), and stage of metamorphosis for settling Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*). Symbols indicate metamorphic stage. Also shown is the proportion of variation explained by otolith radius (r^2) in both species and by metamorphic stage in Dover sole. One stage 4 Dover sole was a statistical outlier and was excluded from analyses.

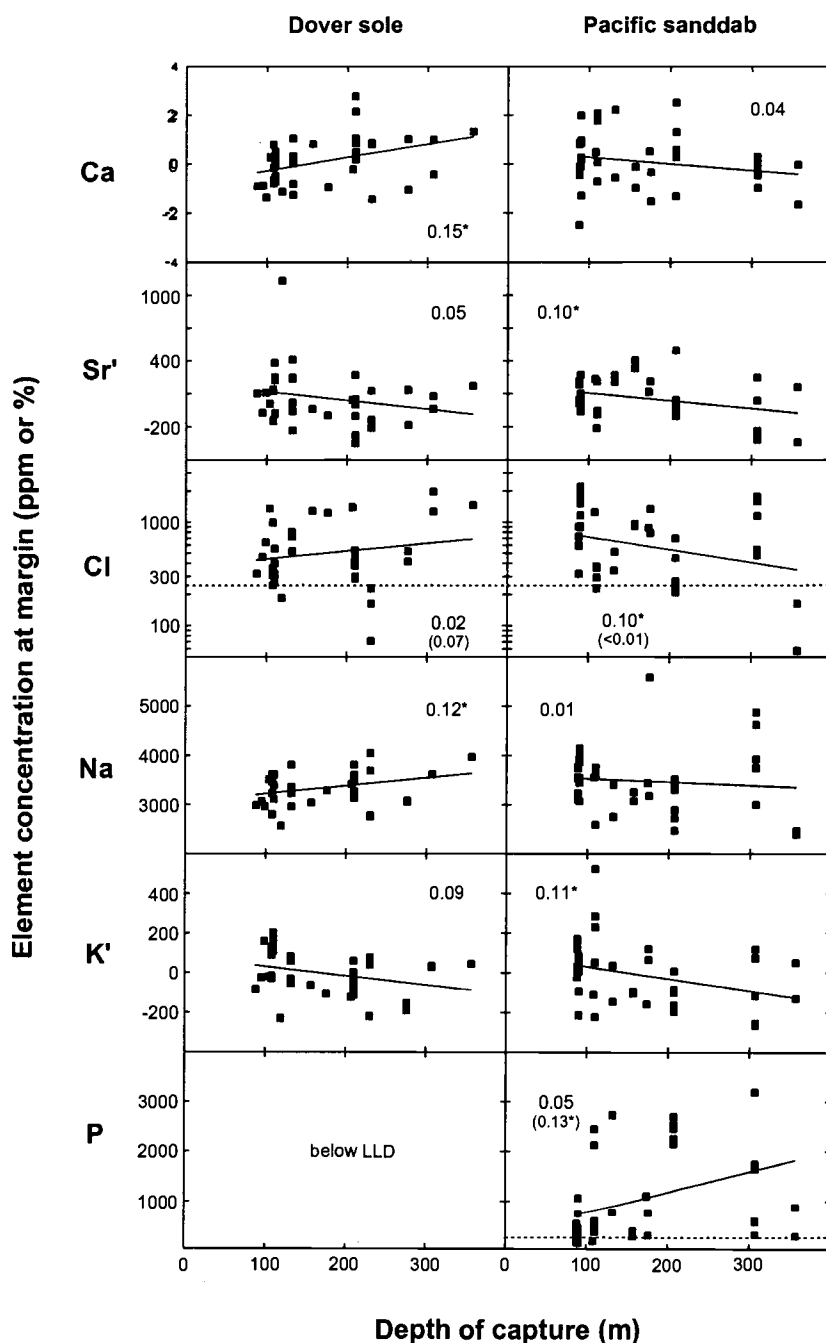


Figure 4.10. Relationship between mean element concentration or normalized concentration (Sr, K) at the otolith margin and depth of capture for 38 Dover sole (*Microstomus pacificus*) and 40 Pacific sanddab (*Citharichthys sordidus*). Concentrations were measured at five points along the otolith margin and then averaged. Coefficients of determination (r^2) are shown. Significant regressions are indicated with asterisks; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Concentrations (by weight) are in ppm for all elements except Ca, which is a percentage. Values in parentheses are for censored data.

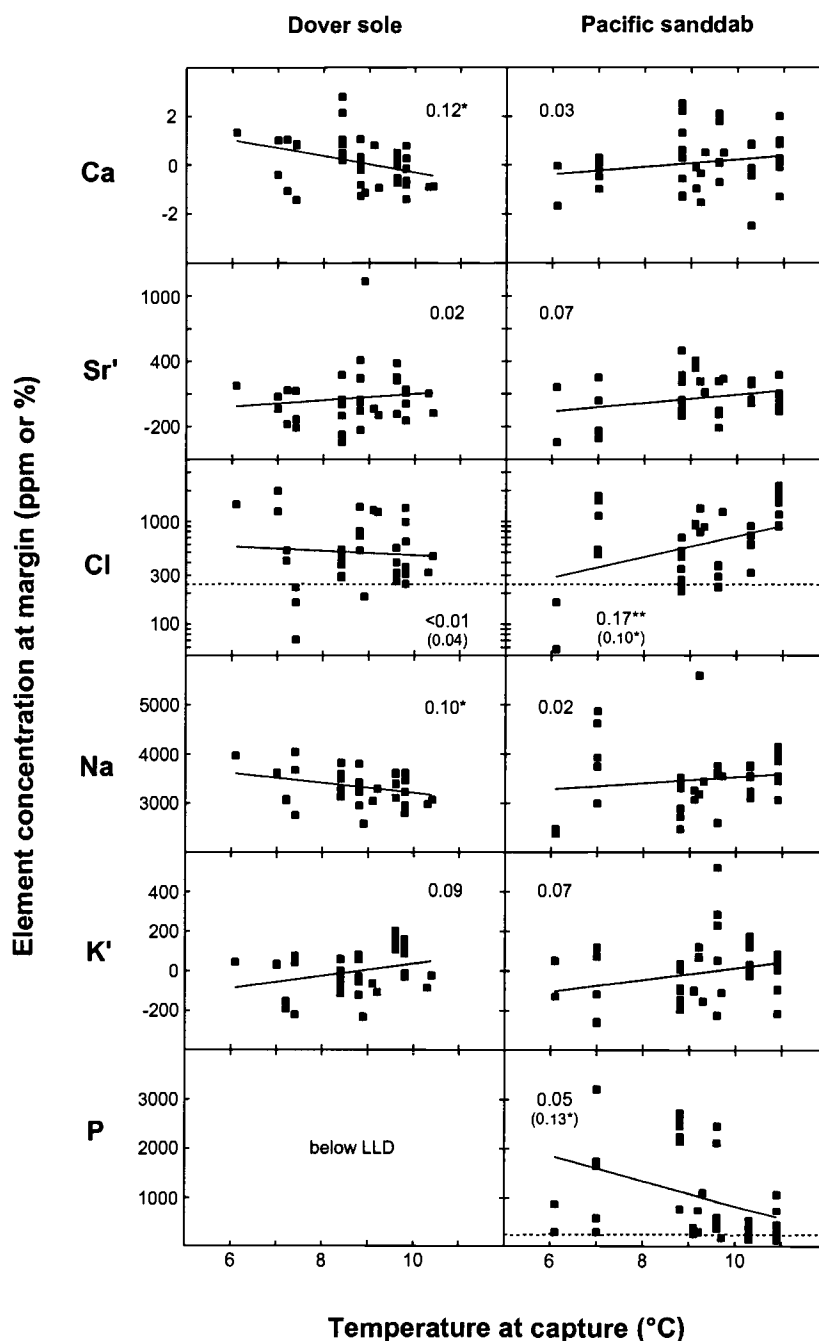


Figure 4.11. Relationship between mean element concentration or normalized concentration (Sr, K) at the otolith margin and water temperature at time of capture for 38 Dover sole (*Microstomus pacificus*) and 40 Pacific sanddab (*Citharichthys sordidus*). Concentrations were measured at five points along the otolith margin, and then averaged. Coefficients of determination (r^2) are shown. Significant regressions are indicated with asterisks; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Concentrations (by weight) are in ppm for all elements except Ca, which is a percentage. Values in parentheses are for censored data.

concentrations of Cl increased with temperature ($n=40$, $r^2=0.17$). However, relationships between Cl, P, and temperature were influenced by data below the LLD. If values below the LLD are replaced with the detection limit (245 ppm for both elements), these relationships become less significant for Cl and significant for P (Figure 4.10 and Figure 4.11). No element showed a significant relationship with depth or temperature at capture in both species.

Length of fish used in the analysis did not covary with depth of capture for either species ($P=0.32$ and $P=0.11$, Figure 4.12). However, regression showed that individuals of both species caught at shallower depths tended to have larger otoliths ($r^2=0.19$, $P<0.01$; $r^2=0.30$, $P<0.001$). Larger otoliths indicate fish were further through metamorphosis because otolith size increases rapidly at metamorphosis in both species.

Sediment experiment

Sediment type appeared to have little effect on concentration of elements in otoliths of laboratory reared Dover sole (Figure 4.13). Mean concentrations of Na decreased 260 ppm (9.0%) as fish were moved from 126 to 179 m sediments (treatment 1) and also decreased 90 ppm (3.3%) as fish were moved from 179 to 155 m sediments (treatment 3), but sample size in this treatment was small ($n=2$ fish). However, no reciprocal increase in Na concentration was observed for fish moved from 155 to 126 m sediments (treatment 2) as would be expected given the declines observed in treatments 1 and 3. Mean concentration of K decreased 100 ppm (13.5%) as fish were moved from 126 to 179 m sediments (treatment 1), but reciprocal increases were not observed in other treatments. No changes in mean concentrations of Ca, Sr, or Cl due to sediment type were detected.

Although unaffected by sediment type, Sr concentrations increased in otoliths of nearly all juvenile Dover sole during laboratory rearing, regardless of sediment treatment. Sr concentrations increased an average of 140 ppm (7.8%) while fish were reared on native sediments, although this increase was not significant in any of the four treatments (Figure 4.13).

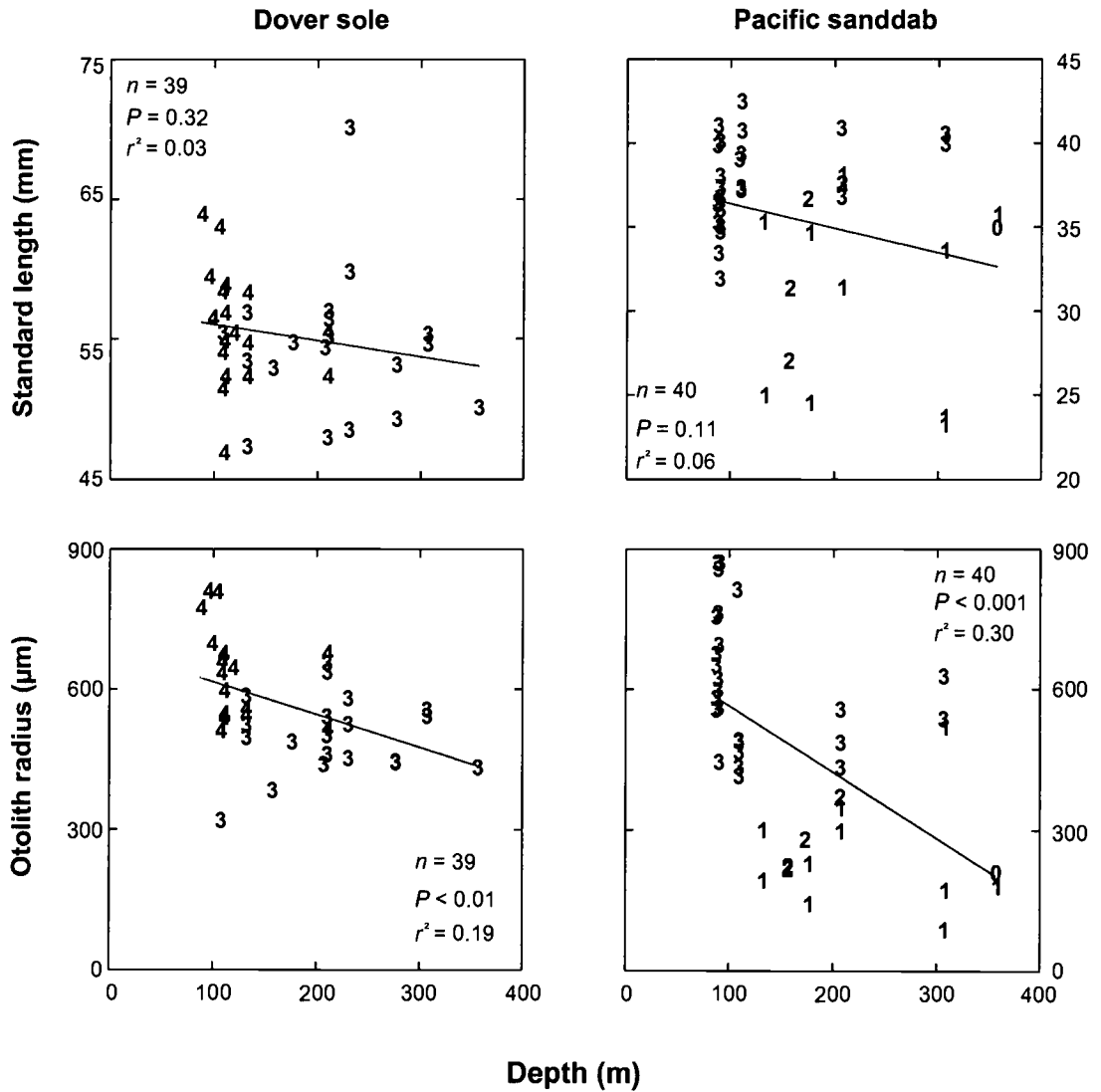


Figure 4.12. Relationships between standard length, otolith radius, and depth of capture for settling Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*). Symbols indicate metamorphic stage.

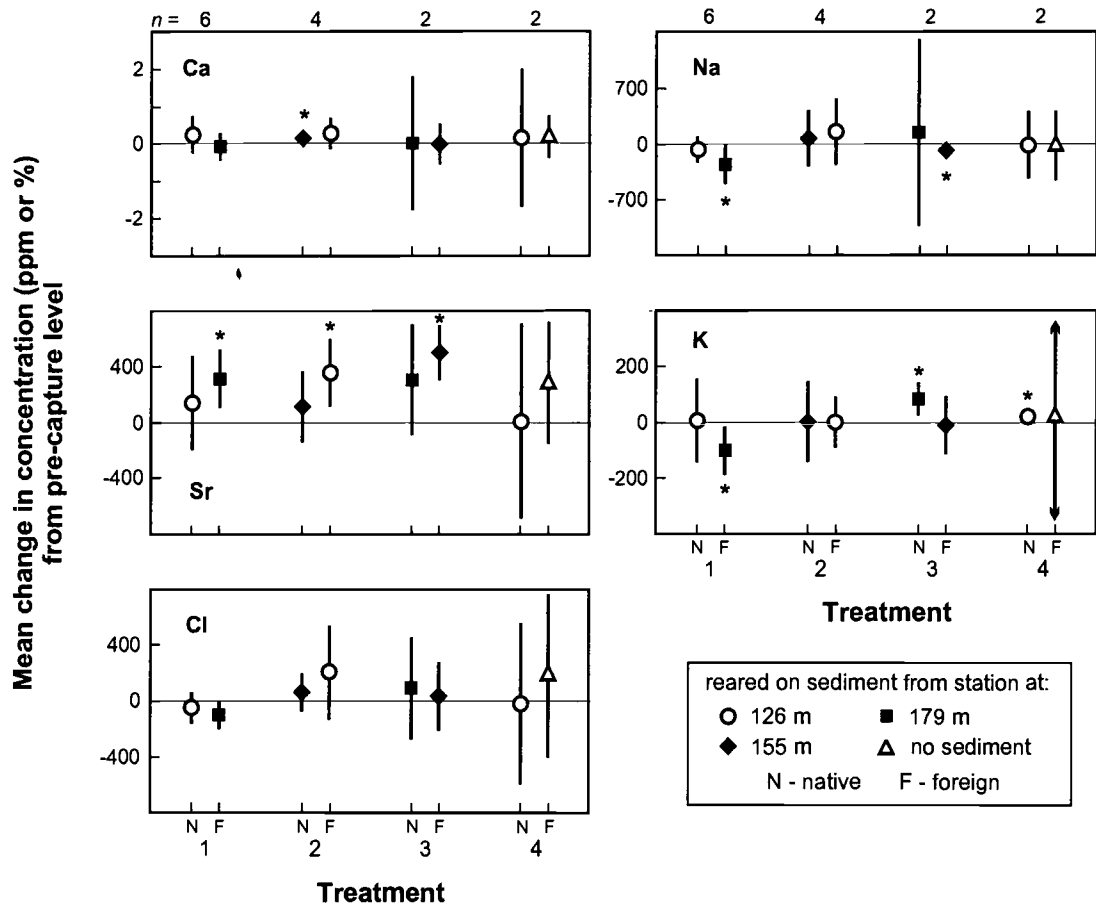


Figure 4.13. Effect of sediment type and laboratory rearing on element concentrations in otoliths of Dover sole (*Microstomus pacificus*). Points are the mean change in element concentration (and 95% confidence intervals) between the region of the otolith formed prior to capture (in the field) and the region formed in the laboratory first on native sediment (lab effect) and then on one of three foreign sediments or no sediment (lab + sediment effect). Fish and sediments were collected from three stations at depths of 126, 155, and 179 m (see Figure 4.1). Number of fish in each treatment is indicated at top of graph.

Sr concentrations continued to increase after fish were moved onto foreign sediments (and no sediment), increasing an average of 350 ppm (18.4 %), significantly greater than pre-capture levels in three of four treatments. Other elements were largely unaffected by the initial 54 d of laboratory rearing. However a few small (0.4-12.4%) but statistically significant increases were observed for Ca and K in some treatments.

Distribution of settling flatfish

Results showed that differences in margin concentrations of Cl and K among Dover sole and in Cl among Pacific sanddab were established early in life (Figure 4.8). These elements were therefore stable characters useful for classifying settling fish. Concentrations of these elements were compared for fish collected from stations 5-122 km apart to determine if there was small-scale structure within the settling year class.

Settling flatfishes did not appear to be randomly distributed among stations. Mean combined concentration of Cl and K' at the otolith margin differed among Dover sole collected at different stations (MANOVA, $F = 6.41$, $P < 0.001$, Table 4.4). Post-hoc contrasts showed that combined concentrations differed among stations 113-116 km apart and also among stations only 5-9 km apart ($P < 0.05$). Otolith compositions of Dover sole from station D did not overlap those from station 2 (113 km away) or station J (5 km away). Otolith composition did not differ among stations 2 and H (122 km apart). Univariate tests confirmed that mean concentrations of Cl and K' differed among stations 5-116 km apart (ANOVA, $P < 0.05$, Figure 4.14).

Cluster analysis based on concentrations of Cl and K' showed that Dover sole with similar otolith composition often occurred at the same station. Dover sole clustered into 5 indistinct groups (Figure 4.15). Two clusters included fish from only one station and one cluster included fish from the three stations 5-9 km apart (D, H, and J). Two clusters included fish from stations over 100 km apart (2 and J, 2 and H).

Table 4.4. Distances between stations and corresponding *P*-values for pairwise comparisons of mean margin concentrations. For Dover sole, concentrations of Cl and K' were compared using MANOVA. For Pacific sanddab, Cl concentrations were compared using the Tukey HSD test.

Dover sole

station	<i>P</i> -value \ distance (km)			
	2	D	H	J
2	---	113	122	116
D	<0.001	---	9	5
H	0.16	0.02	---	6
J	0.03	<0.001	0.04	---

Pacific sanddab

station	1	A	D	O	P
1	---	74	83	103	100
A	0.02	---	9	31	32
D	<0.001	0.06	---	23	25
O	<0.001	0.06	1.0	---	8
P	0.69	0.39	0.001	0.001	---

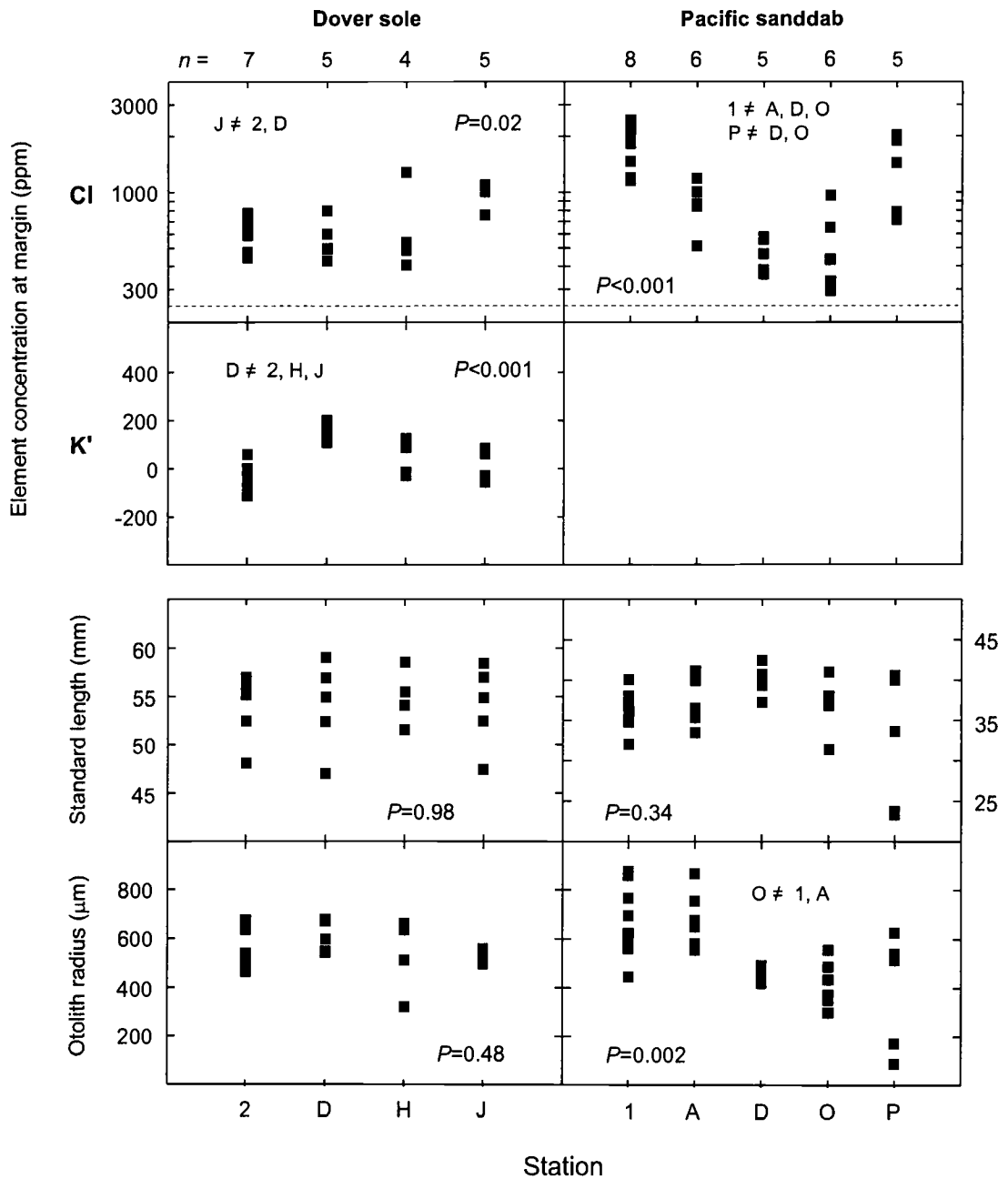


Figure 4.14. Variation in margin concentrations, fish length, and otolith radius among stations for settling Dover sole (*Microstomus pacificus*) and Pacific sanddab (*Citharichthys sordidus*). Element concentrations were measured at five points along the otolith margin and then averaged. Concentrations of K were normalized to remove size-related bias. Differences in mean concentrations were tested using ANOVA and post-hoc pairwise comparisons using the Tukey HSD. Differences in length and otolith radius were tested using the Kruskal-Wallis test. Dashed lines represent the average minimum 99% lower limit of detection.

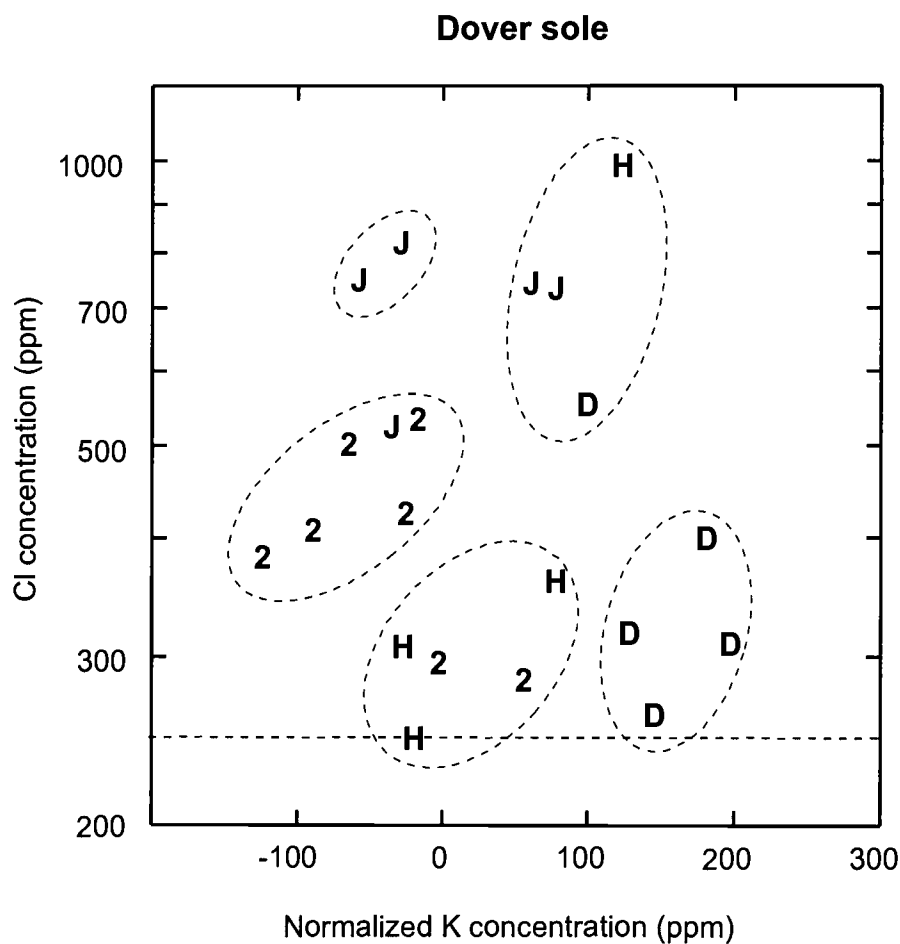


Figure 4.15. Scatterplot showing margin concentrations of Cl and normalized K in otoliths of Dover sole (*Microstomus pacificus*) collected at four stations on the continental shelf and upper slope. Letters indicate stations. Ellipses indicate major groups formed by cluster analysis using standardized elemental concentrations, euclidean distances, and average linkage.

In Pacific sanddab, mean concentrations of Cl at the otolith margin differed among stations (ANOVA, $P < 0.001$, Figure 4.14). Post-hoc pairwise comparisons showed that mean Cl concentration differed among stations 8-103 km apart (Table 4.4). Ranges in Cl concentrations for several stations did not overlap (Figure 4.14). However, Pacific sanddab with similar Cl concentrations always occurred at two or more stations. Fish with high Cl levels were caught primarily at stations I and P (100 km apart), those with low Cl levels were caught primarily at stations D and O (23 km apart), and fish with moderate Cl levels were caught at stations A, O, and P (8-32 km apart).

Length of settling fish did not differ among stations for either species (Kruskal-Wallis, $P=0.98$ and $P=0.34$, Figure 4.14). Otolith size also did not differ among stations for Dover sole ($P=0.48$), but Pacific sanddab caught at two shallow stations (I and A) had larger otoliths than those caught at station O in deep water ($P=0.002$).

DISCUSSION

Elemental variation

Cross-otolith patterns

Our analyses revealed consistent cross-otolith patterns in concentrations of Sr, K, and P in both species and in Ca for Dover sole. These patterns demonstrate a strong influence of either environment or ontogeny (or both) on concentrations of these elements during the larval and early juvenile periods. Although we cannot discriminate between the effects of environment and ontogeny with certainty, several of our results suggest that cross-otolith patterns in element concentrations are not related to environmental experience but are primarily ontogenetic (endogenous).

The lack of a consistent change in concentrations of Ca, Sr, Cl, Na, and K at or near otolith landmarks associated with settlement (Figures 4.3 and 4.4) clearly shows that cross-otolith patterns in these elements are not reliable records of settlement. Phosphorous may be an

exception. Increases in P concentrations at settlement in >50% of Pacific sanddab suggest P may be a response to the change in habitat (Figures 4.3 and 4.4), but because settlement and metamorphosis coincide in Pacific sanddab, the observed increase could also be related to an internal process. Other results suggest these increases in P are not a response to settlement.

Poor relationships between margin concentrations of P (and other elements) and environmental factors suggests that element concentrations are not determined primarily by temperature or other factors associated with depth (Figures 4.10 and 4.11). None of the elements examined was strongly related to temperature even though temperatures ranged from 6 to 11°C at the time (Figure 4.11). Poor relationships could result if settling fish had only recently arrived at the capture depth. Dover sole and Pacific sanddab initially settle to the outer continental shelf and upper slope, then move inshore to nurseries on the middle shelf (Toole et al., 1997; Donohoe and Markle, MS [Ch. 3]). In addition, some margin analyses did not include the most recently formed increments due to rounding during polishing. However the effect of these biases was probably small because settling fish move in the same direction (inshore) and the rate of movement appears to be slow in both species (Toole et al., 1997; Donohoe and Markle, MS [Ch. 3]). Because margin concentrations were poorly related to depth of capture, we conclude that cross-otolith patterns after settlement, including the observed increases in P, are not records of settlement and inshore movement. Our results are consistent with those of Thresher et al. (1994) who concluded that settlement had no effect on otolith concentrations of Ca, Na, Cl, K, or S, and only a slight effect on Sr in *Nemadactylus macropterus* entering estuarine nursery areas.

The stability of most elements at settlement also suggest that element concentrations are not sensitive to changes in environment. Both species probably experience the largest change in environmental conditions at settlement. Although differences in salinity and water chemistry among pelagic and benthic habitats are probably small, temperatures on the bottom are several degrees colder than in the upper water column and there is also a shift in available prey.

However except for P, element concentrations were stable at settlement. This disparity suggests that the large variations in Sr and P before settlement are not a response to a smaller change in environment during the larval period. Because element concentrations did not shift in response to settlement and were not related to temperature or depth after settlement, it is unlikely that cross-otolith patterns are records of environmental experience, which in turn suggests that the observed patterns in Sr, K, P, and Ca in Dover sole and Pacific sanddab are primarily ontogenetic.

Previous studies have suggested that Sr concentrations (and Sr/Ca ratios) are inversely related to temperature (Radtke, 1989; Townsend et al., 1989, 1995). However the cross-otolith patterns in Sr concentration in Dover sole and Pacific sanddab do not correspond to thermal histories. If Sr concentrations were inversely related to temperature, the observed Sr pattern (Figures 4.3 and 4.4) would suggest both species begin life in cool water, continue to move into progressively warmer water throughout the pelagic period, and then settle and remain in warm water. This sequence is not consistent with our knowledge of the early life history. Eggs and early stages of both species are offshore in relatively warm upper 50 m of the water column (Pearcy et al., 1977; Urena, 1989; Doyle, 1992). Dover sole appear to move deeper into colder water as metamorphosis begins, then move inshore, perhaps with upwelling water masses (Markle et al., 1992). Late larval Pacific sanddab also move deeper in the water column as metamorphosis progresses (Sakuma and Larson, 1995). Both species are likely to experience colder water as they settle to the upper slope and then warmer water as they move inshore. Thus the disparity between the Sr and temperature histories supports our earlier conclusion that Sr concentrations are not inversely related to temperature in either species.

Sadovy and Severin (1992, 1994) suggested that Sr/Ca ratios are inversely related to growth rate, and that observed relationships between Sr/Ca ratios and temperature were due to correlations between temperature and growth. Sr concentrations in Dover sole and Pacific sanddab do appear to be inversely related to otolith growth during the larval period. The steady

decrease in Sr concentration in the clear central region coincides with a gradual increase in increment widths in the clear central region in both species (Toole et al., 1993; Donohoe and Markle, MS [Ch. 2]). During metamorphosis however, as the opaque region and accessory primordia form, otolith growth rates increase dramatically, tripling in Pacific sanddab, and somatic growth in length temporarily slows or halts (Toole et al., 1993; Donohoe and Markle, MS [Ch. 2]). Sr concentrations did not dramatically decrease or increase as the opaque region formed as would be expected if Sr concentrations were tightly coupled to either otolith growth or somatic growth in length. The relative stability of Sr during this period suggests that if Sr concentrations are related to otolith or somatic growth, the relationships are weak. Toole et al. (1993) also noted that Sr/Ca ratios in Dover sole were not inversely related to somatic growth during metamorphosis, but a seasonal inverse relationship was observed in larger juveniles. General relationships between Sr/Ca ratios and growth rate have been observed in several species, but much of variation remained unexplained (Kalish, 1989; Sadovy and Severin, 1994). In one of the few studies that have directly compared Sr/Ca ratios to otolith growth, Sr/Ca ratios were not related to increment widths in juvenile *Girella elevata* (Gallahar and Kingsford, 1992).

The exact cause of the cross-otolith pattern in Sr remains unclear. Similar cross-otolith patterns in Sr and Sr/Ca ratios during the larval and early juvenile period have been observed in several groups of fishes, but interpretation of these patterns has differed. Kalish (1991) suggested that a decrease in Sr during the larval period was due to increased discrimination between Sr and Ca by the gills and integument during development. Tzeng and Tsai (1994) observed a decline in Sr around metamorphosis in otoliths of young *Anguilla japonica* and concluded the pattern was related to decreased salinity as fish migrated into freshwater. Otake et al. (1997) observed a similar decline in Sr/Ca ratios in otoliths of metamorphosing *Conger myriaster*, but concluded the pattern was related to metamorphosis and the break down of a unique Sr-rich matrix. Furthermore, Tzeng and Tsai (1994) noted that the Sr pattern in *Anguilla japonica* was inversely related to the pattern of increment widths and an analysis of data

presented by Otake *et al.* (1997) show that Sr/Ca ratios in *Conger myriaster* were inversely related to increment widths ($r^2 \sim 0.80$). These studies do suggest a link between Sr concentration and metabolic rate.

Sediment experiment

Results of the laboratory experiment suggest that element concentrations were not sensitive to sediment type (Figure 4.13), but the power of the experiment was probably low. Conditions at sea prevented collection of sediments and fish from a greater range of depths and habitats. Sample sizes were also small because some Dover sole and all Pacific sanddab died on board ship. In addition, increases in Sr concentrations in 3 of 4 treatments may indicate that Dover sole were stressed by laboratory rearing. Kalish (1992) observed a similar response of elevated Sr due to stress in both laboratory and wild fish. Laboratory-induced stress can also alter the relationship between temperature and Sr concentration (Townsend *et al.*, 1989). Stress may have influenced deposition of other elements as well. Increments formed in the laboratory were also less distinct than those formed in the wild. Similar changes in otolith growth in captive fish have been reported for many species (Kalish, 1989). Consequently, the use of laboratory experiments for the study of elemental composition in Dover sole, and perhaps other larval flatfishes, is limited.

Individual bias

Strong correlations between concentrations near the core and concentrations near the margin show that much of the variation in Cl (both species) and K (Dover sole) among fish was present early in life and persisted in juveniles. These correlations suggest there are large baseline (fixed) differences in concentrations of Cl and K among individuals. Early differences in Cl concentration persisted later in life because Cl was generally unaffected by ontogeny or environmental experience in either species (Figures 4.3 and 4.4). In contrast, K concentrations showed strong ontogenetic trends in both species. Early differences in K concentration

persisted in Dover sole because K concentrations increased at similar rates in all fish (Figure 4.3). However, K concentrations increased at different rates among developing Pacific sanddab, which obscured early differences (Figure 4.4). Early differences in Ca concentration were also partially obscured by variable rates of increase during development.

There is some evidence of large baseline differences in Cl concentration among individuals in other species. Differences in otolith composition among geographic groups were greatest for Cl in *Nemadactylus macropterus* and *Thunnus maccoyii* (Thresher et al., 1994; Proctor et al., 1995). Differences in Cl among *Thunnus maccoyii* were present across the otolith (Proctor et al., 1995), indicating that Cl concentrations were established early in life. Concentrations of K near the otolith core also differed among *Nemadactylus macropterus* from different geographic locations (Thresher et al., 1994).

Although differences in concentrations of Cl and K were set early in life, it is not known if these differences have a genetic basis. Baseline differences may be genetic or may have been established during the egg or early juvenile period. Microprobe analyses cannot distinguish between these two hypotheses because elemental concentrations, even those measured entirely within the core region, may reflect environmental experience during the egg stage or maternal experience (Kalish, 1990; Reiman et al., 1994). Thresher et al. (1994) tentatively concluded that baseline differences in elemental concentrations have a genetic basis. We suspect that baseline differences in Cl and K in Dover sole and Pacific sanddab also have a genetic basis. However, a genetic analysis or controlled laboratory experiment rearing sibling and non-sibling groups is required to determine if concentrations of Cl and K are affected by genotypes.

Distribution of settling flatfish

Our results show that margin concentrations of Cl and K' in Dover sole and Cl in Pacific sanddab differed among stations as little as 5-8 km apart, and that fish with similar

margin concentrations tended to occur at the same station. Differences in otolith composition among stations did not appear to develop after settlement in response to local environmental conditions. As previously shown, differences (and similarities) in margin concentrations of Cl and K' were present early in life, neither element appeared sensitive to environmental conditions, and concentrations did not converge after settlement (Figures 4.6 and 4.7). Proctor and Thresher (1998) have suggested recently that concentrations of Cl, K, and other elements can be affected by standard specimen handling and otolith preparation techniques. The methods we used, freezing of larvae and rinsing polished otoliths with distilled water, had the smallest effect on element concentrations in that study (Proctor and Thresher, 1998). More importantly, after otoliths were extracted, the order of preparation and analysis was mixed, reducing the possibility of systematic bias among stations. We conclude that differences among stations are not artifacts of otolith preparation and analysis. Differences therefore suggest that recently settled flatfishes are not distributed at random over the continental shelf and slope, but are segregated in groups or patches.

If differences in otolith composition are genetic, then the observed distributions suggest meso-scale genetic heterogeneity or patchiness at settlement in both species. At a broader scale, a genetic analysis of adult Dover sole suggested the population along the west coast of North America was well-mixed, but also revealed evidence of regional population structure (Stepien, 1995). This pattern of fine- to meso-scale genetic patchiness (chaotic patchiness) within a broader panmictic population has been observed in other marine fishes (Johnson et al., 1994; Doherty et al., 1995) and invertebrates (Johnson and Black, 1984; Johnson et al., 1993; Hedgecock, 1994; McMillen-Jackson et al., 1994). Genetic patchiness may result from differential mortality of particular phenotypes, or from temporal or spatial patchiness in settlement. Differential selectivity and survival of particular phenotypes among stations seem unlikely for settling Dover sole and Pacific sanddab given the apparent uniformity of the continental shelf habitat. Genetic patchiness probably resulted from patchy settlement.

Patchiness among benthic fish implies patchiness in the plankton. Furthermore, these groups of larvae must have formed early in life and tended to remain together for the entire pelagic period. This conclusion is somewhat surprising given the long pelagic phase of both species. Dover sole are pelagic for 9 months to 2 years and Pacific sanddab are pelagic for 4-7 months (Markle et al., 1992; Butler et al., 1996; Donohoe and Markle, MS [Ch. 3]). Both species are probably transported long distances by strong alongshore currents. Markle et al. (1992) hypothesized that Dover sole larvae drift south in the California Current then migrate into deeper water and are returned by the northward flowing Davidson Current. Larval patches might be established by initial conditions such as time and place of spawning and maintained by behavior (schooling, feeding on aggregated prey), ontogenetic changes in buoyancy, and oceanographic processes such as meso-scale eddies and fronts. High densities of Pacific sanddab larvae have been observed near fronts off central California (Sakuma and Ralston, 1995). Females are batch spawners and genetic half-sibs are likely to be released over an extended period so apparent patchiness likely has several levels of complexity. Analysis of a highly variable genetic locus combined with otolith microchemistry analysis is needed to better understand meso-scale larval patches.

The size of these patches is difficult to estimate from our limited data. Margin concentrations were similar among fish at stations 9-122 km apart, but it is not clear if these fish are members of a single large patch or members of several smaller patches that have overlapping otolith composition. Because fish were classified based on only one or two elements that showed fixed differences, our ability to discriminate among patches was limited. However, differences among stations only 5-8 km apart suggest some benthic patches may be small, on the order of 5-10 km. This estimate is consistent with patch sizes observed in other species. Collections of reef fish larvae or settled juveniles at multiple sites suggest that larval patches vary in size from ~1 km to >40 km (Victor, 1984; Doherty, 1987; Williams and English, 1992; Thorrold et al., 1994).

Otolith composition has not been used previously to discriminate among cohorts. Previous studies have used otolith composition or 'elemental fingerprints' to discriminate among stocks, populations, or among geographic areas. Otolith composition has been shown to differ among groups of marine fish from sites 10-100s of km apart (Edmonds et al., 1989, 1992) and among sites within the same bay (Thorrold et al., 1998). Our results suggest that otolith composition is a useful tool for discriminating among settling cohorts or sub-cohorts. While some cohorts can be identified based on differences in length-frequency distributions or backcalculated spawn dates, differences in otolith composition can reveal the presence of multiple cohorts when lengths and spawn dates overlap or for species that are difficult to age. Thus otolith composition can serve as a natural tag that may aid the study of larval drift, patch dynamics, and small scale patterns of settlement.

Conclusions

In conclusion, our study suggests that elemental histories are not reliable records of settlement and environmental experience in Dover sole and Pacific sanddab. We found little evidence that element concentrations were sensitive to environmental conditions. Rather, otolith microchemistry of larvae and early juveniles appears to be influenced primarily by ontogeny and individual (possibly genetic) biases. However, 50 to 72% of the variation in Ca, K, Na, and P in individual fish was unexplained. This short-term variation may be induced by environmental events or represent random variation. The interaction between ontogenetic trends and individual bias for K shows that the relationship between otolith composition and controlling factors is complex and that ontogenetic bias may be difficult to eliminate. Differences in Cl and K among fish were largely inherent, may have a genetic basis, and revealed small-scale population structure not evident from other characters. These results suggest otolith composition can serve as natural tags that are useful for discriminating among cohorts and may aid the study of larval drift and patch dynamics.

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CHAPTER 5

Sources of Variation in Time Series of Otolith Growth of Settling Pacific Sanddab, *Citharichthys sordidus* (Paralichthyidae)

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ABSTRACT

We examined variation in time series of daily increment widths to understand factors influencing growth of late larval and early juvenile Pacific sanddab (*Citharichthys sordidus*). Recently settled fish were collected off central Oregon in March 1992, 1993, and 1994 and pelagic fish were collected off central California in May 1994. Otolith radius had a strong effect on otolith growth rate, explaining 48% of the overall variation (ANOVA, $F=541.1$, $P<0.001$, $n=20,232$). After removing the effect of otolith radius, calendar date explained 12-26% of the variation in daily otolith growth anomalies for the 4 survey periods. Regression showed that daily otolith growth anomalies increased with sea surface temperature (SST) in 1992 and 1994 ($r^2=0.49$ and 0.53) although the significance was marginal ($P=0.06$ and 0.07) due to strong autocorrelation in both time series. Mean otolith growth rates were ~30% higher in 1992 and 1993 than in 1994 during settlement and inshore movement. Slower growth in 1994 appears to be due to a combination of slightly lower temperatures, earlier settlement, and changes in the stratification of the water column that provide a potential thermal advantage to late settlers.

Daily otolith growth rates of individual fish varied during early life. Day-to-day changes (within fish) accounted for 67-78% of the variation in daily otolith growth anomalies. Correlation coefficients (r) for all possible pairs of growth histories ranged from -0.92 to +0.97. Asynchronous growth of most fish does not support the hypothesis that larval growth is regulated primarily by broad scale processes. Cluster analysis identified 3-4 major growth patterns in each of the 4 surveys. Discriminant analysis correctly classified 71% of pelagic fish and 25-45% for benthic fish using the jackknife method, suggesting that major growth patterns were distinct in pelagic fish.

Pelagic fish with the same major growth pattern tended to occur at adjacent stations, indicating segregated distributions. This segregation broke down at settlement, perhaps due to the vertical migration behavior of settling fish. Pelagic fish with growth pattern 'B' occurred

most often around Monterey Bay. Moreover, growth pattern B resembled the SST history in Monterey Bay, suggesting that growth patterns reflect the local temperature regime and can serve as natural tags that allow study of larval patch dynamics and patterns of settlement.

INTRODUCTION

Recruitment processes are thought to operate at a variety of spatial and temporal scales (Haury et al., 1977; Doherty, 1987; Mullin, 1993; Doherty et al., 1995; Brodeur, 1997). Synchronous time series of recruitment of species or stocks provide evidence that broad-scale spatial processes influence year class size (Koslow, 1984; Hollowed et al., 1987; Thompson and Page, 1989). Similarly, decadal patterns of fish recruitment, oceanographic conditions, and zooplankton biomass have been described (Roemmich and McGowan, 1995; Brodeur et al., 1996; Beamish et al., 1997; Francis et al., 1998; Hare et al., 1998). At the other end of the spectrum, small-scale and meso-scale processes, such as those that affect the distribution and abundance of food (Lasker, 1975), larval patchiness (McGurk, 1986), or transport of larvae (Shanks, 1983) are also thought to be important. Identifying the appropriate scales of the processes regulating recruitment is a prerequisite for designing sampling programs and testing relationships between environmental and recruitment data (Taggart and Frank, 1990; Mullin, 1993).

Growth rate is one of several processes affecting recruitment and is especially important because small changes during early life may result in large changes in stage duration, survival, and ultimately year class strength (Houde, 1987, 1989). Although research has focused on the earliest larval stages, growth and survival of late larval and early juvenile stages may also be critical determinants of year class success (Sissenwine, 1984; Peterman et al., 1988; Bradford, 1992; Campana, 1996).

Pacific sanddab, *Citharichthys sordidus*, occur along the western coast of North America from Baja California to the Bering Sea (Miller and Lea, 1972). Spawning occurs throughout the year with a seasonal peak from August to October and a smaller peak in January and February (Arora, 1951; Urena, 1989; Doyle, 1992; Moser et al., 1993). Eggs and pelagic larvae are dispersed offshore, beyond the edge of the continental shelf (Pearcy et al., 1977; Doyle, 1992; Moser et al., 1993; Sakuma and Ralston, 1995) and occur in the California

Current, a system influenced by large-scale processes (Chelton et al., 1982; Francis et al., 1998). Late-staged larvae move inshore and settle to nurseries on the middle continental shelf (Sakuma and Larson, 1995; Donohoe and Markle, MS [Ch. 3]). The settlement process is complex with individuals apparently moving between the pelagic and benthic habitats (Donohoe and Markle, MS [Ch. 3]). During the period 1992-1994, Pacific sanddab off central Oregon showed significant variation in settlement abundance in March, mean larval growth rate, and mean date of settlement (Donohoe and Markle, MS [Ch. 3]).

In this study, we examine variation in time series of daily otolith increment widths to understand patterns of growth variation of Pacific sanddab during the late larval and early juvenile stages. We partition growth variation into ontogenetic, seasonal, and individual components, relate mean growth and temperature, and determine the extent of growth synchrony of three year-classes.

METAMORPHOSIS AND SEASONALITY

Pacific sanddab larvae complete eye migration at 30-52 mm SL and an age of 4-7 months (Sakuma and Larson, 1995; Donohoe and Markle, MS [Ch. 2]). Off Oregon, late-staged Pacific sanddab larvae move inshore and settle to middle continental shelf nurseries in late fall and winter (Donohoe and Markle, MS [Ch. 3]). During the season of maximum settlement, sea surface temperature (SST) tends to decline from October to January and rise from January to March (Figure 5.1). Although differences among years varied with season, SSTs were often on the order of 1-2 °C cooler in 1994 than in 1992 or 1993. Estimated bottom temperature at 100 m showed greater short term and interannual variability (Figure 5.1). Thermal stratification, the difference between SST and estimated bottom temperature, showed a consistent seasonal pattern. The difference between temperatures at the surface and 100 m was about 3-4 °C in October, declined to a minimum in January, and rose to 2-3 °C by late March (Figure 5.1). Temperatures recorded during our March surveys show a similar pattern, with mean bottom

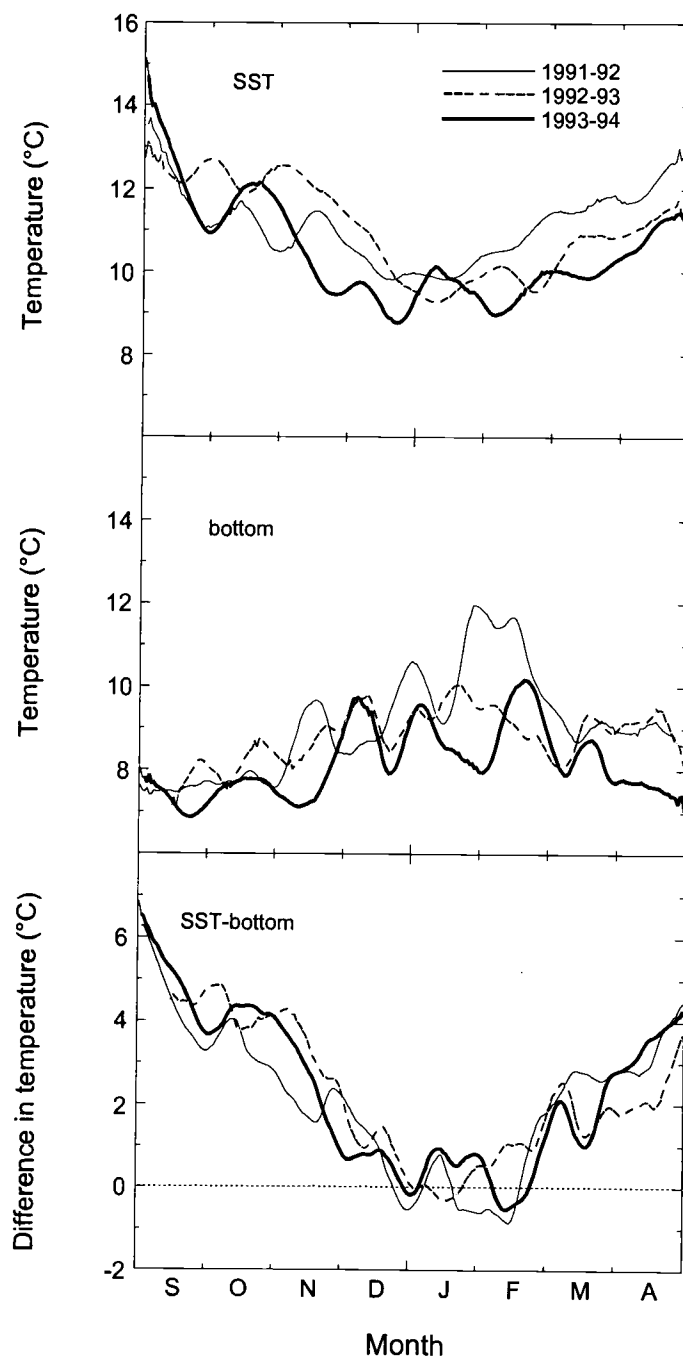


Figure 5.1 Seasonal variation in sea surface temperature (SST) and estimated bottom temperature at the 100 m isobath off Newport, Oregon in 1991-1994. SST is the mean of daily temperatures at Coos Bay and buoys off the Columbia River and Stonewall Bank. Bottom temperatures were estimated from sea level height at Neah Bay, Washington using the equation of Kruse and Huyer (1983).

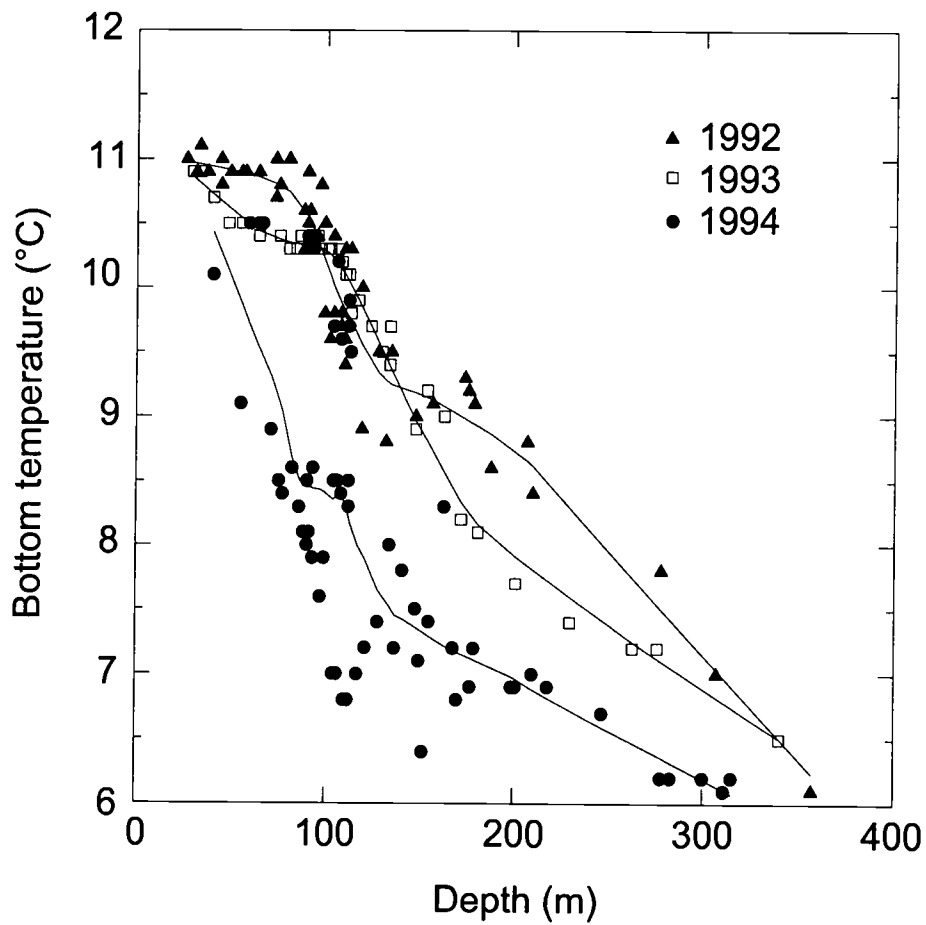


Figure 5.2 Near bottom temperatures at stations on the continental shelf and upper slope off central Oregon during surveys in March 1992, 1993, and 1994. Temperatures were recorded by a bathythermograph attached to trawl headrope.

temperatures on the continental shelf around 2 °C cooler in 1994 than in 1992 or 1993 (Figure 5.2).

Although the importance of temperature on growth is still debated (Campana et al., 1996; Sinclair and Swain, 1996), it is one of the most important environmental variables regulating growth of larval and early juvenile fishes. Early-spawned Pacific sanddab probably settle early during declining or low surface water temperatures and experience relatively little thermal change during settlement while those spawned later should settle during rising surface water temperatures and experience stratified thermal conditions. The spring transition to seasonal upwelling and offshore transport may be a major factor confining settlement to late fall and winter.

METHODS

Collections

Benthic larval and early juvenile Pacific sanddab (18-49 mm SL) were collected from the continental shelf and upper slope off central Oregon (Figure 5.3). Benthic tows were made at depths of 75 to 357 m for five minutes using a 27.4 m headrope commercial shrimp trawl lined with 6.4 mm mesh in the cod end. Surveys were conducted in two transects located about 100 km apart (Figure 5.3). The northern transect was sampled in March 1992, 1993, and 1994. The southern transect was sampled in March 1992 and 1994, but few Pacific sanddab were caught at these stations. We examined fish from 3-8 stations in each of the 3 years (Table 5.1). Distance among stations ranged from 4 to 103 km, but most were <32 km apart. We also examined a few fish collected from the same general area in May 1994 to increase seasonal coverage.

Pelagic Pacific sanddab (30-46 mm SL) were obtained from the 1994 juvenile rockfish survey conducted by NMFS scientists off central California (cruise number DSJ-9406). Fish were collected from the upper 30 m of the water column using a 26 m x 26 m modified Cobb

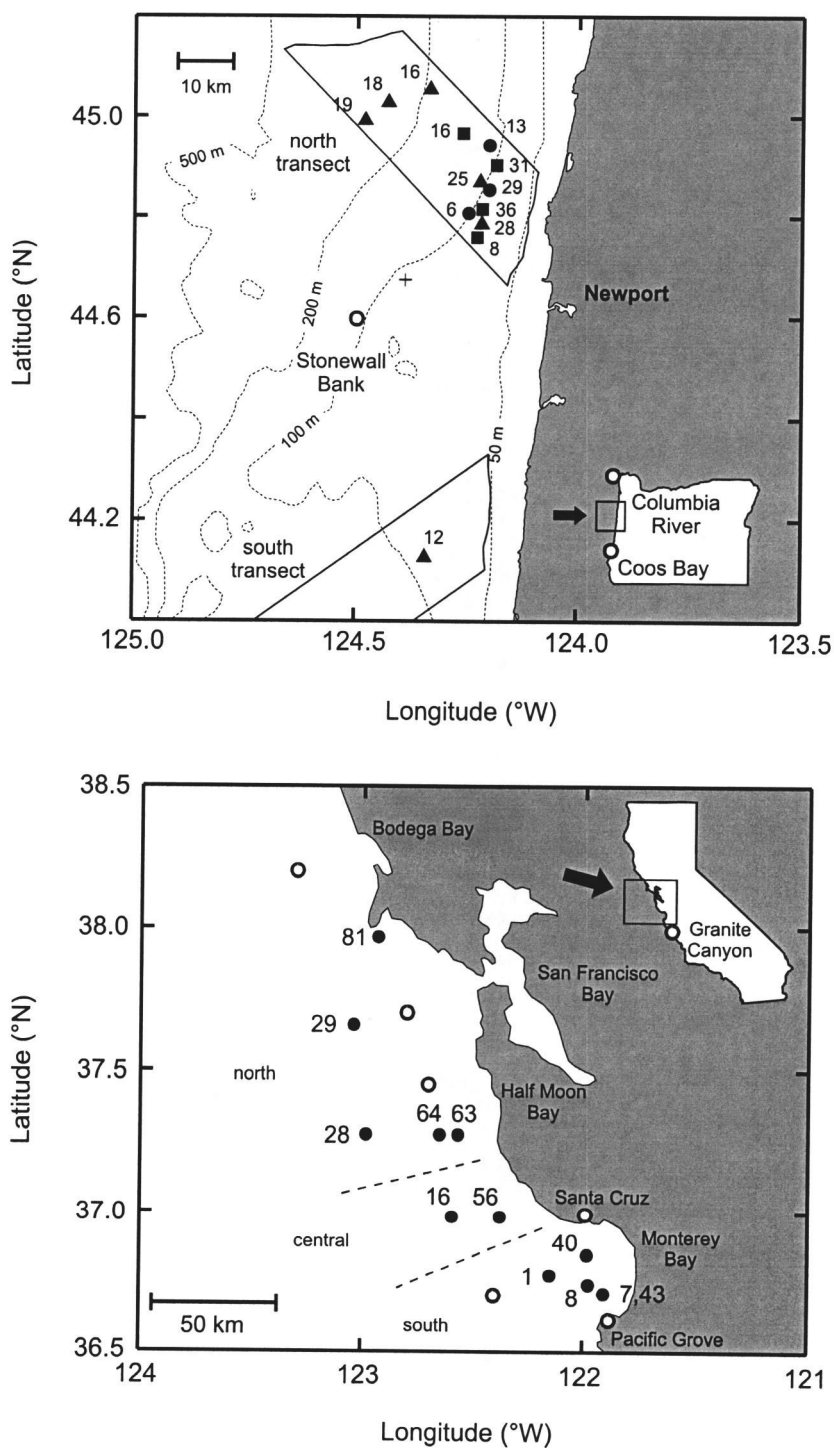


Figure 5.3. Location of stations where Pacific sanddab were collected. top: benthic tows off central Oregon in: \blacktriangle = March 1992, \blacksquare = March 1993, \bullet = March 1994, $+$ = May 1994. bottom: NMFS midwater tows off central California in May 1994. Open circles are locations of buoys and shore stations that monitored surface temperatures.

midwater trawl. We examined a non-random subsample of fish collected at 12 stations located between Point Reyes and the Monterey peninsula over a 2 week period (Figure 5.3, Table 5.1). Stations were sampled in two sweeps of the survey area. Stations 1-29 were sampled in the first sweep from May 18-25 and stations 40-81 from May 26 - June 1 in the second sweep. Distance among stations ranged from 5 to 153 km. Stations were grouped into 4 regions based on location and time of collection; north, central, south (Monterey Bay) during sweep 1, and south during sweep 2. Details of the survey design are provided in Wyllie Echeverria et al. (1990).

Otolith preparation and measurement

In the laboratory, standard length (SL) was measured to 0.1 mm. Benthic fish were frozen at sea and pelagic fish were preserved in ethanol but lengths were not corrected for potential shrinkage, which prior experience suggested would be small. Fish were classified into four metamorphic stages based on the position of the right (migrating) eye: stage 0 - eyes symmetrical, stage 1 - eye beginning to migrate but right of midline, stage 2 - eye intersecting the midline, and stage 3 - right eye migrated to left side. Individuals classified as stage 3 have not necessarily completed metamorphosis. Sagittae were not suitable for analysis because their growth is complicated by the formation of accessory primordia during metamorphosis (Donohoe and Markle, MS [Ch. 2]). Asterisci were removed, cleaned of adhering tissue, and mounted in thermoplastic resin. Otoliths were ground in the sagittal plane on both faces to the level of the central primordium (core) to expose increments, then polished with 0.05 μm alumina powder.

Increment widths were measured from the otolith core to the margin along the longest growth axis (Figure 5.4) to produce a time series of daily otolith growth for each fish. Previous studies suggest that increments form daily in asterisci of Pacific sanddab (Donohoe and Markle, MS [Ch. 2], MS [Ch. 3]). Measurements were made at 400-1000x with the aid of an image

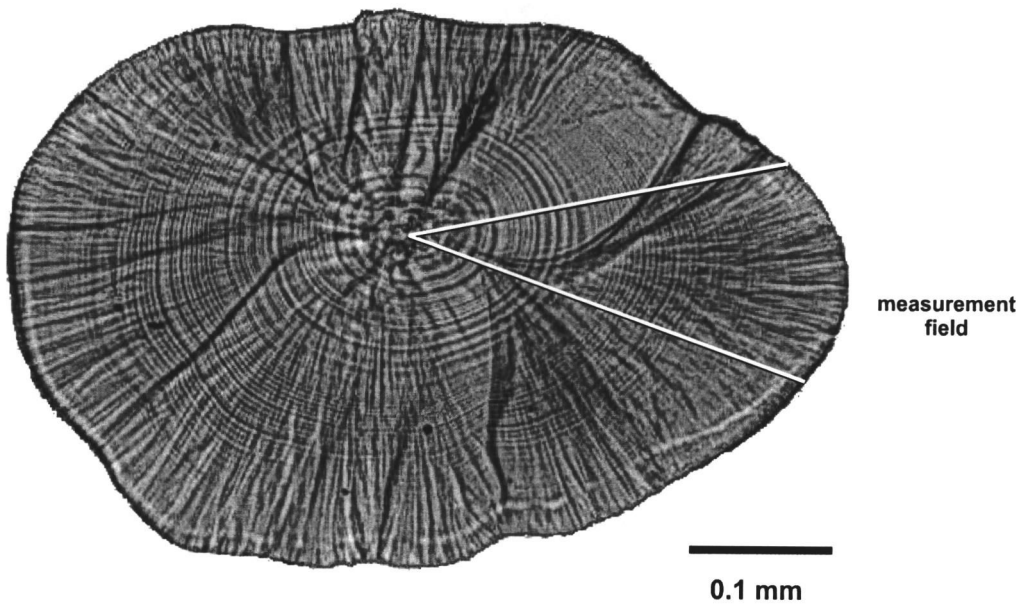


Figure 5.4 Photograph of a polished asteriscus from a 43.7 mm SL stage 3 Pacific sanddab (*Citharichthys sordidus*). Increment widths were measured along the longest growth axis within the wedge-shaped region.

analysis system (Optimas). Resolution of the system at was generally better than 0.1 μm .

Otoliths from the 4 surveys were mixed within the analysis sequence to reduce potential bias.

Radial distance of each increment from the otolith core (otolith radius at increment formation) was also recorded. The calendar date that each increment formed was backcalculated from date of capture and increment number counted back from the otolith margin.

Time series of increment widths (μm) were log-transformed using $\ln(\text{width}+1)$, then filtered using a 5-day moving average function to reduce noise. Because the asteriscus does not form until ~ 50 d after hatching (Donohoe and Markle, MS [Ch. 2]), time series do not provide a record of growth during the early larval period. We have adopted much of the terminology of Ralston (1995) to describe components of otolith growth.

Analysis of mean growth patterns

The effect of ontogeny on otolith growth rate is usually large and can be modeled as a function of either size or age. Previous studies have used age or increment number as the ontogenetic covariate (Maillet and Checkley, 1991; Ralston, 1995). However a preliminary analysis showed that in Pacific sanddab, otolith growth rate was more closely related to otolith size than to increment number. Consequently, otolith growth rate was modeled as function of otolith radius. Because fish from any one survey had similar birthdates, otolith radius covaried with the calendar date of increment formation. This covariation precluded the use of a two-way analysis of variance to simultaneously identify radius and date effects (Ralston, 1995). To reduce this covariation, data from all surveys were pooled to include fish which were spawned over the broadest possible range of dates and environmental conditions. The mean radius-specific growth rate (\bar{G}_r) was calculated as follows. For each fish, increments within each 0.01 mm interval in otolith radius were pooled, and the mean growth rate [$\ln(\text{width}+1)$] was calculated for each interval. Interval means for all fish were pooled by otolith radius. Least-squared means (grand means) for each radius interval were calculated using one-way analysis of

variance. Finally, a polynomial model was fit to the least-squared means to produce a smooth continuous function that allowed estimation of \overline{G}_r for any otolith radius.

The effect of otolith radius on otolith growth was removed by subtracting the mean radius-specific growth rate for all fish (\overline{G}_r) from each observation. Specifically, this deviation or otolith growth anomaly (A) was calculated as: $A_{ir} = (G_{ir} - \overline{G}_r) / \overline{G}_r$ where G_{ir} is the otolith growth rate for individual i at radius r and \overline{G}_r is the radius-specific growth rate. Otolith growth anomalies were expressed as a proportion because preliminary analysis showed that the variance of deviations covaried with the mean (\overline{G}_r).

The radius-specific pattern of somatic growth was estimated from otolith growth and the relationship between standard length and asteriscus radius. This relationship was best described by a three segment model which incorporates a function to smooth the transition between segments (Bacon and Watts, 1971; Laidig et al., 1991). The slope of this relationship was multiplied by mean increment width (untransformed) to yield mean somatic growth rate.

The effect of calendar date on otolith growth rate was evaluated for each of the 4 surveys using one-way analysis of variance (ANOVA). Daily otolith growth anomalies served as the dependent variable and calendar date as the grouping variable.

The date of settlement was estimated based on otolith radius. Pacific sanddab initially land on the upper slope prior to completion of eye migration (CEM) then move inshore, reaching the middle shelf around CEM (Donohoe and Markle, MS [Ch. 3]). Asterisci of fish on the upper slope and outer shelf are generally <0.225 mm in radius while those on the middle shelf are >0.225 mm (Donohoe and Markle, unpublished). Settlement was estimated to occur on the date the asteriscus increment at a radius of 0.225 mm formed.

Environmental data

Records of daily sea surface temperatures (SST) for 1991-1994 were obtained from shore stations and moored buoys located along the coasts of Oregon and central California (Figure 5.3). Shore station data were compiled by Scripps Institution of Oceanography, San Diego and buoy data were obtained from the National Data Buoy Center (NDBC), a part of the National Oceanic and Atmospheric Administration (NOAA). Daily temperatures from several locations within each region were averaged to represent the broad-scale temperature and reduce the occurrence of missing data. Off California, SST data from shore stations at Santa Cruz and Granite Cove and buoys off Bodega Bay and San Francisco Bay were averaged (Figure 5.3). SST data from buoys at Half Moon Bay and Monterey Bay were incomplete, but were used in some meso-scale analyses. Off Oregon, SST data from the shore station at Coos Bay and buoys at Stonewall Bank and Columbia River were averaged. In addition, bottom temperatures at the 100 m isobath off Newport, Oregon were estimated from sea level height at Neah Bay, Washington using the equation of Kruse and Huyer (1983). Surface temperature and temperature profiles were also recorded at each station during all surveys.

Cross-correlations and adjustments for autocorrelations

Relationships between time series of mean otolith growth anomalies and SST were evaluated using linear regression. Significance of relationships was evaluated after compensating for serial autocorrelations in both time series. Serial autocorrelations were estimated using the methods of Box and Jenkins (1976). Both the otolith growth and temperature time series were found to be highly autocorrelated, and thus observations were not independent. To compensate, sample size was adjusted downward using the "modified Chelton" method of Pyper and Peterman (1998). Briefly, the product of the autoregressive parameters for the first $N/5$ lags for the growth and temperature time series were summed and used to calculate the effective sample size (N^*) and critical value of r at the $\alpha=0.05$ level.

Cross-correlations between time series of temperature and otolith growth were estimated at lags of up to ± 30 d to determine if the response of otolith growth lagged behind changes in temperature. All statistical analyses were performed using the Systat statistical package (Wilkinson, 1990).

Individual growth histories

Individual time series of otolith growth were compared to determine if otolith growth of the cohort was synchronous or asynchronous (random). For each survey, individual time series of otolith growth anomalies were compared for fish from 3-6 stations. To maximize the length of the period of comparison, a few of the youngest fish, those with short growth histories, were dropped from the analyses. The number of fish examined for each survey and the length of the period of comparison are shown in Table 5.2. Similarity among individual time series of daily otolith growth anomalies (growth histories) were evaluated using the Pearson correlation coefficient (r) for all possible pairs of fish. To compensate for the effect of autocorrelation on correlations, effective sample sizes and critical values of r were calculated using the methods described above.

Cluster analysis was used to identify natural groups within the variety of growth histories within each survey. Distance (dissimilarity) among individual growth histories was calculated as $1-r$. These distances are not affected by differences in amplitude or means of the time series; shape alone is important. Clusters were joined (linked) using Ward's minimum-variance method. Ward's method uses an analysis of variance approach such that new members are added to a cluster if the addition produces the smallest increase in within-group variance. Groups identified by cluster analysis were fed into a discriminant analysis and jackknife classification success was calculated to determine if the major growth patterns were distinct. Frequency analysis was used to test if fish from particular stations were randomly distributed among clusters.

RESULTS

Mean growth patterns

Ontogenetic variation

Otolith radius had a strong effect on otolith growth rate. Mean otolith growth rate ($\ln[\mu\text{m/d} + 1]$) for fish from all surveys declined slightly after otolith formation, gradually increased, and then declined with otolith radius (Figure 5.5). The equivalent untransformed values indicate that mean growth rate increased from a low of 1.5 $\mu\text{m/d}$ at a radius of 0.04 mm to a peak of 3.4 $\mu\text{m/d}$ at 0.18 mm and declined to 1.7 $\mu\text{m/d}$ at a radius of 0.35 mm. Analysis of variance showed that radial distance (0.01 mm intervals) explained 48% of the variation in otolith growth rate ($\ln[\mu\text{m/d} + 1]$) (ANOVA, $F=541.1$, $P<0.001$, $n=20,232$).

The observed increase in otolith growth rate with radius was due in part to a shift in relative otolith growth. The relationship between standard length and otolith size was not linear, but shifted twice during metamorphosis (Figure 5.6). Changes in slope indicate that relative otolith growth rate temporarily increased 3-fold at a radius of 0.15 mm, remained relatively constant up to 0.38 mm, then decreased 4-fold. The relationship was strong however. A three segment regression model fit to the relationship explained 94% of variation in standard length. The first shift occurred prior to completion of eye migration (stage 3) and roughly coincided with the formation of accessory primordia (AP) in the sagitta, while the second shift coincided with completion of metamorphosis (Donohoe and Markle, MS [Ch. 2]).

Mean somatic growth rate was estimated as the product of otolith growth rate (untransformed) and the slope of the standard length-otolith radius relationship (Figure 5.7). Results indicate that mean somatic growth rate increased from 0.23 mm SL/d at a radius of 0.05 mm to 0.32 mm SL/d at a radius of 0.1 mm, declined to 0.13 mm SL/d at 0.18 mm, then decreased to 0.07 mm SL/d. Mean somatic growth rate declined as mean otolith growth rate continued to increase.

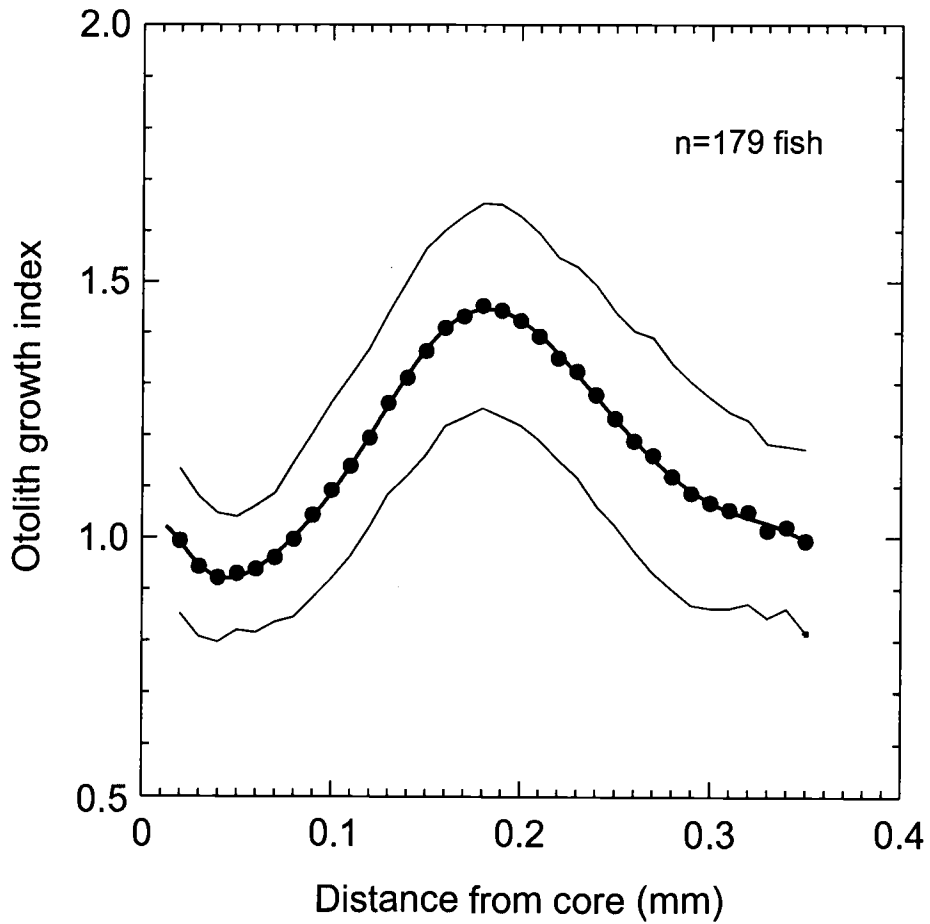


Figure 5.5 Effect of otolith radius on otolith growth rate of Pacific sanddab. Points are the mean otolith growth rate ($\ln[\mu\text{m}/\text{d} + 1]$), thick line is a polynomial fit to the means, and thin lines are ± 1 SD. Data are from 179 fish.

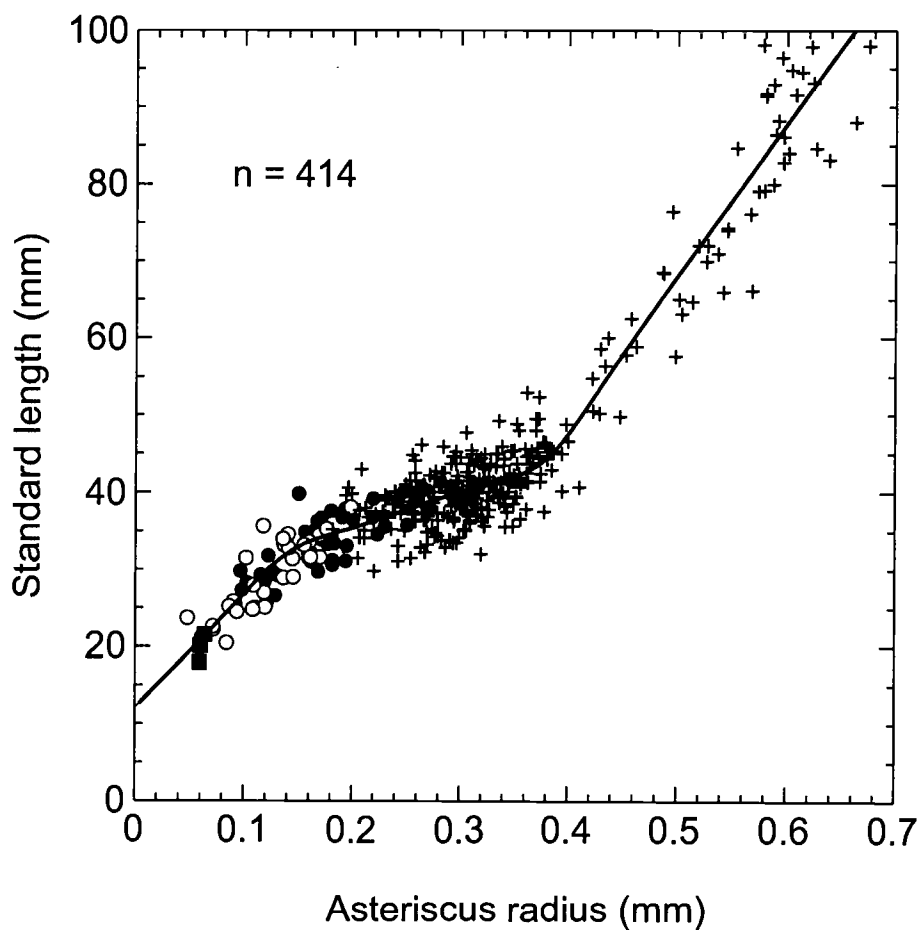


Figure 5.6 Relationship between standard length and asteriscus radius for Pacific sanddab. Symbols indicate metamorphic stage: ■ = 0, ○ = 1, ● = 2, + = 3. Line is a 3 segment regression with a smoothing function between segments.

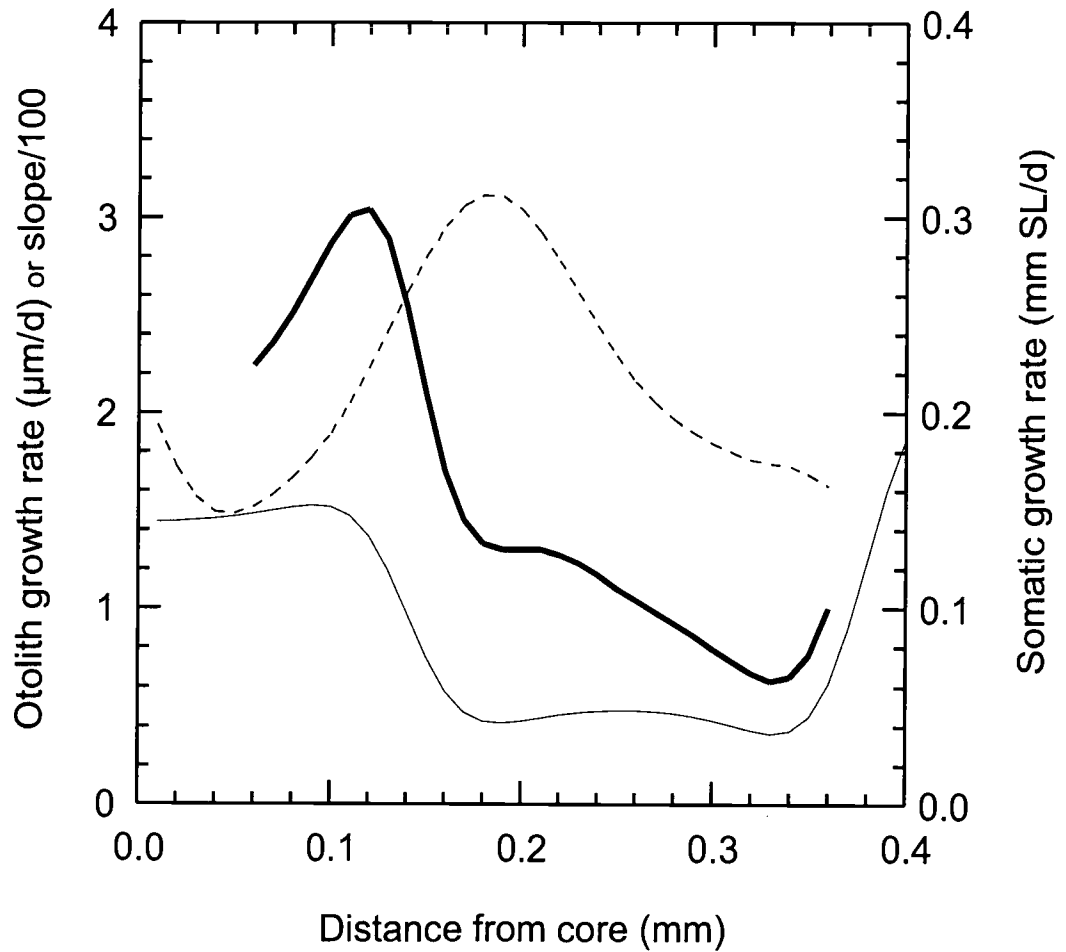


Figure 5.7 Size-related variation in mean otolith and somatic growth rates for Pacific sanddab. Somatic growth rate (thick line) was estimated as the product of the untransformed otolith growth rate (dashed line) and the slope of the relationship between standard length and asteriscus radius (thin line).

Settlement date

Fish from 1994 settled earlier than those from 1992 or 1993 (Donohoe and Markle, MS [Ch. 3]). Relative to February 1, 93% of 1994 fish in this analysis had settled by this date whereas, only 40% of 1992 fish and 32% of 1993 fish had settled by 1 February. Mean otolith growth anomalies were plotted against otolith surrogates for metamorphic stage and were distinctly negative during settlement in 1994 and positive in 1992 and 1993 (Figure 5.8). In contrast, mean anomalies during the pelagic phase of life were quite similar in the three years (Figure 5.8).

Seasonal variation

Seasonal patterns in growth anomalies also showed interannual differences and similarities (Figure 5.9). Early-settling fish in 1994 had negative growth anomalies in February compared to 1992 and 1993 fish. Within years, early settling fish also had negative growth anomalies in February in 1992 and 1993 and in January 1994 (Figure 5.10). During fall and early winter, seasonal growth was similar with positive anomalies in October and November and negative anomalies in December and early January in all 3 years (Figure 5.11). Mean otolith growth anomalies off California in 1994 fluctuated from month to month, with positive anomalies in January and again in late March and early April. Calendar date explained 12-26% of the variation in daily otolith growth anomalies for the 4 survey periods (one-way ANOVA, $P < 0.001$, $n = 3,888-5,506$). The effect of calendar date was strongest in 1992 and 1993 (26% and 25%) and weaker in 1994 off Oregon and 1994 off California (10% and 14%).

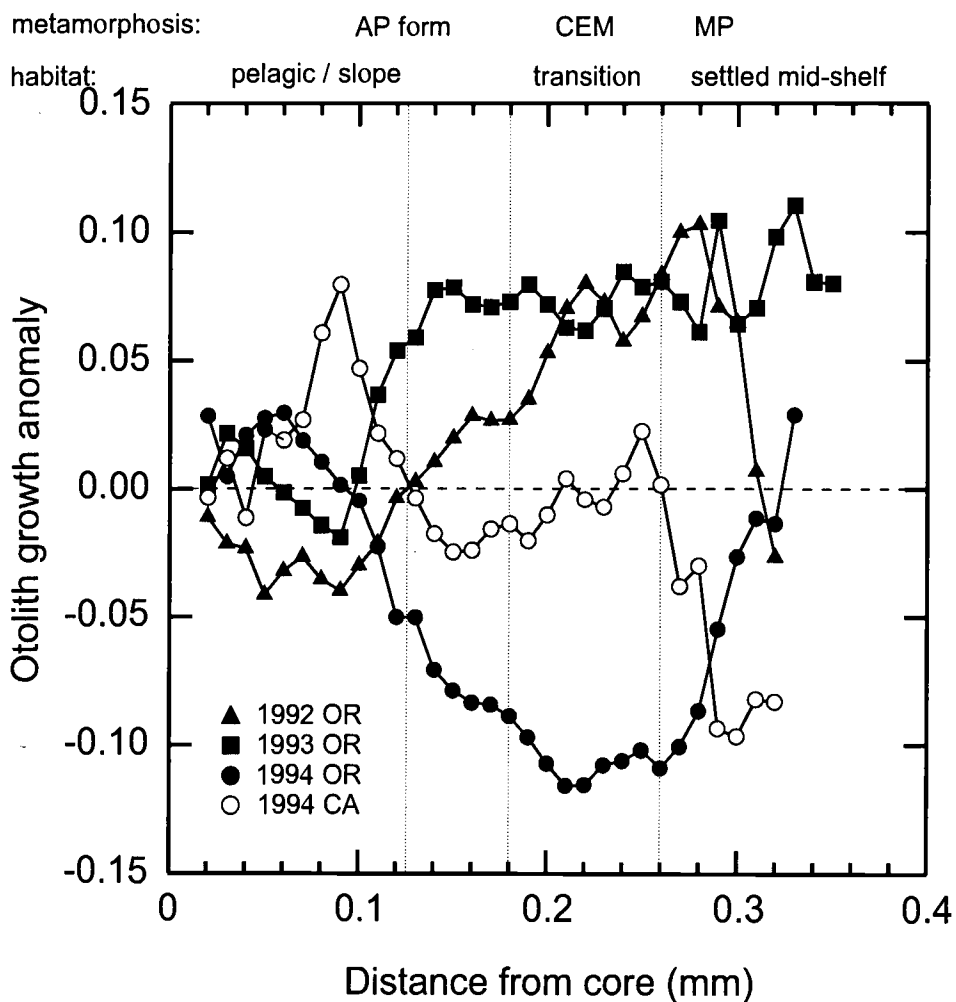


Figure 5.8 Mean otolith growth anomaly by otolith radius for Pacific sanddab for the 4 surveys. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m}/\text{d} + 1]$) for all fish. CEM=completion of eye migration, MP=start of 'metamorphosis proper', AP=accessory primordia.

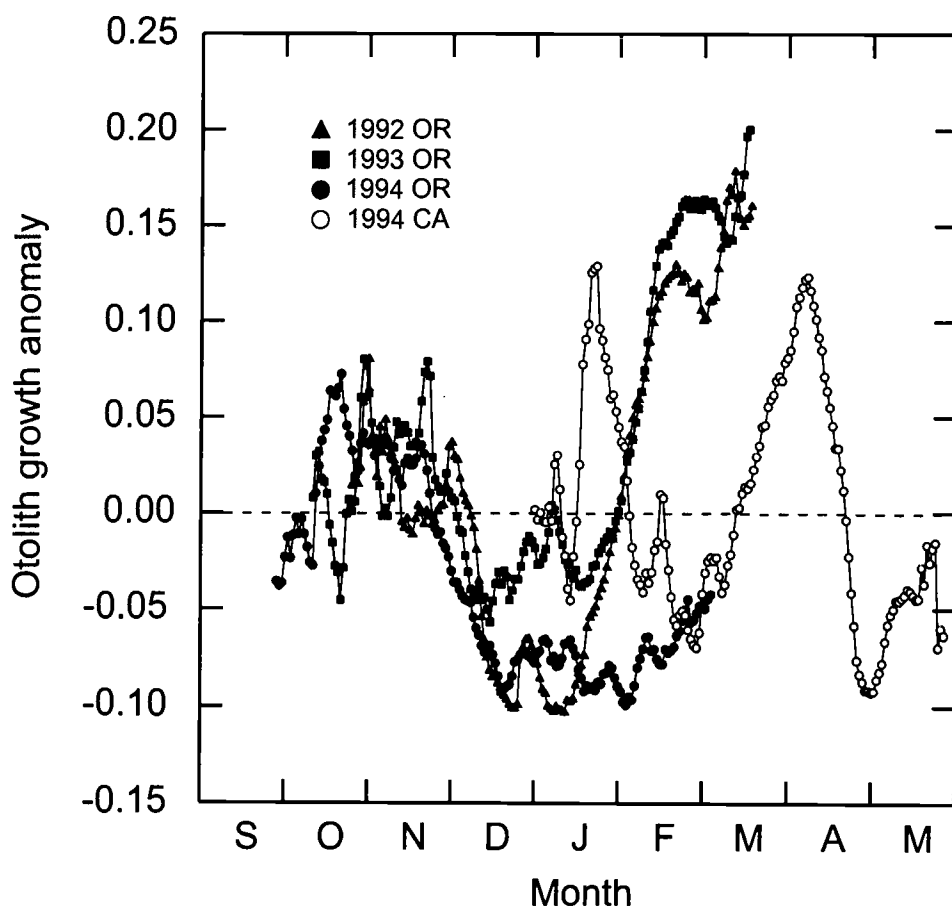


Figure 5.9 Mean daily otolith growth anomaly by calendar date for Pacific sanddab for the 4 surveys. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m/d} + 1]$) for all fish.

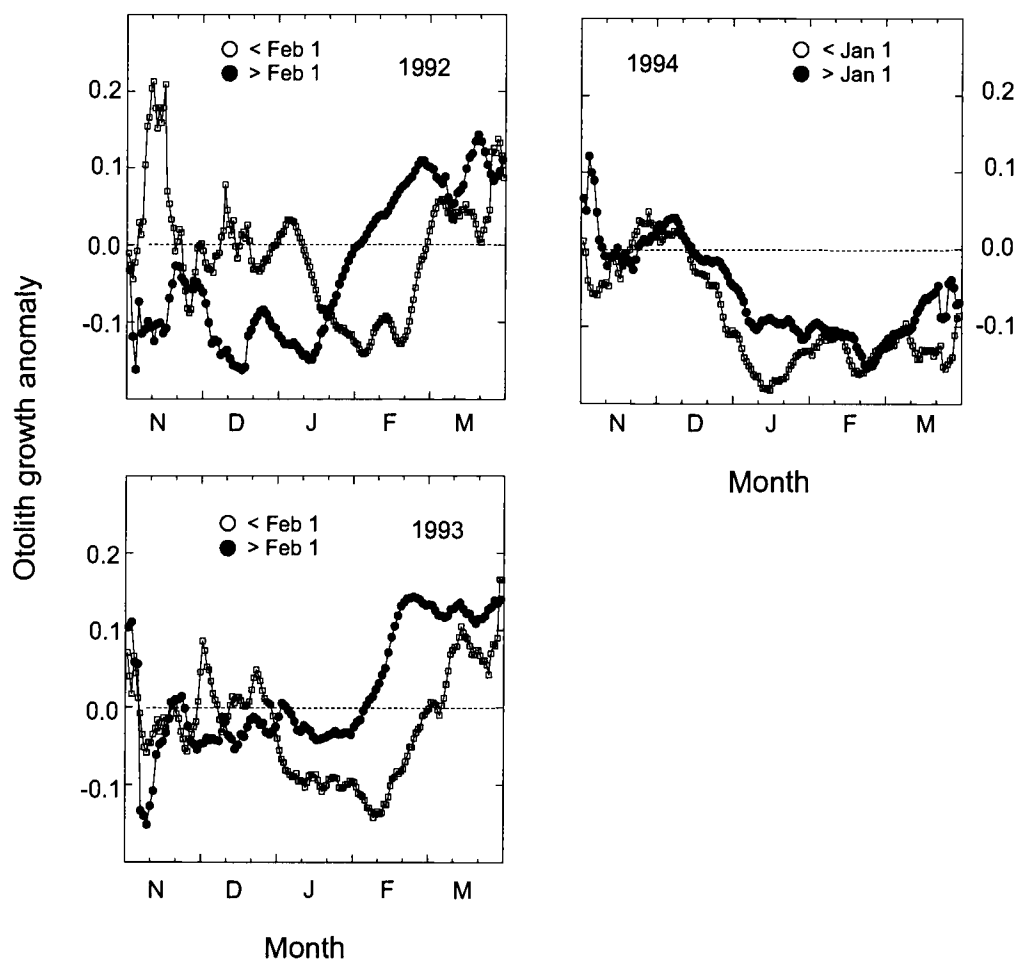


Figure 5.10 Mean daily otolith growth anomaly for early and late settlers by calendar date for Pacific sanddab for the 3 Oregon surveys. Settlement date was estimated from the date of completion of eye migration. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m}/\text{d} + 1]$) for all fish.

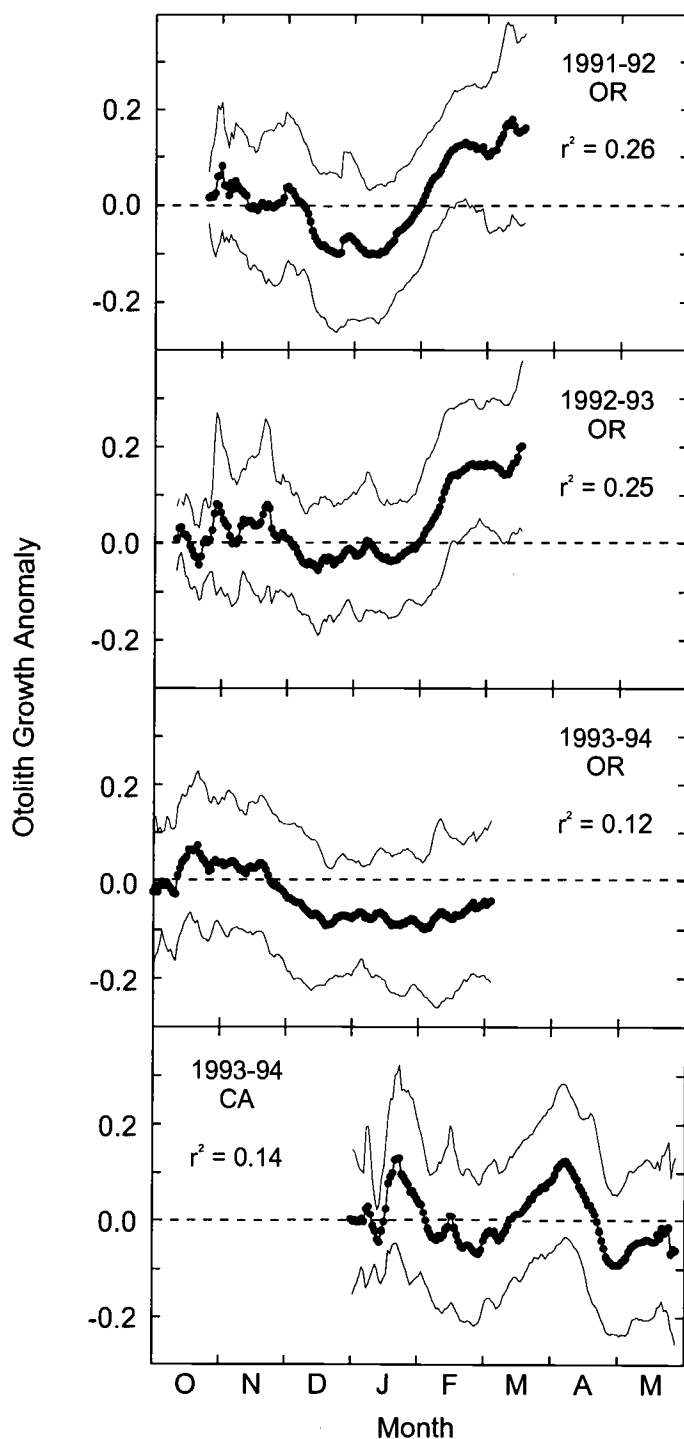


Figure 5.11 Mean daily otolith growth anomaly by calendar date for Pacific sanddab for the 4 surveys. Points are means, thin lines are ± 1 SD. Variation explained by calendar date (ANOVA r^2) is shown. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m}/\text{d} + 1]$) for all fish.

Annual variation

Interannual differences in the seasonal pattern of otolith growth were greatest from mid-January through March. Mean otolith growth rates were higher in 1992 and 1993 than in 1994 (one-way ANOVA for March 1, $F=33.736$, $P<0.001$, $n=134$). Mean otolith growth rates in December and January were slightly higher in 1993 than in 1992 and 1994, but differences were not significant (one-way ANOVA for January 1, $F=1.708$, $P=0.186$, $n=126$). Mean growth rates in October and November did not differ among years (Figure 5.11).

Mean radius-specific otolith growth rates differed among the 4 survey periods. Differences in mean otolith growth rates were small at radial distances of <0.1 mm (Figure 5.8). This portion of the otolith represents growth during the mid-larval period since the first 50 d of life is not recorded in the asteriscus (Donohoe and Markle, MS [Ch. 2]). Interannual differences in mean otolith growth rate began to develop at a radial distance of 0.1 mm and were greatest at distances of 0.15 to 0.25 mm. Otolith growth rates at these distances were significantly higher in 1992 and 1993 than in 1994, and intermediate in 1994 off California (ANOVA for radius=0.22 mm, $F=20.07$, $P<0.001$, $n=135$). The observed difference at radius of 0.22 mm is equivalent to 30% faster otolith growth in 1992 and 1993 than in 1994. Differences in mean otolith growth rate declined at radial distances >0.3 mm.

Relationship to temperature

Seasonal variation in otolith growth rate was related to SST in 2 of 4 surveys. Time series of mean daily otolith growth anomalies showed a positive relationship with daily SST in 1992 and 1994 (regression, $r^2=0.49$ and 0.54 , Figure 5.12). Relationships were marginally significant ($P=0.06$ and 0.07) after adjusting effective sample sizes for the effects of autocorrelation in both time series. Relationships for 1993 and 1994 off California were not significant (Figure 5.12). The slopes of the relationships differed among years (ANCOVA, $F=42.8$, $P<0.001$).

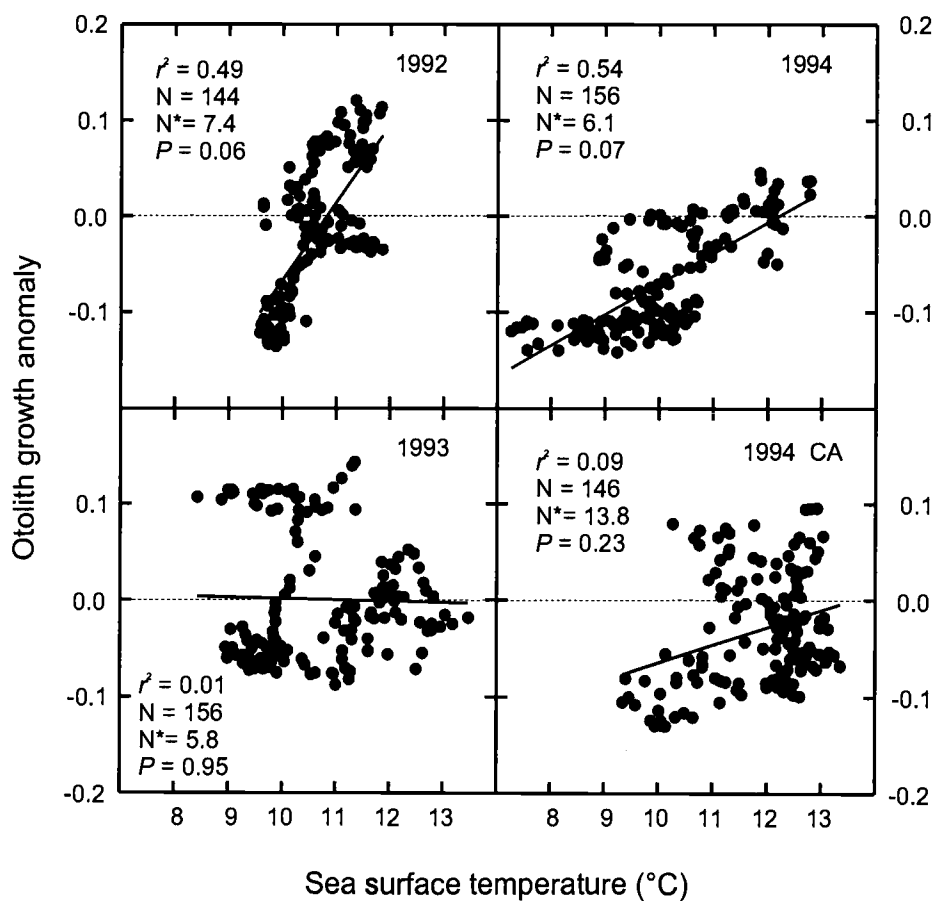


Figure 5.12 Relationship between the mean daily otolith growth anomaly for Pacific sanddab and mean daily sea surface temperature for the 4 surveys. N^* is the effective sample size after adjusting for autocorrelations in both time series. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m/d} + 1]$) for all fish.

Correlations between time series of otolith growth and SST were also calculated for time lags of ± 30 d to test the possibility that changes in otolith growth rate lagged behind changes in SST. Small increases in correlations were observed at lags ranging from -25 d to +23 d indicating that the direction and timing of the lag was not consistent among the 4 surveys.

Individual growth patterns

Growth synchrony

Growth histories of individual fish were examined in an attempt to explain some of the 74-88% of variation in daily otolith growth anomalies not explained by calendar date. Mean daily otolith growth rates during the 56-103 d period of common growth (Table 5.2) differed among fish in each of the 4 surveys (one-way ANOVA, $P < 0.001$, $n = 2223-3960$). Analysis of variance showed that differences among fish accounted for 22%, 28%, and 27% of variation in daily otolith growth anomalies in the 1992-1994 Oregon surveys and 33% of the variation in the 1994 survey off central California. Thus the remaining 67-78% of the variation was due to day-to-day changes in otolith growth rate.

Individual patterns of otolith growth were variable and not synchronous among all fish within a year class. Time series of daily otolith growth anomalies (growth histories) were compared for the 56-103 d period of common growth (Table 5.2). Correlation coefficients (r) for all possible pairs of growth histories ranged from -0.92 to +0.97 (Figure 5.13). Mean r for the 4 surveys ranged from 0.07 to 0.393. Distributions of r were strongly skewed in 1992 and 1993, with large proportions of positive correlations. A mean critical value of r was estimated for each survey by adjusting the sample size to compensate for autocorrelation in both series. First order autocorrelations were high, ranging from 0.81 to 0.99, reducing the effective number of observations from 56-103 to an average of roughly 6-10. Based on the mean critical value of r , the proportion of significant correlations ranged from 0.013 to 0.032 for the 4 surveys, less than the 0.05 expected by chance.

Table 5.2 Reduced number and date ranges of time series of daily otolith growth anomalies used in the cluster analyses.

cruise	date range	no. days	no. fish
Oregon			
March 1992	18 Dec - 26 Feb	70	45
March 1993	29 Dec - 11 Mar	72	36
March 1994	19 Nov - 2 Mar	103	40
California			
May 1994	21 Mar - 16 May	56	38

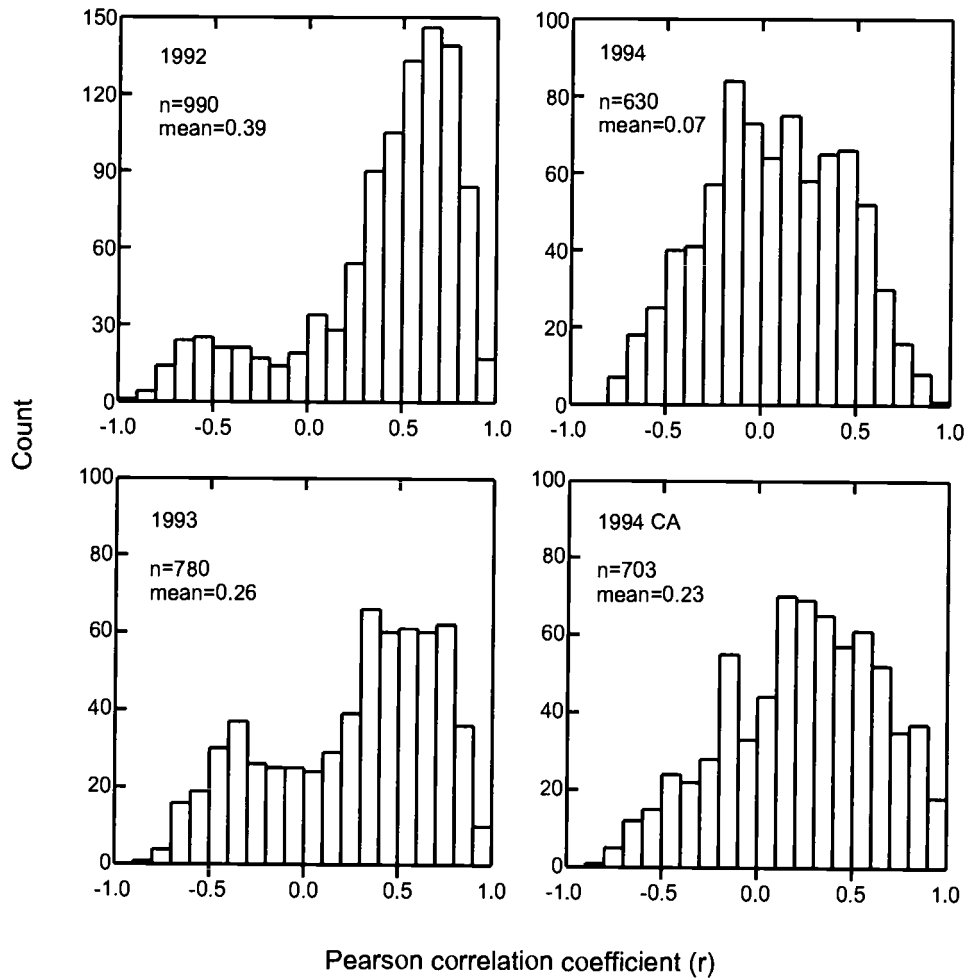


Figure 5.13 Similarities between all possible pairs of time series of daily otolith growth anomalies for Pacific sanddab from each of the 4 surveys. The length of time series and period of comparison for each survey is listed in Table 5.2.

Time series analysis showed that growth histories of many pairs of fish were most strongly correlated at time lag=0. However growth histories of some pairs of fish were more strongly correlated at time lags of 1-10 days. In some cases, correlations increased markedly at lags of a few days. For example, the correlation between growth histories for specimens 5060 and 5069 increased from $r=0.28$ at lag 0 d to 0.75 at lag of 6 d.

Major growth patterns

Cluster analysis identified 3 or 4 major patterns of otolith growth in each of the 4 surveys (Figure 5.14-Figure 5.17). Mean growth patterns for each cluster are shown in Figure 5.18 and individual patterns in Appendix 1. To test the distinctiveness of the major patterns, cluster memberships were used in a discriminant analysis to create models of the major growth patterns. Jackknife reclassification success of the individual growth patterns was 71% for pelagic fish collected off California in May 1994, suggesting that major growth patterns were fairly distinct. In contrast, jackknife reclassification success was 25%, 36%, and 45% for benthic fish collected off Oregon in March 1992-1994.

Patch dynamics and settlement

Cluster analysis showed that pelagic Pacific sanddab with similar growth histories tended to occur at the same station or in same region (Figure 5.14). Most fish with growth patterns A and B were caught in the central region or south region during sweep 2. Nearly all fish with growth pattern B were stage 2 larvae (Figure A.1). In contrast, most fish with growth pattern C were caught in the north region or south region during sweep 1 (Figure 5.3), and had completed eye migration (stage 3). Although expected frequencies were low, frequency analysis suggest that fish were not randomly distributed among clusters A+B and C (Chi-square =19.33, df=11, $P=0.06$).

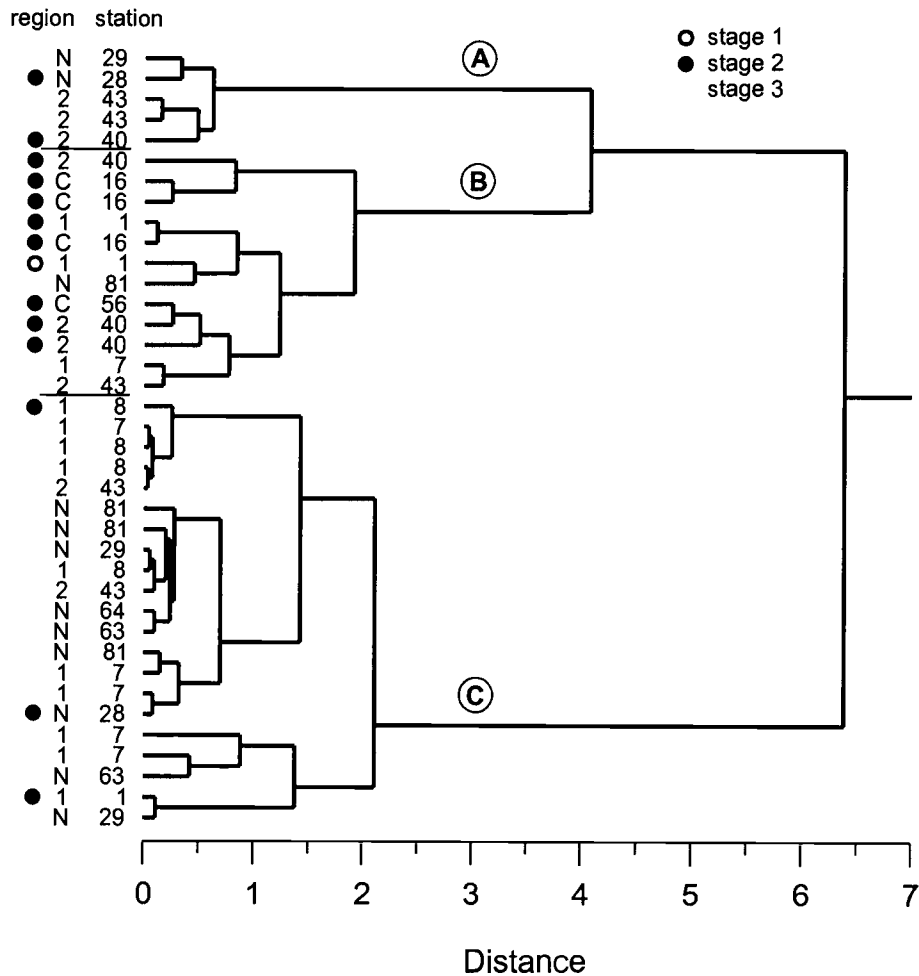


Figure 5.14 Similarities among time series of daily otolith growth anomalies for 38 Pacific sanddab caught at 12 stations off California in May 1994. Similarity is based on the Pearson correlation coefficient (r). Clusters were linked using Ward's minimum variance method. Distance is a measure of within-cluster variance. Regions: N=north, C=central, 1= south-1st sweep, 2=south-2nd sweep.

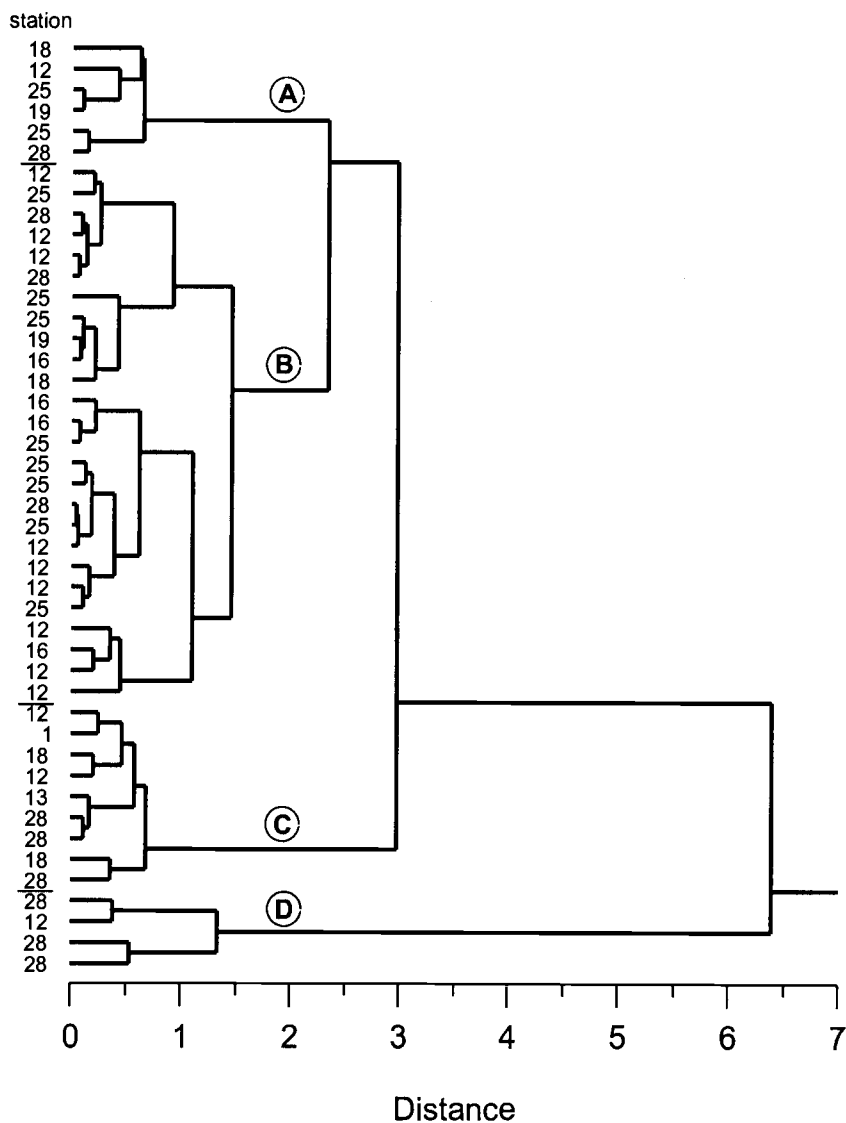


Figure 5.15 Similarities among time series of daily otolith growth anomalies for 45 Pacific sanddab caught at 8 stations off Oregon in March 1992. Similarity is based on the Pearson correlation coefficient (r). Clusters were linked using Ward's minimum variance method. Distance is a measure of within-cluster variance. Stations 1 and 12 located in south transect, all others in north transect.

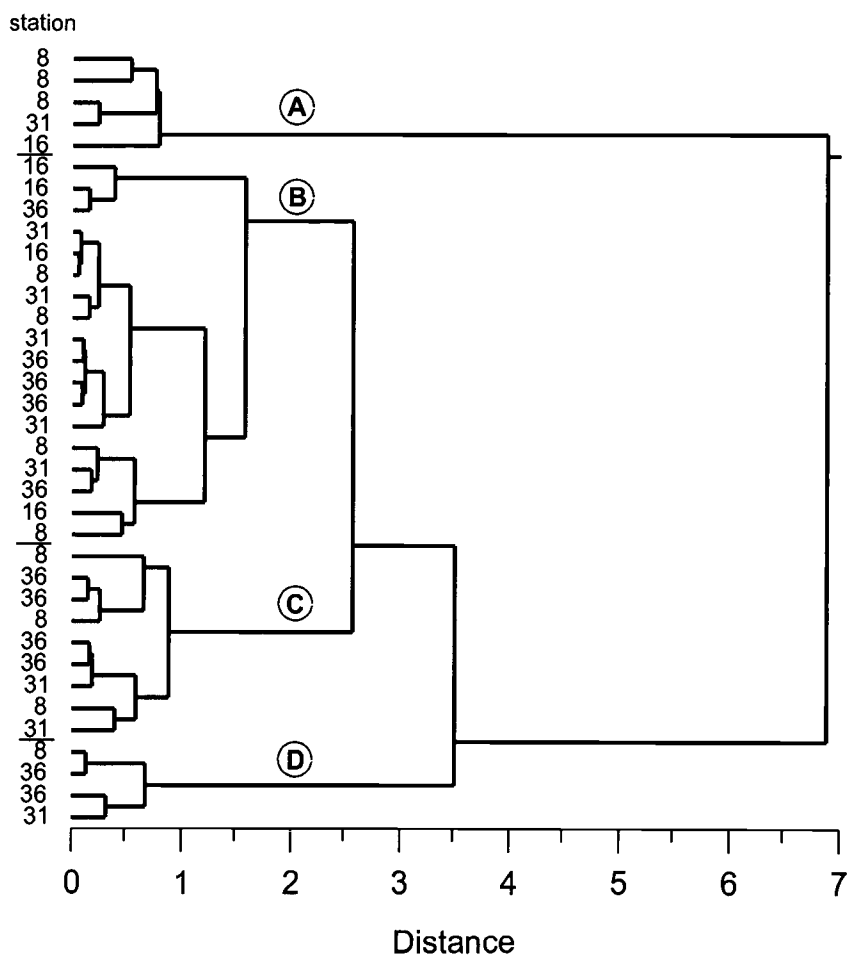


Figure 5.16 Similarities among time series of daily otolith growth anomalies for 36 Pacific sanddab caught at 4 stations off Oregon in March 1993. Similarity is based on the Pearson correlation coefficient (r). Clusters were linked using Ward's minimum variance method. Distance is a measure of within-cluster variance. All stations located in north transect.

Growth patterns of benthic fish collected in March 1992 were more evenly distributed among stations, but some differences were observed (Figure 5.15). Most fish from station 25 had growth pattern A or B while most fish from station 28, only 9 km away, had growth pattern C or D. Likewise, 9 of 12 fish from station 12, located ~100 km south of most other stations, had growth pattern B (Figure 5.3). Expected frequencies were low, but frequency analysis suggest that the distribution of fish among clusters A+C+D and B was not completely random (Chi-square =13.36, df=8, $P=0.10$). Growth patterns of benthic fish collected in March 1993 and 1994 were evenly distributed among stations (Figure 5.16 and Figure 5.17). Frequency analysis confirmed that the distribution did not differ from random (1993 - Chi-square =7.50, df=9, $P=0.59$; 1994 - Chi-square =3.08, df=6, $P=0.80$).

Two of the 3 major patterns of otolith growth observed for pelagic fish from central California in 1994 appear to be related mesoscale variation in temperature. Fish with growth pattern B, caught primarily in the central and south regions, showed a sharp, temporary decrease in otolith growth anomalies in late April, followed by an increase in early May (Figure 5.14, Figure 5.19, A.1). SST recorded at the buoy in Monterey Bay showed a similar decrease in late April (Figure 5.19). Temperature data prior to April 6 were missing. A regression of mean otolith growth for pattern B on SST at the Monterey Bay buoy was not significant ($r^2 = 0.25$, $n=48$, $N^*=11.4$, $P=0.40$). In contrast, fish with growth pattern C, most common in the north and south regions, generally showed a steady decline in otolith growth anomalies in April and into May. Mean SST outside of Monterey Bay (buoys off Bodega Bay, San Francisco, Half Moon Bay, and the shore station at Granite Cove) showed a similar gradual decline over this same period. A regression of mean otolith growth for pattern C on SST outside Monterey Bay was not significant ($r^2 = 0.33$, $n=140$, $N^*=8.2$, $P=0.34$).

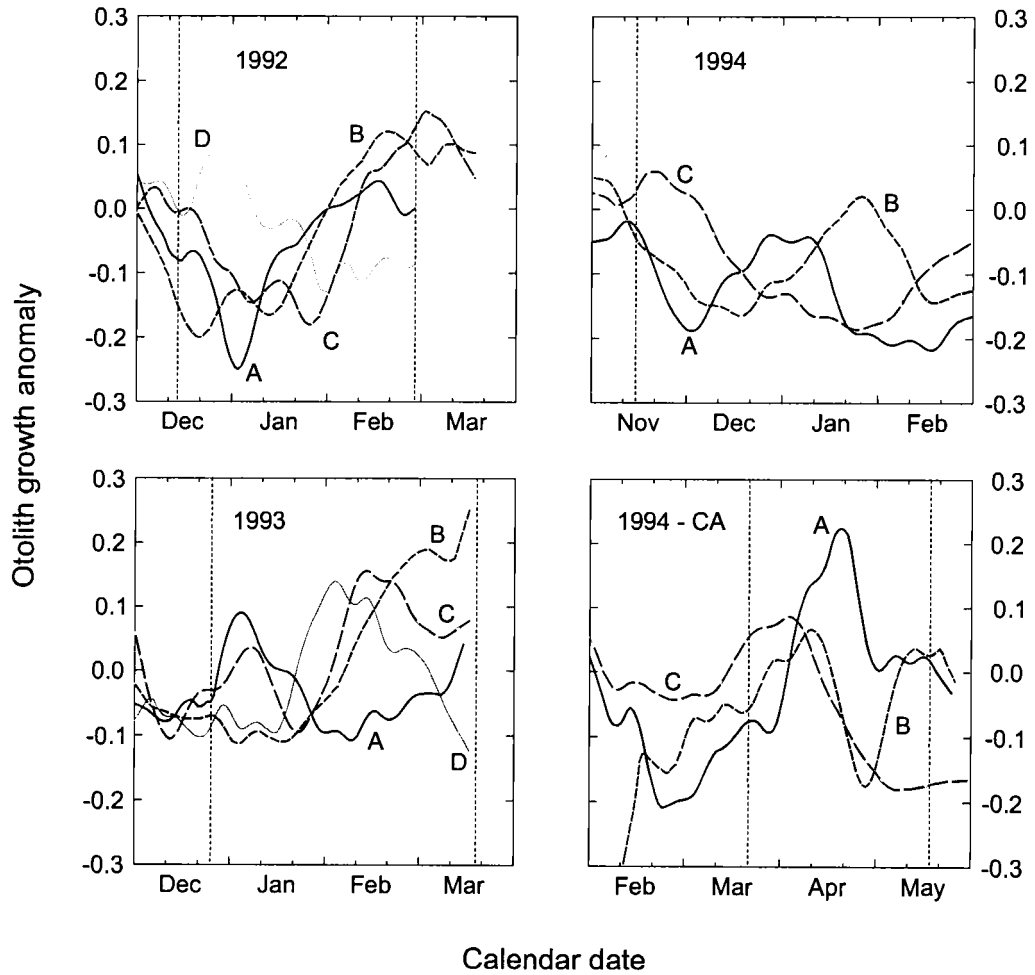


Figure 5.18 Mean growth patterns for the 3-4 main groups of Pacific sanddab identified by cluster analysis for the 4 surveys. Letters indicate clusters. Vertical lines mark the range of dates used in the cluster analysis. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m}/\text{d} + 1]$) for all fish.

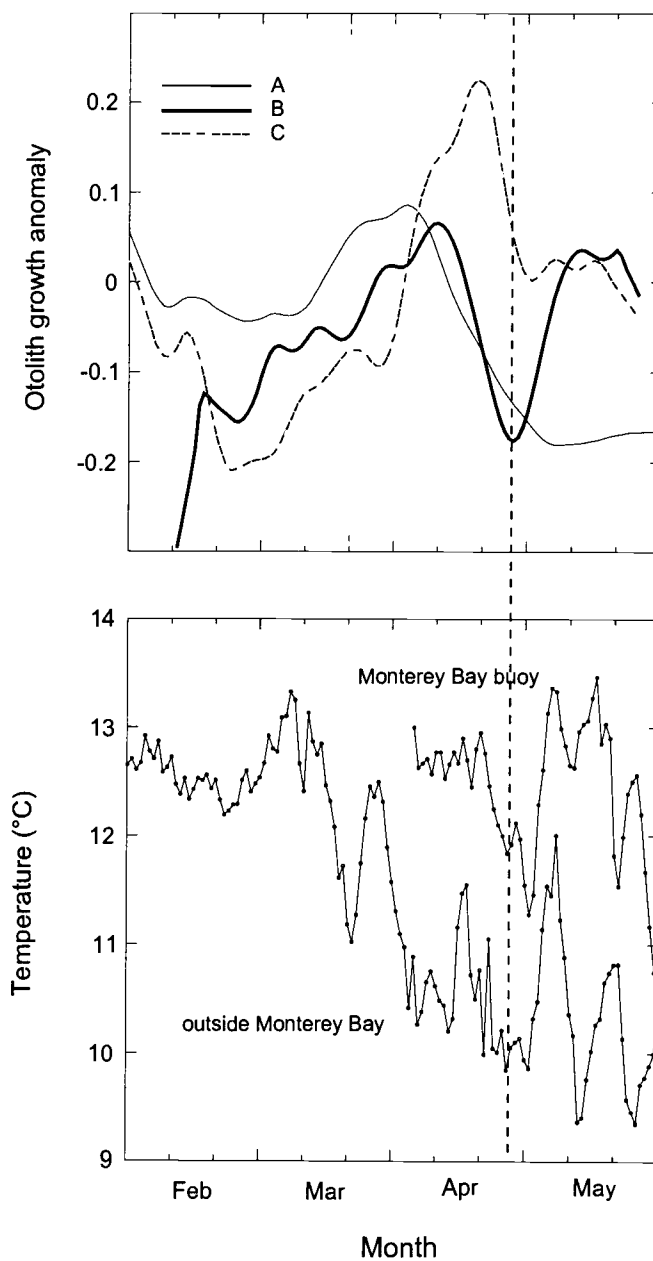


Figure 5.19 Top: Mean growth patterns for the 3 main groups of Pacific sanddab identified by cluster analysis for the 1994 survey off central California. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m}/\text{d} + 1]$) for all fish. Bottom: Sea surface temperature (SST) in 1994 recorded at the Monterey Bay buoy and the mean SST for the shore station at Granite Cove and buoys at Bodega Bay, San Francisco, and Half Moon Bay.

DISCUSSION

Mean growth patterns

Time series of daily otolith increment widths provide detailed information about growth of larval and early juvenile Pacific sanddab that is not available from size and age at capture. Daily otolith growth rate showed considerable ontogenetic, seasonal, annual, and individual variation. Ontogeny (otolith radius) explained 48% of the total variation in otolith growth rate. Season (calendar date) accounted for 12-26%, differences among fish (mean growth rate) explained 22-33%, and day-to-day (within fish) accounted for 67-78% of the variation in daily otolith growth anomalies. These sources of variation are discussed below.

Otolith radius had the largest effect on otolith growth rate, explaining 48 % of the total variation (Figure 5.5). This ontogenetic variation was due to changes in both somatic and relative otolith growth as fish completed metamorphosis (Figure 5.7). Because this ontogenetic effect was large and probably varied among individuals, deviations from the mean radius-specific growth rate (otolith growth anomalies) most likely include residual effects of ontogeny. These ontogenetic residuals may have added variation to our analysis of calendar date and environmental effects. Several methods have been used to remove the dominant effect of ontogeny from time series of otolith growth and to calculate growth variability (Maillet and Checkley, 1991; May and Jenkins, 1992; Ralston, 1995). In our study, growth anomalies were calculated as proportional deviations from the radius-specific mean. Some authors have used deviations that were not scaled to fish size. Because otolith growth potential and thus the potential response to changes in the environment will increase as larval and otolith size increase, scaling is required to make meaningful comparisons of otolith growth rates of small and large fish.

Calendar date explained 12-26% of variation in otolith growth anomalies in the 4 surveys, indicating moderate seasonal variation in mean otolith growth rate. Off Oregon, calendar date effects were strongest in 1992 and 1993, due primarily to the large increase in

otolith growth anomalies in February and March. Mean otolith growth anomalies were lowest in December and January (Figure 5.9). Seasonal variation in mean otolith growth rate suggests that timing of spawning may have a strong affect on early survival. Pacific sanddab spawn all year with a seasonal peak from August to October and a minor peak in January and February (Moser et al., 1993). Our results suggest that fish spawned in late summer or early fall would complete the early larval stage more quickly than those spawned later in the year, and thus may experience lower cumulative mortality (Houde, 1987, 1989). Fish spawned in January and February should experience the slowest early growth that may result in higher cumulative mortality.

The relationship between the seasonal pattern of otolith growth and temperature differed among surveys. Time series of otolith growth anomalies and SST were related for 1992 and 1994 surveys but not 1993, even though SSTs off Oregon were similar in all 3 years, ranging from 9 to 13 °C (Figure 5.12). Slopes of the relationships for 1992 and 1994 also differed markedly. Otolith growth rate of pelagic Pacific sanddab off California in 1994 also was not correlated with broad-scale SST. This variability suggests a strong interaction (synergism) between temperature and other factors that also affect growth, e.g. the availability of food. Ralston (1995) also noted a surprisingly small effect of temperature on time series of otolith increment widths in *Sebastes* larvae and speculated this was due to errors in time series of SST which dampened the observed relationship.

Annual variation in the mean ontogenetic and seasonal patterns of otolith growth appear related to timing of settlement. Interannual variation in mean otolith growth rate was greatest at radial distances of 0.15 to 0.25 mm, with much slower growth in 1994 (Figure 5.8). Pacific sanddab complete eye migration (CEM) and start 'metamorphosis proper' at an asteriscus radius of 0.18 to 0.26 mm. Settlement to the middle continental shelf generally coincides with CEM (Donohoe and Markle, MS [Ch. 3]). The process of inshore movement appears to be gradual, taking an average of 50-60 d. Otolith growth rate is therefore most variable during

metamorphosis and settlement. In terms of season, mean otolith growth rate was most variable in February and March with much slower growth in 1994 than in 1992 and 1993 (Figure 5.9). Peak settlement occurred from December to March in the 3 survey years (Donohoe and Markle, MS [Ch. 3]). We attribute differences in both patterns to a combination of 3 factors: earlier settlement, slightly cooler bottom temperatures in 1994, and seasonal changes in the stratification of the water column. Pacific sanddab settled earlier in 1994 than in 1992 and 1993 survey years (Donohoe and Markle, MS [Ch. 3]). The 1994 year class probably settled in December and January, while most of the 1992 year class settled in January-February and the 1993 year class settled from December-March with a peak in March (Donohoe and Markle, MS [Ch. 2], MS [Ch. 3]). Early settlement from warm surface waters to colder bottom water explains the much slower growth of the 1994 year class in February and March. The effect of early settlement on otolith growth rate in 1994 is compounded by slightly cooler bottom temperatures in 1994 and an increase in stratification of the water column as the settlement season progressed (Figure 5.1). In all 3 years, the difference between surface and bottom temperatures increased by 2-3 °C from January to March. Thus Pacific sanddab spawned late in the season or that remain in the water column in February and March may gain a thermal advantage of several degrees over fish that settled earlier. Off Oregon, this potential advantage may be offset by an increased risk of offshore advection at the abrupt onset of the upwelling season in late March and April (Huyer, 1983; Strub et al., 1987).

Individual patterns

Individual time series of daily otolith growth were correlated among some fish in each of the 4 surveys (Figure 5.13). Strong correlations suggest that growth of some Pacific sanddab was synchronous during the late larval and early juvenile periods.. These correlations, along with the finding of a significant calendar date effect, suggest that broad scale processes have only a weak influence on otolith growth of Pacific sanddab during the larvae and early juveniles

period. Higher degrees of growth synchrony in 1992 and 1993 were associated with stronger calendar date effects and faster growth (Figure 5.8 and Figure 5.13), and suggest the relative influence of broad scale processes varies among years. In contrast, mean daily otolith growth rates were strongly correlated among 5 species of larval rockfishes (Ralston, 1995) suggesting broad synchrony in the growth of those fishes.

Individual time series of daily otolith growth of many fish were not correlated (Figure 5.13). Poor correlations among the growth histories of many fish do not provide evidence of broad synchrony in growth during the late larval and early juvenile period. In turn, asynchronous growth histories do not support the hypothesis that growth of the year class is determined primarily by broad-scale environmental factors. However our ability to detect synchrony was limited by several factors. Poor correlations among growth histories of some pairs of fish improved markedly at time lags of 1-10 d, suggesting the two series were slightly offset. Offsets may be caused by small aging errors. Increments near the otolith margin were difficult to interpret in large fish. Even with error-free time series, broad-scale environmental variation can produce slightly offset time series if fish are at different locations and therefore experienced the same signal at slightly different times. The rapid change in correlation coefficients at lags of a few days suggests that tests of similarity among time series using time domain models (e.g. correlations) are sensitive to small lags or errors in time series. Use of a frequency domain models such as Fourier (Finn et al., 1997), elliptical Fourier (Campana and Casselman, 1993), or eigenshape analysis (Lohmann and Schweitzer, 1990) to characterize growth patterns should be less sensitive to small offsets among time series.

Although we have limited our discussion to variation in otolith growth, there is strong interest in the corresponding variation in somatic growth. Otolith growth rate in Pacific sanddab is not an exact record of somatic growth. Many studies have shown that the relationship between otolith and somatic growth rate is not linear, but varies with growth rate (Reznick et al., 1989; Secor and Dean, 1989; Secor et al., 1989). Non-linearity can occur

particularly during periods of very rapid or very slow growth. However, the general conclusion is that otolith growth is a conservative process relative to somatic growth. Consequently, changes in somatic growth or metabolic rate are probably larger than indicated by changes in otolith growth rate. Our results show that the relationship between otolith and somatic growth in length is complex (Figure 5.7). Shifts in this relationship were largely accounted for by examining the residuals or anomalies from the mean radius-specific growth rate. However, otolith growth and somatic growth in length appear to become temporarily uncoupled during metamorphosis proper (Donohoe and Markle, MS [Ch. 2]). Thus rapid otolith growth did not always correspond to rapid somatic growth. Otolith growth rate during this period may be more closely related to changes in metabolic rate than somatic growth rate (Wright, 1991).

Patch dynamics and settlement

Pelagic Pacific sanddab with similar growth histories tended to occur at adjacent stations while benthic fish with similar growth histories were more broadly distributed. Although pelagic were captured off California and benthic fish off Oregon, these patterns suggests that pelagic fish are segregated and that this segregation breaks down during the process of settlement. Benthic fish are probably less segregated than pelagic fish because multiple pelagic cohorts accumulate in the benthos. The most distinctive and aggregated group of pelagic Pacific sanddab, those with growth pattern B, is composed almost entirely of earlier (stage 2) larvae (Figure 5.14). Stage 3 pelagic-caught larvae, those with growth pattern C, were more broadly distributed. Although our data are limited, it appears that segregation of larvae begins to break down before larvae have completed settlement. Settling Pacific sanddab appear to make extensive vertical migrations during stage 2 and 3 as they move from offshore to nurseries on the continental shelf (Donohoe and Markle, MS [Ch. 3]). Segregation of pelagic fish breaks down as fish spend more time on the bottom. Thus ontogenetic changes in the

diversity of growth histories (natural tags) within a sample may indicate a change in behavior of larvae.

Although benthic fish appear to be randomly distributed in 1993 and 1994, benthic fish with similar growth histories tended to co-occur in 1992 ($P=0.10$, Figure 5.15). For example, the proportion of fish with growth histories A-D differed among stations 25 and 28, only 9 km apart. This small scale segregation of benthic fish was most likely due to segregated or patchy settlement. A previous sister study has shown that otolith composition of benthic Pacific sanddab collected in 1992 also differed over small spatial scales (Donohoe and Markle, MS [Ch. 4]). The observed patterns suggested that some Pacific sanddab larvae remain together in the plankton for long periods and settle together on shelf (Donohoe and Markle, MS [Ch. 4]). Growth histories provide some evidence to corroborate this hypothesis. Some fish from the same station had remarkably similar growth histories (Figures A.1-A.4). These similarities may be due to chance, but for some pairs similarities extend back several months prior to capture, suggesting that the pair had similar experiences and may have remain together in plankton for months. Larval patches might be established by initial conditions such as time and place of spawning and maintained by behavior (schooling, feeding on aggregated prey), ontogenetic changes in buoyancy, and oceanographic processes such as mesoscale eddies and fronts. These results are suggestive, but not conclusive. As we concluded previously, analysis of a highly variable genetic locus combined with growth history data and otolith microchemistry analysis is needed to better understand meso-scale larval patch dynamics.

Our results suggest an association between the growth histories of Pacific sanddab collected in Monterey Bay and the local temperature history recorded at the Monterey Bay buoy (Figure 5.19). Although we could not demonstrate a statistical relationship among the growth patterns and SST, such a relationship is not unreasonable nor necessarily surprising. Many studies have demonstrated that larvae are patchily distributed at spatial scales of <1 m to 100s of

kilometers (Victor, 1984; Doherty, 1987; Williams and English, 1992; Thorrold et al., 1994).

Growth of these larval patches is likely to be dictated by local environment.

Distinct patterns of daily otolith growth histories of marine fishes may serve as natural tags that allow study of patch dynamics and larval transport. Distinct patterns of otolith growth are most likely to occur among larval fishes that occur in regions with diverse oceanographic conditions. This may include temporary meso-scale features such as gyres, fronts, and eddies, and more permanent features such as upwelling associated with headlands or bays. Broader-scale episodic events may also produce distinct marks in a portion of a cohort. For example, storm events (Maillet and Checkley, 1991) will most strongly affect fishes in the upper water column and coastal upwelling will affect inshore fishes over those further offshore. Otolith growth patterns have been used previously as natural tags. Otolith banding patterns formed during incubation have been used to discriminate among populations of sockeye salmon *Oncorhynchus nerka* (Finn et al., 1997) and increment widths formed in estuarine nurseries have been used to discriminate among cohorts of Atlantic menhaden *Brevoortia tyrannus* spawned in different months (Fitzhugh et al., 1997). In addition, temperature fluctuations have been widely used to thermally mark otoliths of hatchery fish (Volk et al., 1999). Several other natural tags have been used to discriminate among fish stocks, including otolith composition or 'elemental fingerprints' (Campana et al., 1994, 1995; Thorrold et al., 1998a, b), otolith shape (Campana and Casselman, 1993), and frequency of parasites (Bailey et al., 1988). Advantages of using growth histories as tags is that the pattern may vary over small temporal and spatial scales, and the pattern can be readily related to widely available oceanographic data. Understanding the patterns of larval transport and dispersal is especially relevant given the recent emphasis on using marine reserves to conserve and manage coastal fishes (Fogarty, 1999).

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APPENDIX

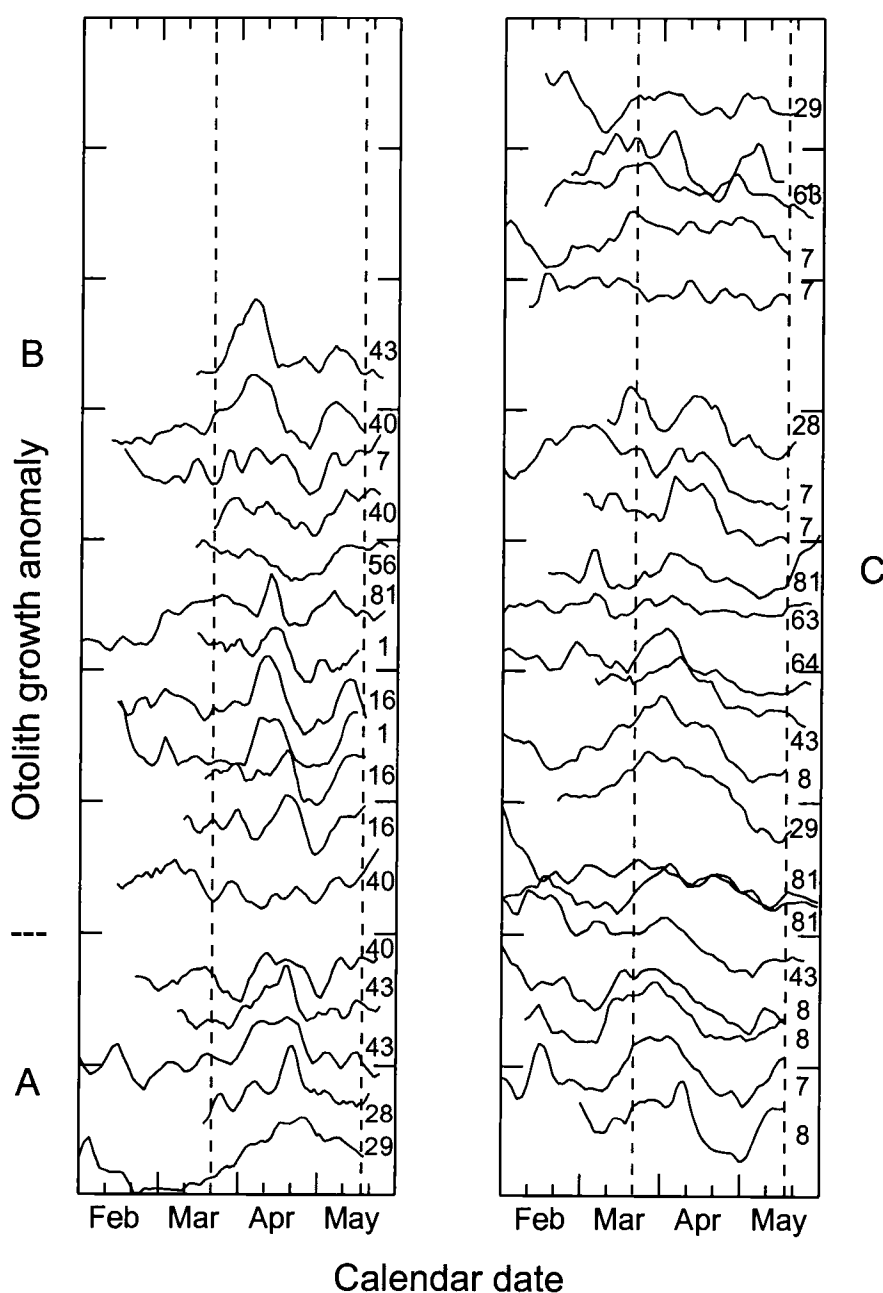


Figure A.1 Individual variation in time series of daily otolith growth anomalies for 38 pelagic Pacific sanddab collected off central California in May 1994. Letters=cluster groups, numbers=stations, vertical lines show range of dates used for clustering. All time series are on the same scale; tick marks equal a range of 1.0 units for anomalies. Anomalies are proportional deviations from the mean radius-specific otolith growth rate ($\ln[\mu\text{m/d} + 1]$) for all fish.

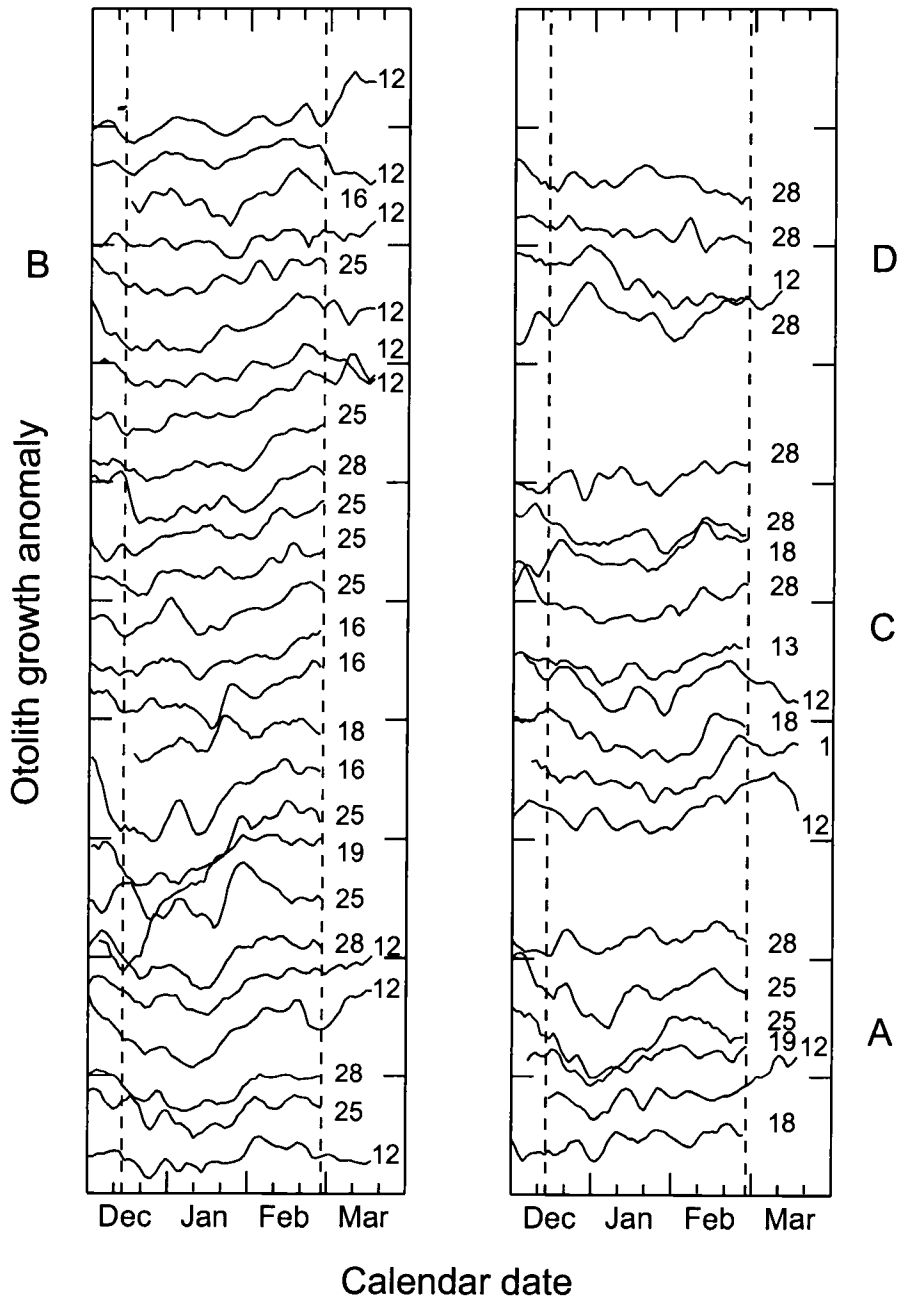


Figure A.2 Individual variation in time series of daily otolith growth anomalies for 45 benthic Pacific sanddab collected off central Oregon in March 1992. All other features the same as Figure A.1.

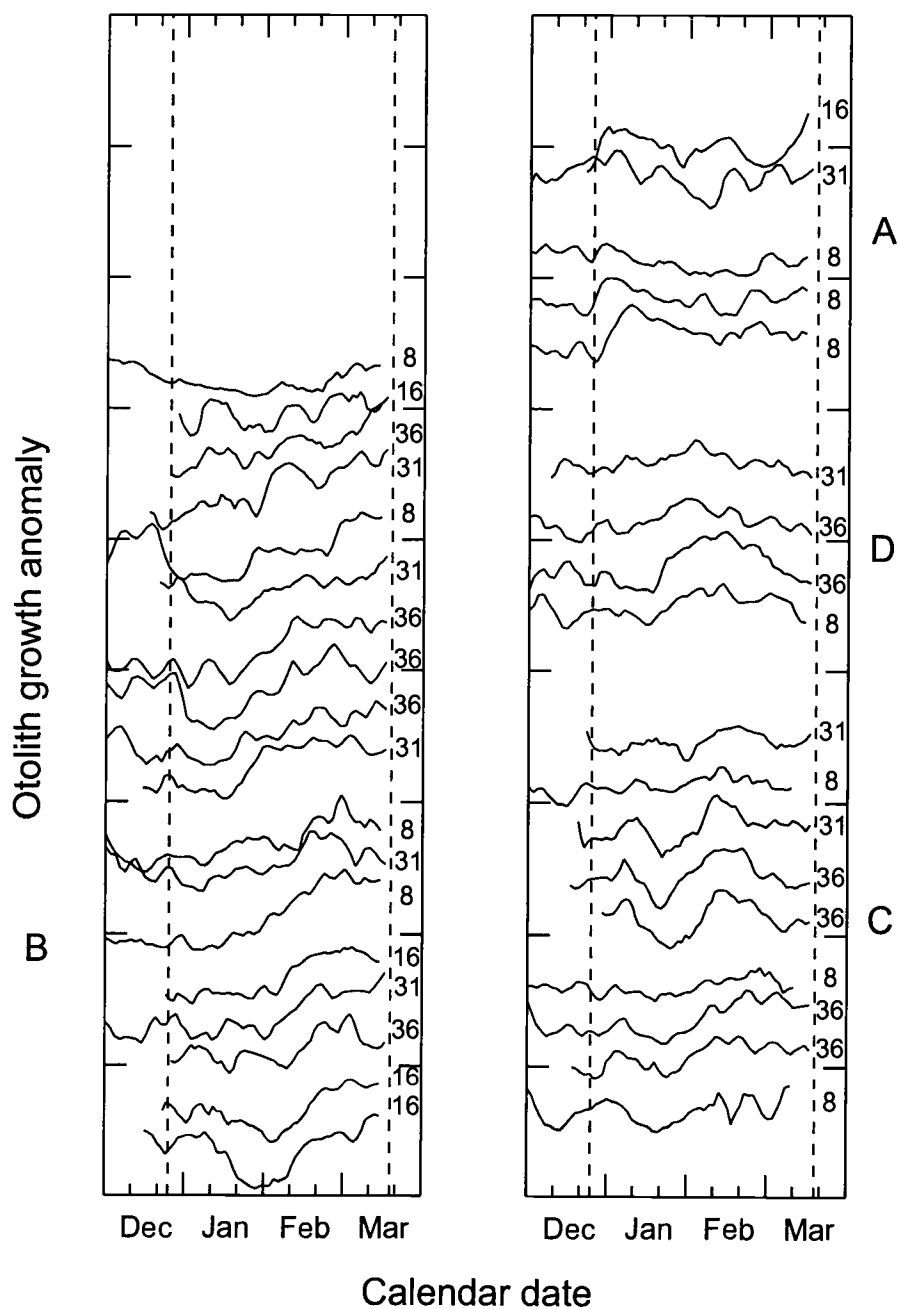


Figure A.3 Individual variation in time series of daily otolith growth anomalies for 36 benthic Pacific sanddab collected off central Oregon in March 1993. All other features the same as Figure A.1.

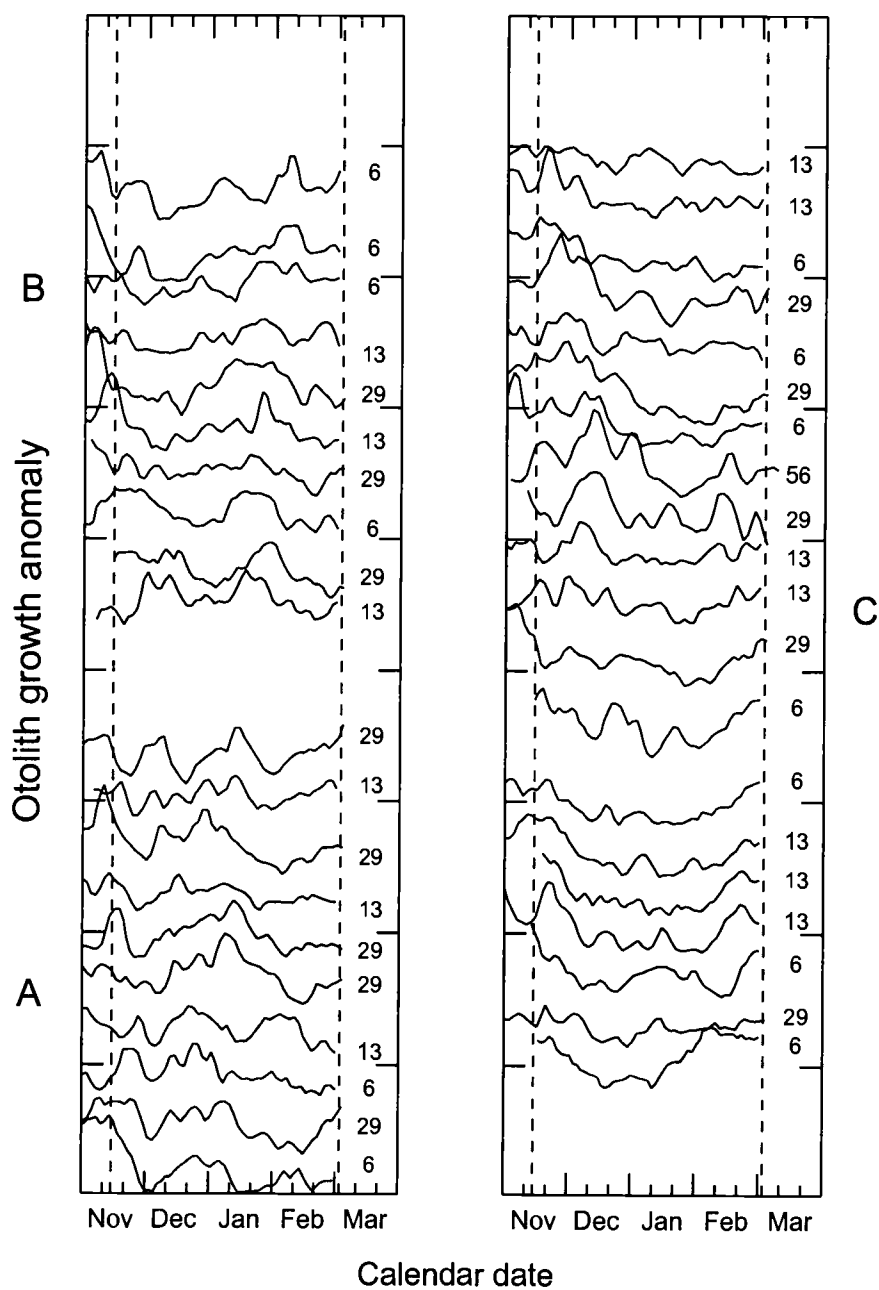


Figure A.4 Individual variation in time series of daily otolith growth anomalies for 39 benthic Pacific sanddab collected off central Oregon in March 1994. All other features the same as Figure A.1.

CHAPTER 6

Summary

The transition from a symmetrical pelagic larvae to an asymmetrical benthic juvenile represents a major physiological and ecological shift in the early life of flatfishes. Most flatfishes metamorphose at 10-25 mm SL, have short pelagic periods, and many settle to shallow juvenile nurseries. A smaller number of species transform at larger sizes and have long pelagic periods, but these species are not well studied. Research on the early life history and population dynamics of flatfishes has also focused on one family, the Pleuronectidae. These manuscripts describe metamorphosis, settlement, associated changes in otolith microstructure and microchemistry, and variation in growth of Pacific sanddab (*Citharichthys sordidus*), a paralichthyid that transforms at large sizes and settles to deep nurseries on the continental shelf.

Unlike many flatfishes that transform at small sizes, metamorphosis in Pacific sanddab is a gradual process that takes a total of 4-5 months (Chapter 2). Metamorphosis consists of two phases, eye migration and metamorphosis proper. Eye migration takes 3 months and is completed at 30-52 mm SL and age of 4-7 months. As a result, the right eye is partially migrated for half the larval period. Eye migration is also interrupted in Dover sole, *Microstomus pacificus*, which complete metamorphosis at 49-79 mm SL (Markle et al., 1992). This pattern of development may be a consequence of the evolution of large size at metamorphosis in these species. Gradual metamorphosis is contrary to the idea of saltatory ontogeny (Balon, 1981) and challenges the assumption that transitional or intermediate forms are poorly adapted to the pelagic habitat. Curiously, metamorphosis proper begins after completion of eye migration (CEM) and takes an additional 1-2 months. Settlement appears to coincide with CEM (Chapter 3). Thus Pacific sanddab retain most larval traits during eye migration and while pelagic and develop juvenile traits after settlement.

The gradual metamorphosis of Pacific sanddab allowed study of the relationship between metamorphosis and changes in otolith microstructure. In flatfishes with rapid metamorphosis, the formation of accessory primordia (AP) in the sagitta often coincides with the end of metamorphosis and settlement (Alhossaini et al., 1989; Sogard, 1991). In Pacific sanddab, AP and an opaque region formed 2-7 weeks before CEM and the start of metamorphosis proper and 2-3 months before metamorphosis was complete. AP appear to form in response to a temporary increase in relative otolith growth rate during metamorphosis, not to settlement. These results confirm an earlier study which showed that AP and an opaque region form at the start of metamorphosis proper in sagittae of Dover sole, which also transforms at large sizes and has a protracted metamorphosis (Markle et al., 1992; Toole et al., 1993).

Settlement of Pacific sanddab off central Oregon appears to be facilitated by Ekman transport (Chapter 3). Peak settlement of Pacific sanddab to the continental shelf occurred in late fall and winter, coinciding with seasonal onshore Ekman transport off Oregon and Washington. In addition, abundance of recently settled Pacific sanddab in March 1989-1994 was correlated with onshore Ekman transport during the previous 30 d. Previous studies have shown that settlement of fishes and invertebrates to nearshore or intertidal habitats is related to onshore movement of surface waters (Nelson et al., 1977; Boehlert and Mundy, 1987; Farrell et al., 1991). The results of the present study suggests that settlement of fishes to mid-shelf nurseries is also facilitated by cross-shelf currents. However, Pacific sanddab apparently settle at times and in locations when surface transport is predominantly offshore (e.g. in June off central California), suggesting that Pacific sanddab use other mechanisms to move inshore such as swimming, subsurface currents, or relaxation events. Additional studies are needed to clarify the relative importance of these mechanisms and whether timing and manner of settlement varies with latitude or season.

Pacific sanddab complete metamorphosis at large sizes (30-52 mm SL) and settle to deep nurseries on the continental shelf (50-120 m). This strategy is consistent with the general

flatfish pattern of increasing size and age at metamorphosis with increasing depth of the juvenile nursery (Moser, 1981; Minami and Tanaka, 1992). The reason for this pattern is unclear however. Moser (1981) suggested that a long pelagic period is dispersal mechanism. Large size at settlement is also advantageous if there are predators in the nursery (Minami and Tanaka, 1992). This relationship between mean metamorphic size and depth suggests that individual size may be important determinant of post-settlement survival in Pacific sanddab.

The early life history strategy of Pacific sanddab is similar to that of two pleuronectids which also occur off Oregon. Like Pacific sanddab, Dover sole and rex sole, *Errex zachirus*, complete metamorphosis at large sizes and settle to nurseries on the outer continental shelf in winter. Early larvae of all 3 species are advected offshore during summer upwelling and depend upon onshore transport to return to the shelf. This strategy exploits the pelagic habitat and is in contrast to that of many coastal fishes in the California Current region which appear to have evolved reproductive strategies to minimize offshore advection of eggs and early larvae (Parrish et al., 1981).

Otolith microchemistry of Pacific sanddab and Dover sole were examined for the presence of an elemental settlement mark to allow more precise estimation of settlement timing. Electron microprobe analysis revealed strong cross-otolith trends in concentrations of Sr, K, Ca, and P in recently settled Pacific sanddab and Dover sole (Chapter 4). These trends were not related to settlement, thermal experience, or otolith and somatic growth, but appear to be ontogenetic. This interpretation differs from that of Toole et al. (1993) who observed cross-otolith patterns in Sr/Ca ratios in Dover sole, and speculated the pattern was related to stress, temperature, or changes in growth rate.

Pacific sanddab with similar otolith composition (Chapter 4) and similar otolith growth histories (Chapter 5) tended to co-occur. This segregation suggests that groups of larvae remain together during much of the larval period and then settle together. These results are somewhat surprising given that Pacific sanddab are pelagic for up to 7 months and Dover sole for up to 2

years. Fine to meso-scale genetic patchiness (chaotic patchiness) has been observed in marine fishes (Johnson et al., 1994; Doherty et al., 1995) and invertebrates (Johnson and Black, 1984; Johnson et al., 1993; Hedgecock, 1994; McMillen-Jackson et al., 1994), although none have such long pelagic lives. Additional studies are needed to confirm these patterns. A genetic analysis of highly variable loci may indicate if settled flatfish that co-occur are closely related and provide insight into the processes of transport and settlement off Oregon. Understanding the patterns of larval transport, mixing, and dispersal is especially relevant given the recent interest in establishing marine reserves to manage and conserve coastal fishes.

Analysis of time series of otolith growth showed that otolith growth rate (OGR) of Pacific sanddab varied with ontogeny, season, and year (Chapter 5). Seasonal variation in OGR was related to sea surface temperature (SST), but there appeared to be strong interaction with other factors. Mean OGR also varied among years, with the greatest variation (~30% higher in 1992 and 1993 than in 1994) during February and March during settlement. Growth rates during the pelagic period were similar among years. Slower growth in 1994 was attributed to slightly cooler temperatures and to earlier settlement. Increases in the thermal stratification of the water column in February and March in all 3 years suggests that fish may gain a thermal advantage by remaining in the warmer surface layer and settling later. This advantage may be offset by greater risk of offshore advection after the transition to upwelling in early spring. The influence of the observed variation in otolith growth rate on somatic growth rate and cohort survival was not examined, but is a topic for continued studies. Small changes in somatic growth rate during the larval and early juvenile period can theoretically result in large changes in survival and year class size (Houde, 1987, 1989).

Otolith growth histories also varied greatly among individuals. Variation in otolith growth was not synchronous among most fish in the year class and thus does not support the hypothesis that growth is controlled by a single large-scale processes. Cluster analysis identified 3 major patterns of otolith growth among pelagic Pacific sanddab caught off central

California in 1994. The presence of a few distinct growth patterns suggests that meso-scale processes may be important determinants of individual growth. The time domain approach used to analyze growth time series proved to be sensitive to small aging errors. Frequency domain methods such as Fourier analysis and eigenshape analysis should provide a more robust approach to analysis of otolith growth histories, and thus warrant further development. These results also demonstrate that otolith growth histories can serve as natural tags allowing the study of patch dynamics and patterns of settlement. Distinct growth histories are likely to found among fish in regions with diverse oceanography.

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