Abstract.—Upwelling and its associated offshore advection of surface waters can affect the recruitment of nearshore organisms. Late-stage pelagic Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, were collected with a midwater trawl off central California during the spring and summer upwelling season. In both species, otolith size increased linearly with metamorphic development; standard length, however, increased asymptotically. Earlier stages of both species occurred shallower in the water column, whereas later stages occurred deeper. The deeper distribution of later stages may have been due to decreased buoyancy as a result of increased otolith size and ossification of bony structures coincident with metamorphosis. Earlier stages of both species were more abundant offshore and less abundant in areas of upwelling, whereas later stages were more abundant nearshore regardless of upwelling. The difference in the horizontal distributions of early and late stages may have been passively driven by different current patterns as a result of the difference in vertical distributions between early and late stages.

Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California

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Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, are abundant along the Pacific coast of North America (Miller and Lea, 1976). In both species, spawning peaks during the summer months but also occurs at lower levels during the remainder of the year; individuals may spawn more than once during a given season (Arora, 1951; Ford, 1965; Goldberg and Pham, 1987; Matarese et al., 1989; Rackowski and Pikitch, 1989). Sanddabs have a long pelagic stage, which may exceed 324 days in speckled sanddabs and 271 days in Pacific sanddabs (Kendall, 1992; Brothers[1]), and settle at a relatively large size (20 to greater than 39 mm standard length (SL) for Pacific sanddabs and 24 to greater than 36 mm for speckled sanddabs) (Ahlstrom et al., 1984; Matarese et al., 1989). Kramer (1990) noted that flatfish with nearshore nurseries had brief pelagic stages and settled at small sizes, whereas those with less restricted coastal nurseries had longer pelagic stages and settled at larger sizes. Kramer (1990) placed sanddabs in the latter category; however, speckled sanddabs, in particular, have a somewhat restricted bathymetric distribution as settled individuals (usually found at depths of 40 m and less)(Rackowski and Pikitch, 1989; Kramer, 1990). Both species are widely distributed as pelagic larvae (as far as 724 km offshore for Pacific sanddabs and 320 km offshore for speckled sanddabs) (Rackowski and Pikitch, 1989), but settled individuals occur within a somewhat more restricted coastal region.

The existence of late-stage Pacific and speckled sanddabs in midwater trawls conducted off central California by the National Marine Fisheries Service (NMFS) Tiburon Laboratory (Wyllie-Echeverria et al., 1990) provided an opportunity to examine ontogenetic changes in distribution associated with metamorphosis and settlement of these two sanddabs. In this paper we investigated the vertical and horizontal distribution of pelagic-stage sanddabs, with the general purpose of elucidating the changes that take place at metamorphosis and settlement. Because the NMFS collections were made during the spring

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and summer upwelling season, when the associated offshore advection of surface waters can adversely affect marine organisms with pelagic life stages (Parrish et al., 1981; Bailey and Francis, 1985; Roughgarden et al., 1988), the effect of upwelling on pelagic-stage sanddabs was also investigated.

Methods

Data collection

Pelagic Pacific and speckled sanddabs were collected in conjunction with the annual juvenile rockfish surveys conducted by NMFS Tiburon Laboratory scientists aboard the National Oceanic and Atmospheric Administration (NOAA) research vessel *David Starr Jordan*. Standard stations extending from Point Reyes to Cypress Point (Fig. 1) were sampled with a 26 × 26 m modified Stauffer midwater trawl with a codend liner of 9.5-mm stretched mesh (Wyllie Echeverria et al., 1990). Standard trawling depth was 30 m except at shallow-water stations where trawls were conducted at 10 m. At certain standard stations a series of three depth-stratified trawls (depths=10 m, 30 m, and 110 m) were conducted to determine bathymetric distributional patterns (Fig. 1). As time permitted, additional trawls, both standard depth and depth-stratified, were conducted at nonstandard stations. All trawls were 15 minutes in duration and were completed between the hours of 2100 and 0600. Stations were sampled during a 10-day "sweep" of the survey area. Three replicate sweeps were completed from mid-May to mid-June of each year; in some years one additional sweep was completed in early April.

CTD (conductivity, temperature, and depth) casts were made at each trawl station to obtain temperature and salinity information at depth. Additional CTD casts were made during the day along tracklines interspersed between the trawl station lines (Schwing et al., 1990). Surface temperature and salinity were also recorded continuously by a thermosalinometer aboard the vessel. CTD and thermosalinometer data were used to determine the relation between upwelling and the spatial distributions of the different pelagic stages of both sanddabs.

Although the annual juvenile rockfish surveys began in 1983, sanddabs were not identified to species before 1987. Therefore, data were analyzed only from the 1987 through 1991 surveys. In addition to the May–June surveys in each year, sampling was carried out in April of 1987, 1988, and 1990. Sanddabs were identified and enumerated on board the research vessel at sea. In 1990 and 1991, samples were frozen after identification and enumeration and brought back to the laboratory where standard length (SL) and stage of metamorphosis were additionally recorded for each specimen collected. Five metamorphic stages, based on the staging system used by Pearcy et al. (1977), were defined as follows:

Stage 1 = left and right eyes positioned symmetrically on both sides of head;
Stage 2 = right eye has begun to move dorsally;
Stage 3 = upper edge of right eye within close proximity to the top of the right side of the head;
Stage 4 = right eye has begun to cross over to the left side of the head;
Stage 5 = right eye completely crossed over to left side of the head.

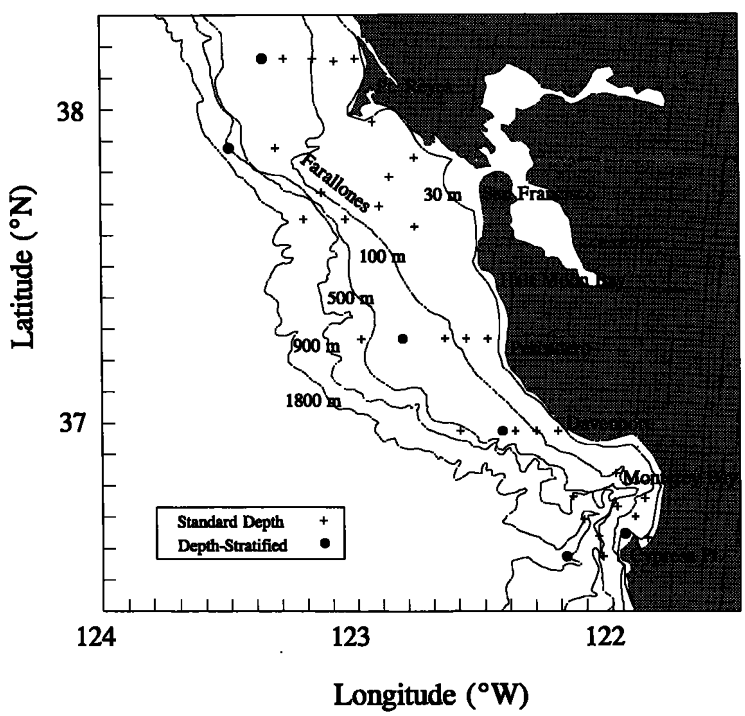

Figure 1
Location of standard trawling stations for Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected during 1987–91.

No stage-1 individuals were collected, probably because their small size allowed them to pass through the net.

To determine if metamorphic stage was a more useful character than SL in resolving spatial patterns, twenty individuals from each metamorphic stage of each species were randomly selected from the May to June survey of 1991, and their otoliths were removed. The diameter of the largest otolith, the sagitta, was measured with a compound microscope connected to a video camera, monitor, digitizer, and computer.

Data analysis

Statistical analyses were performed by using the program SAS (SAS Institute, Inc., 1988). Abundances were transformed by $\ln(x+1)$ to normalize the data. Mean abundances from the April surveys and for each sweep of the May–June surveys were then calculated for all standard stations successfully sampled to describe temporal differences in abundance.

Means and ranges of SL's of the metamorphic stages of both sanddab species were calculated by using specimens measured from the April and May–June surveys of 1990 and from the May–June survey of 1991. Mean SL's were calculated separately for the specimens randomly selected for otolith removal in order to compare the observed changes in otolith size relative to metamorphic stage with SL. Tukey's studentized range tests were performed to determine if there were significant differences in SL and otolith diameter with metamorphic development.

Owing to changes in the width of the net mouth with depth (width=8 m at 10 m depth, 11 m at 30 m depth, and 13.5 m at 110 m depth), abundances for the depth-stratified trawls were adjusted prior to analysis (Lenarz et al., 1991). Abundances for 10-m depth trawls were multiplied by 11/8, abundances for 30-m depth trawls were not adjusted, and abundances for 110-m depth trawls were multiplied by 11/13.5. Because of the large spatial variability in abundances and the fact that not all depth-stratified trawls sampled every depth (i.e. because of time constraints only the 10 m and 30 m depths were sampled at some stations, and only the 30 m and 110 m depths were sampled at others), differences in abundance with depth were evaluated by paired comparison t-tests. Pairing was by station; each depth pair available was considered (10 m versus 30 m, 30 m versus 110 m, and 10 m versus 110 m). When both observations of a pair were equal to 0, that pair was deleted from the analysis. To determine if there was a seasonal change in depth distribution, analyses were performed on all the surveys from 1987 to 1991, the April surveys alone, and the May–June surveys alone. To determine changes in vertical distribution with development, the paired comparisons were also carried out on each of the metamorphic stages, by using data from the April and May–June surveys of 1990 and from the May–June survey of 1991.

To determine the similarity of horizontal distributions among metamorphic stages, Spearman rank correlation coefficients were calculated for the abundances of different stages over standard stations during the 1990 and 1991 surveys.

CTD salinity at the surface (average salinity at 3–5 m depth) and at the standard mid-depth of 30 m (average salinity at 28–32 m) from each sweep of the May–June surveys of 1990 and 1991 was contoured by using the Kriging option in the program SURFER (Golden Software, Inc., 1990). Owing to problems with the CTD during the second sweep of the May–June survey of 1991, thermosalinometer data were incorporated into the available CTD data to generate the surface contours. The log-transformed abundances of metamorphic stages 2 and 5 were overlaid onto the salinity contours to observe the relation (if any) between the abundances of these two metamorphic stages and salinity features indicative of coastal upwelling. These two stages had the greatest potential for differences in spatial relations with salinity features, given that stage-2 individuals were not competent for settlement, whereas stage-5 individuals were relatively close to settlement.

Thermosalinometer data were used to determine trawls conducted in areas of recent upwelling. Schwing et al. (1991) designated recently upwelled water as having surface temperatures less than 10.5°C and surface salinities greater than 33.6 ppt. We used surface salinities greater than 33.6 ppt but surface temperatures less than 11.0°C to allow for marginal surface layer warming during the daylight hours prior to the nighttime trawls. Log-transformed abundances obtained at standard stations from the May–June surveys of 1990 and 1991 were converted to standard scores (log-transformed abundances rescaled for each year so that mean=0 and standard deviation=1) to adjust for year effects, allowing the data from both years to be combined. T-tests were used to compare the mean standard scores of metamorphic stages in upwelling and non-upwelling areas. Separate analyses were performed for shallow-depth (10-m) trawls and standard mid-depth (30-m) trawls because of the possibility of a depth effect due to metamorphic stage and the fact that upwelling typically affects only the upper 20 m of the water column (Parrish et al., 1981). To increase sample size, trawls at nonstandard stations were included in the analysis.

Results

Overall abundances and seasonal abundance patterns of the two sanddab species were variable (Fig. 2). In 1991, the abundance of both species increased monotonically during the May–June sampling period, whereas in 1987 and 1988, catches were relatively high in April but showed a marked decrease by the end of May–June, suggesting that pelagic sanddab abundance frequently declines during the April–June period (Fig. 2). However, catches of Pacific sanddabs in April of 1990 were low relative to May–June, and the May–June catches in 1988 and 1989 did not change monotonically, suggesting interannual variation in seasonal patterns (Fig. 2). Although April–June abundances were variable (Fig. 2), the interannual variation in year-class strength of pelagic sanddabs could not be determined without complete seasonal data.

In both species, SL increased asymptotically with metamorphic stage (Fig. 3). In addition, the range of lengths within each stage was quite large (Fig. 3). Pacific sanddabs were generally larger than speckled sanddabs at each metamorphic stage (Fig. 3). Although stage-2 individuals were significantly smaller than individuals of subsequent stages, the mean SL's did not differ significantly among the three later stages (α=0.05, df=76 for Pacific sanddabs and df=75 for speckled sanddabs). Whereas SL increased asymptotically with metamorphic development in both sanddabs, otolith diameter showed a linear increase (Fig. 4). In addition, otolith diameter increased dramatically with SL (Fig. 5), and mean otolith diameter increased significantly with each successive stage (α=0.05, df=76 for Pacific sanddabs and df=75 for speckled sanddabs). It appears that metamorphosis in sanddabs is possible at a range of sizes (30 mm to >50 mm SL in Pacific sanddabs and 25 to 40 mm SL in speckled sanddabs) and that once initiated, there is little growth in length but continued otolith growth (Figs. 3–5).

In general, Pacific sanddabs were relatively evenly distributed throughout the water column; there was a slight decrease in abundance with increasing depth (Table 1). Separate analyses of the April and May–June surveys showed similar results (Table 1).

In contrast to Pacific sanddabs, speckled sanddabs were significantly more abundant in shallow and mid-depth trawls than in deep trawls (Table 2). Analyzed separately, the May–June surveys showed a similar pattern to the overall analysis, but the April surveys showed less distinct differences in depth distribution (Table 2). The April surveys showed a trend of decreased abundance in deep trawls relative to shallow and mid-depth trawls, but the differences were not significant (Table 2).

Depth distributions differed among the metamorphic stages of both sanddab species: Stage-2 individuals of Pacific sanddabs were significantly more abundant in mid-depth trawls than in deep trawls, with a trend for increased abundance in shallow trawls versus deep trawls (Table 3; Fig. 6). Although both stage-3 and stage-4 sanddabs showed a relatively even distribution throughout the water column (with no significant differences among depths), stage-3 individuals tended to be less abundant with increased depth, whereas stage-4 individuals tended to be more abundant with increased depth (Table 3; Fig. 6). Stage-5 individuals were generally less abundant in shallow trawls and showed a tendency toward increased abundance with increased depth (Table 3; Fig. 6).

In speckled sanddabs, stage-2 individuals were significantly more abundant in mid-depth trawls

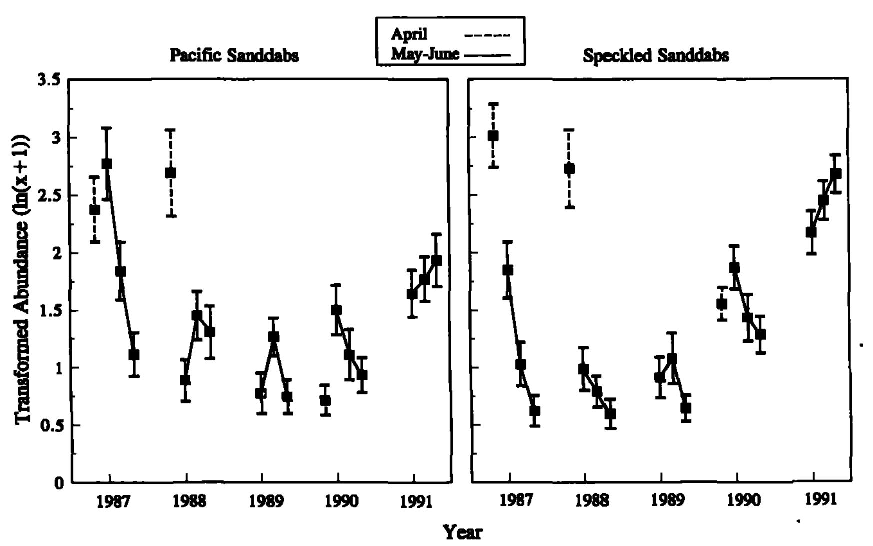

Figure 2

Means and standard errors of the log-transformed abundances of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected at standard stations during April and May–June 1987–91 (means of the three sweeps for the May–June surveys are connected by a line).

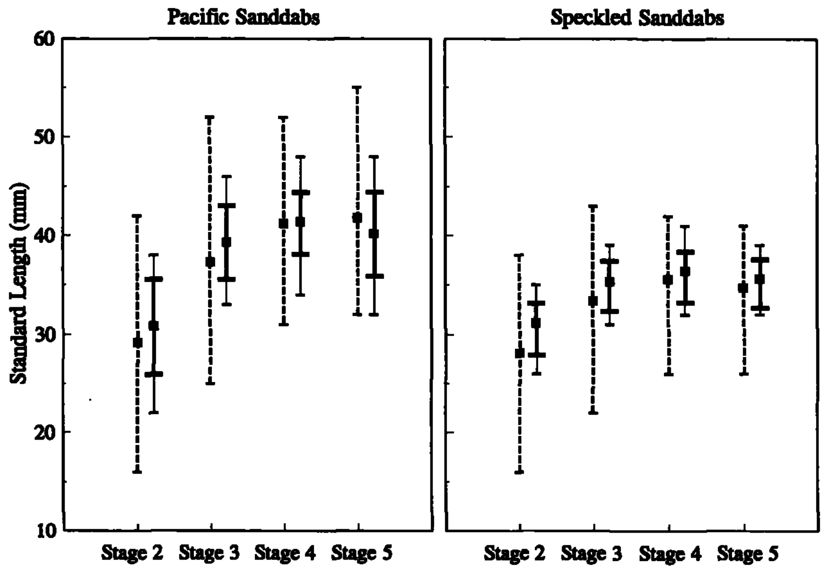

Figure 3

Means and ranges of standard lengths of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, in 1990 and 1991 as a function of metamorphic stage. All specimens measured are represented by dotted lines; those subsampled for otolith removal are represented by solid lines. Standard deviations for the specimens selected for otolith removal are shown with thick lines; ranges are shown with thin lines.

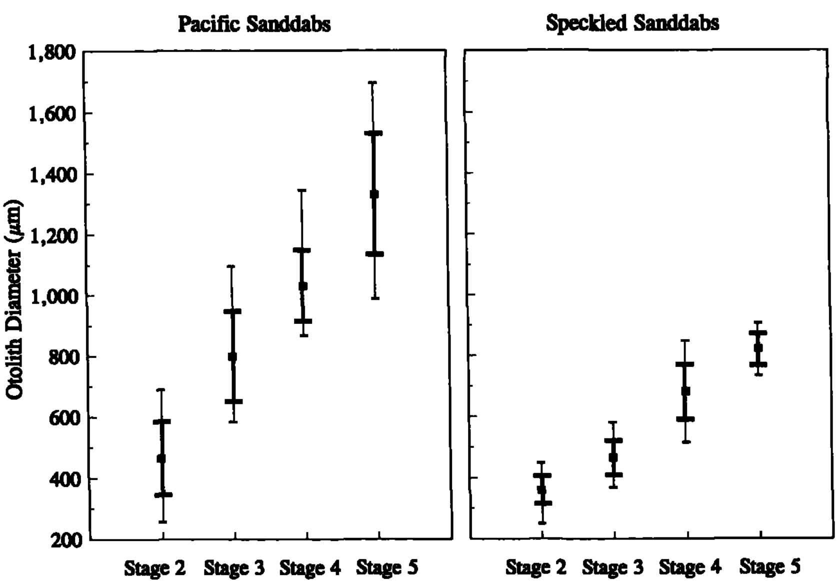

Figure 4

Means, standard deviations, and ranges of otolith diameters of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991. Standard deviations are shown with thick lines; ranges are shown with thin lines.

Table 1

Paired comparison t-tests of log-transformed abundance ($\ln(x+1)$) of Pacific sanddabs, *Citharichthys sordidus*, from 1987 to 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	n	Mean diff.	SE	t	P
All surveys					
10 m – 30 m	57	0.07	0.1723	0.4047	0.6872
30 m – 110 m	63	0.03	0.1358	0.2075	0.8363
10 m – 110 m	39	0.43	0.2122	2.0419	0.0482
April surveys					
10 m – 30 m	15	0.11	0.4375	0.2515	0.8051
30 m – 110 m	11	–0.35	0.3193	–1.0889	0.3018
10 m – 110 m	8	0.53	0.5727	0.9192	0.3886
May–June surveys					
10 m – 30 m	42	0.06	0.1779	0.3109	0.7574
30 m – 110 m	52	0.11	0.1491	0.7223	0.4734
10 m – 110 m	31	0.41	0.2278	1.7962	0.0825

Table 2

Paired comparison t-tests of log-transformed abundance ($\ln(x+1)$) of speckled sanddabs, *Citharichthys stigmaeus*, from 1987 to 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	n	Mean diff.	SE	t	P
All surveys					
10 m – 30 m	54	–0.01	0.1379	–0.1024	0.9188
30 m – 110 m	51	0.62	0.1395	4.4494	0.0001
10 m – 110 m	37	0.69	0.1555	4.4301	0.0001
April surveys					
10 m – 30 m	14	0.02	0.3319	0.0499	0.9610
30 m – 110 m	13	0.59	0.3488	1.7036	0.1142
10 m – 110 m	8	0.75	0.3479	2.1487	0.0687
May–June surveys					
10 m – 30 m	40	–0.02	0.1484	–0.1675	0.8678
30 m – 110 m	38	0.63	0.1476	4.2666	0.0001
10 m – 110 m	29	0.67	0.1768	3.8038	0.0001

than in deep trawls with a trend for increased abundance in shallow trawls versus deep trawls (Table 4; Fig. 6). Stage-3 and stage-4 individuals were most abundant in mid-depth trawls; stage-3 individuals showed a tendency for decreased abundance in shallow trawls versus mid-depth trawls (Table 4; Fig. 6). Stage-5 individuals were distributed relatively evenly throughout the water column, with a tendency toward increased abundance with increased depth (Table 4; Fig. 6). In contrast to Pacific sanddabs, of the four metamorphic stages, only stage-5 individuals of speckled sanddabs were abundant in the deep trawls (Table 4; Fig. 6). Thus, speckled sanddabs generally occurred shallower in the water column than did Pacific sanddabs (Fig. 6).

Within each species of sanddab, abundances of adjacent metamorphic stages were correlated over stations (Table 5). However, the correlations decreased among more dissimilar stages, indicating changes in distribution with advancing metamorphosis (Table 5). The only two stages in either species that were not significantly correlated with each other were stages 2 and 5 (Table 5). Results of the correlation analysis provided a substantial basis for overlaying only stage-2 and stage-5 abundances onto the salinity contours in Figures 8 and 9.

CTD salinity contours showed that many of the patterns at the surface were still noticeable at 30 m (Fig. 7; and Sakuma, 1992). Therefore, only the surface salinity contours were used because they provided the widest horizontal spatial coverage (salinity at 30 m was not available for nearshore stations because of the shallow bottom depth).

Table 3

Paired comparison t-tests of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of Pacific sanddabs, *Citharichthys sordidus*, from 1990 and 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	n	Mean diff.	SE	t	P
Stage 2					
10 m – 30 m	16	0.08	0.3686	0.2217	0.8276
30 m – 110 m	15	0.53	0.2073	2.5674	0.0224
10 m – 110 m	14	0.65	0.3890	1.6758	0.1176
Stage 3					
10 m – 30 m	14	0.09	0.4787	0.1846	0.8564
30 m – 110 m	17	0.25	0.2058	1.2234	0.2389
10 m – 110 m	16	0.34	0.3987	0.8649	0.4007
Stage 4					
10 m – 30 m	10	–0.55	0.4237	–1.3017	0.2254
30 m – 110 m	12	–0.05	0.3156	–0.1684	0.8693
10 m – 110 m	13	–0.51	0.3946	–1.2940	0.2247
Stage 5					
10 m – 30 m	15	–0.77	0.3505	–2.1952	0.0455
30 m – 110 m	16	–0.35	0.2927	–1.1901	0.2525
10 m – 110 m	13	–0.70	0.3931	–1.7859	0.0994

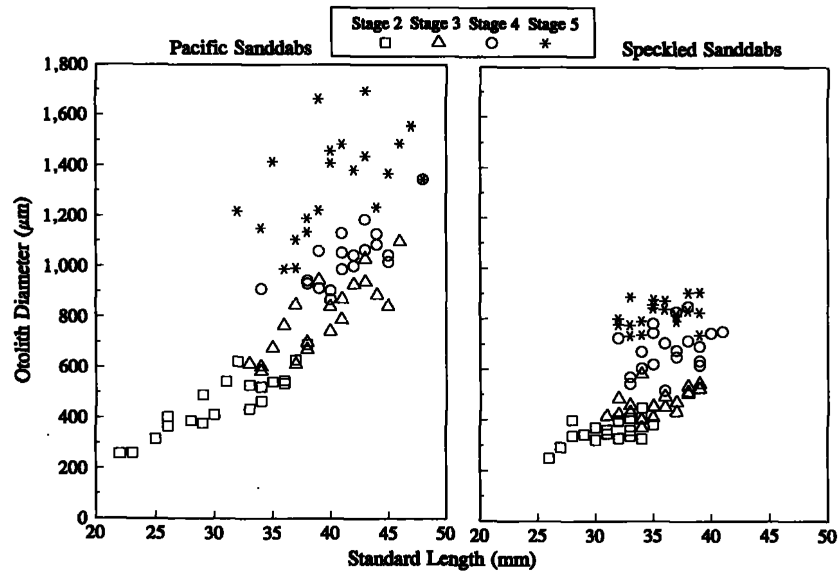

Figure 5

Otolith diameter versus standard length of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991.

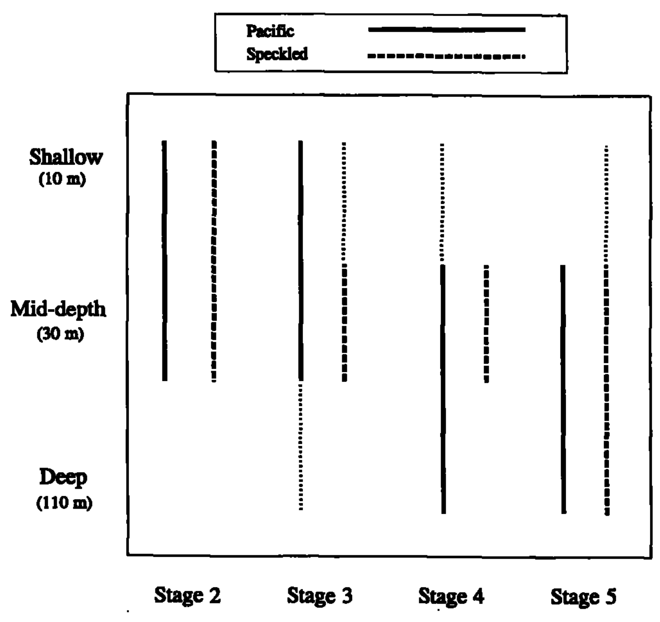

Figure 6

Depth distributions of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991, based on paired comparisons of abundance at different depths (Tables 3 and 4). Small dotted lines indicate nonsignificant (P>0.05) trends of decreased abundance at the given depth.

Contours for sweep 1 of the May–June survey of 1990 showed a pattern of recent or ongoing upwelling occurring off Point Reyes and the Davenport area (see Fig. 1 for place names) as evidenced by the filaments of higher salinity water projecting seaward and shoreward impingement of lower salinity, more oceanic water (Simpson, 1987) at the surface north of Point Reyes (Fig. 8). The contours for sweep 2 indicated a reduction in offshore transport due to upwelling, with lower salinities closer to shore (Fig. 8). The contours for sweep 3 showed upwelling activity occurring off Point Reyes but not off Davenport (Fig. 8).

The contours for the May–June survey of 1991 showed pronounced seaward filaments off Point Reyes and Davenport during sweep 1, which indicated recent or ongoing upwelling (Fig. 9). During sweep 2, upwelling was still evident off Davenport, but owing to problems with the CTD, patterns off Point Reyes were not easily discernible (Fig. 9). During sweep 3, there was a relaxation of upwelling as evidenced by the lack of seaward-projecting filaments of higher salinity water (Fig. 9).

The overlaid abundances of stages 2 and 5 showed that large abundances of stage-5 individuals of both species generally occurred nearshore and could be found within centers of upwelling (Figs. 8 and 9 off Davenport and Monterey Bay; Fig. 9 off Point Reyes). In contrast, large numbers of stage-2 individuals of both species were relatively more abundant in the offshore transitional zone between coastal water (nearshore, high salinity due to upwelling) and oceanic water (offshore, low salinity) (Figs. 8 and 9). In addition, large numbers of stage-2 individuals were observed nearshore in the area north of Point Reyes during sweep 1 of 1990 associated with the shoreward impingement of oceanic water (Fig. 8).

Although the effects of upwelling would be expected to be most intense near the surface, no significant differences in the abundances of the metamorphic stages of either sanddab species were observed between upwelling and non-upwelling areas at the shallow trawl depth of

Table 4

Paired comparison *t*-tests of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of speckled sanddabs, *Citharichthys stigmaeus*, from 1990 and 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
Stage 2					
10m – 30 m	21	–0.08	0.2339	–0.3240	0.7493
30m – 110 m	18	0.49	0.2408	2.0436	0.0568
10m – 110 m	14	0.52	0.3199	1.6392	0.1251
Stage 3					
10m – 30 m	23	–0.46	0.2438	–1.8982	0.0709
30m – 110 m	17	0.51	0.2350	2.1629	0.0460
10m – 110 m	16	0.44	0.2647	1.6492	0.1199
Stage 4					
10m – 30 m	17	–0.79	0.2212	–3.5700	0.0026
30m – 110 m	14	0.67	0.2532	2.6485	0.0201
10m – 110 m	10	0.05	0.2604	0.1739	0.8658
Stage 5					
10m – 30 m	10	–0.72	0.4615	–1.5548	0.1544
30m – 110 m	4	–0.27	0.3705	–0.7186	0.5243
10m – 110 m	5	0.11	0.4416	0.2584	0.8088

Table 5

Spearman rank correlations of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected at standard stations during 1990 and 1991 (significance probabilities of each correlation are listed in bold type under the coefficients).

	Pacific sanddabs (n = 257)			
	Stage 2	Stage 3	Stage 4	Stage 5
Stage 2		0.58	0.31	0.06
		0.0001	**0.0001**	**0.3559**
Stage 3	0.62		0.47	0.13
	0.0001		**0.0001**	**0.0316**
Stage 4	0.15	0.37		0.38
	0.0181	**0.0001**		**0.0001**
Stage 5	0.04	0.13	0.53	
	0.4827	**0.0346**	**0.0001**	
	Stage 2	Stage 3	Stage 4	Stage 5
	Speckled sanddabs (n = 257)			

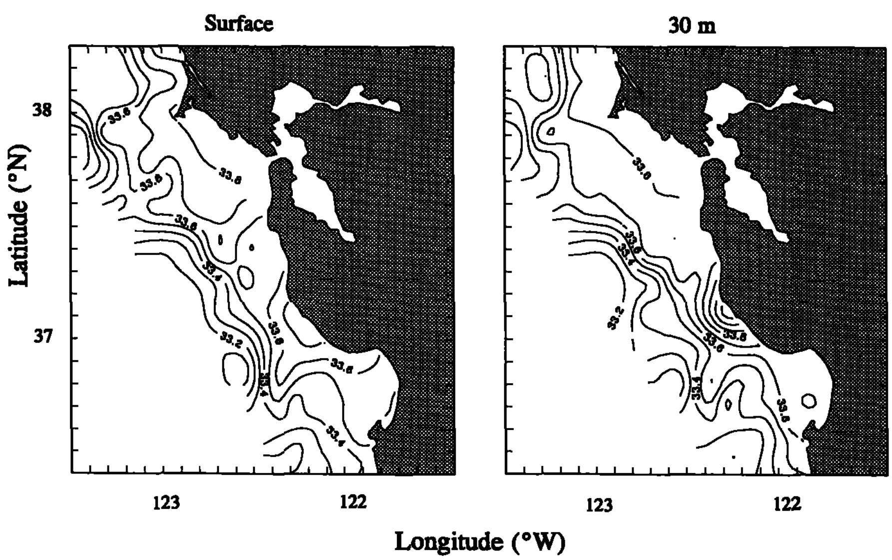

Figure 7

Salinity contours at the surface compared with salinity contours at 30 m depth during 1990 sweep 1.

10 m (Table 6; Fig. 10). However, at the mid-depth of 30 m, stages 2 and 3 of Pacific sanddabs were significantly less abundant in upwelling areas than in non-upwelling areas, and stages 2 and 3 of speckled sanddabs showed a strong tendency for decreased abundance in upwelling areas (Table 6; Fig. 10). In contrast, stage 5 in each species tended to be more abundant in upwelling areas than in non-upwelling areas (Table 6; Fig. 10).

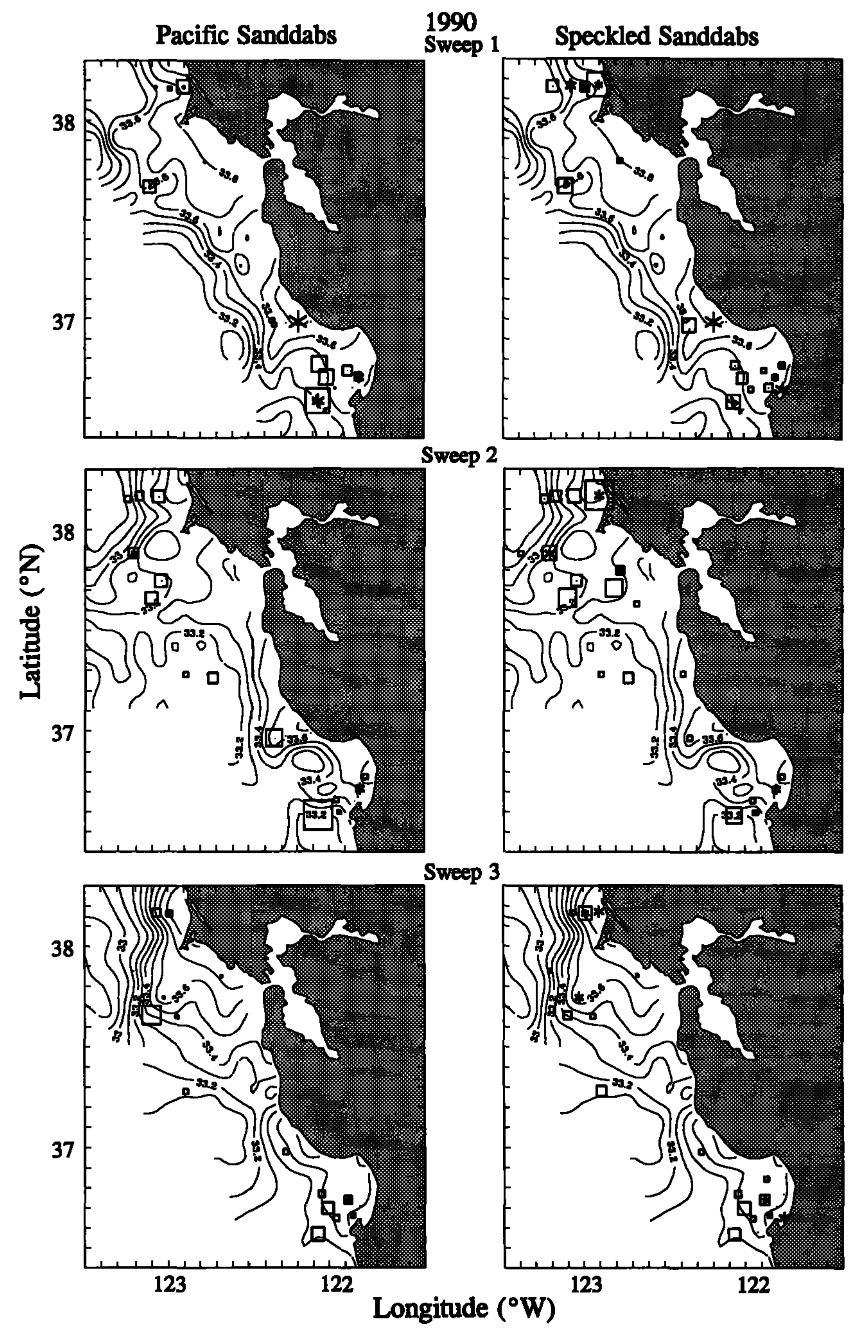

Figure 8

Salinity contours at the surface during the May–June survey of 1990 with overlaid abundances of stages 2 (represented by squares) and 5 (represented by asterisks) of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*. Size of each symbol is proportional to the abundance.

Discussion

During the springtime series covered by this study, metamorphosis in both sanddab species occurred at a wide range of sizes, indicating little growth in body size during metamorphosis (Figs. 3 and 5). Later metamorphic stages tended to occur in deeper water than did earlier stages; Pacific sanddabs shifted to deeper water at earlier stages than speckled sanddabs (Tables 3 and 4; Fig. 6). Later metamorphic stages of both sanddabs occurred nearer to shore than earlier stages, despite the upwelling-associated offshore advection of surface waters (Table 6; Figs. 8–10).

Given the reported variability of size at metamorphosis in both sanddab species (Ahlstrom et al., 1984; Matarese et al., 1989), it was not surprising to observe a large amount of overlap in the SL's of the different metamorphic stages (Fig. 3). Kendall (1992) reported that speckled sanddabs settled at ages ranging from 113 to 324 days. In general, she found that larger, recently settled individuals had spent more time in the plankton than smaller recently settled ones (Kendall, 1992). Kendall (1992) also reported that settlement marks on the otoliths of speckled sanddabs were generally observed at an otolith radius of 400–450 µm. This corresponds to the otolith diameters observed in stage-5 individuals, indicating that these individuals were prepared to settle (Figs. 4 and 5).

An important aspect of metamorphosis in flatfishes is the ossification of bony structures (Ahlstrom et al., 1984). The large increase in otolith size observed in later metamorphic stages of both sanddab species may be attributable to the transition from a planktonic form to a benthic form. Jenkins (1987) observed accelerated otolith growth in relation to growth in length at the beginning of metamorphosis for the flatfish *Rhombosolea tapirina*, which resulted in significant alterations in otolith increment morphology. One alteration in otolith morphology observed in pelagic stage Pacific sanddabs was the formation of accessory growth primordia. Accessory growth primordia first occurred in stage-3 individuals and completely enclosed the otolith by stage 5 (Brothers[1]). Toole et al. (1993) found that the initiation of accessory primordia formation was coincident with the onset of eye migration in Dover sole, *Microstomus pacificus*, and that the completion of accessory primordia formation occurred either during the final stages of eye migration in pelagic individuals or shortly after settlement.

Metamorphosis in some flatfish can take place in as little as five hours, as in *Cynoglossus macrostomus* (Ahlstrom et al., 1984), or up to nine months, as in *Microstomus pacificus* (Markle et al., 1992). The small increase in length seen in metamorphosing sanddabs (Figs. 3 and 5) suggests a relatively rapid metamorphosis relative to growth. However, if metamorphosis occurred very rapidly, then the probability of collecting metamorphosing specimens would be small (Laroche et al., 1982; Ahlstrom et al., 1984). The large numbers of later stages collected in 1991 and the large otolith sizes in later stages suggest that metamorphosis in both sanddab species occurs over a more prolonged period of time (Figs. 5, 8, and 9). Preliminary results from Pacific sanddab otoliths indicate that the transition from stage 3 to stage 5 takes approximately three weeks (Brothers[1]). Kendall's (1992) data on otolith radius at age indicate that the transition from individuals with otolith radii correspond-

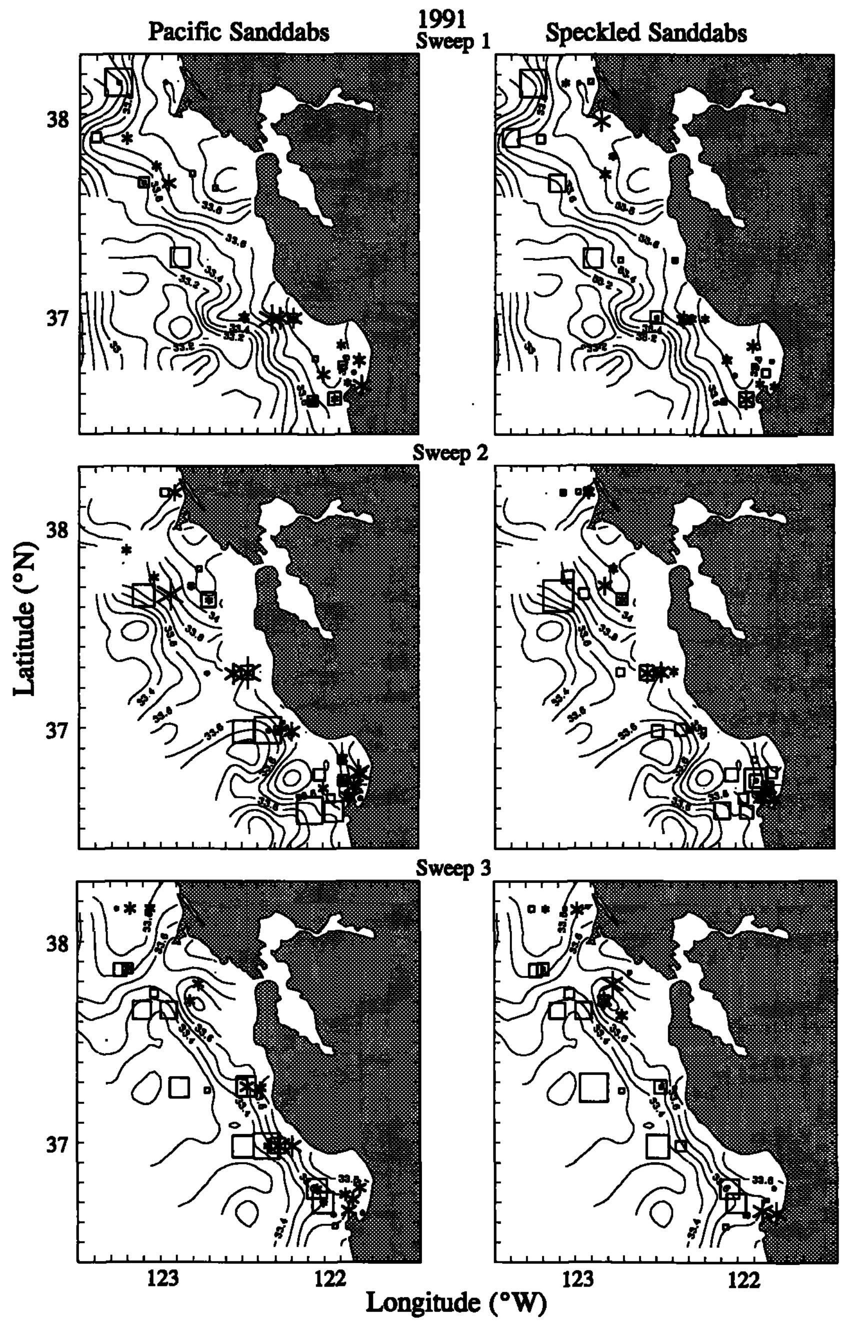

Figure 9

Salinity contours at the surface during the May–June survey of 1991 with overlaid abundances of stages 2 (represented by squares) and 5 (represented by asterisks) of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*. Size of each symbol is proportional to the abundance.

Table 6

Comparison of standard scores of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, in upwelling and non-upwelling areas during 1990 and 1991 (upwelling areas were defined as having surface salinities >33.6 ppt and surface temperatures <11.0°C). Means and standard errors are shown in Figure 10. Degrees of freedom less than $(n_1-1)+(n_2-1)$ indicate cases with unequal variances.

Pacific sanddabs				Speckled sanddabs			
Stage	*t*	df	*P*	Stage	*t*	df	*P*
Shallow trawls (upwelling *n*=36, non-upwelling *n*=44)							
2	0.6797	78.0	0.4987	2	−0.4730	76.2	0.6375
3	0.6911	76.4	0.4916	3	0.6346	78.0	0.5275
4	0.1171	78.0	0.9071	4	0.4846	78.0	0.6293
5	−0.4135	77.0	0.6804	5	−0.3190	78.0	0.7506
Mid-depth trawls (upwelling *n*=63, non-upwelling *n*=99)							
2	−2.3877	159.9	0.0181	2	−1.7268	160.0	0.0861
3	−3.0253	160.0	0.0029	3	−1.7147	160.0	0.0883
4	−0.5325	160.0	0.5951	4	0.7201	160.0	0.4275
5	0.9655	160.0	0.3259	5	1.5650	100.4	0.1207

ing to stage 3 to those corresponding to stage 5 takes approximately five weeks.

Morphological changes associated with metamorphosis probably decrease the buoyancy of pelagic sanddabs. Laroche et al. (1982) found an increase in otolith growth relative to growth in length at metamorphosis for *Parophrys vetulus*, which was similar to that observed for the two sanddab species in this study and for *Rhombosolea tapirina* (Jenkins, 1987). Reared *Parophrys vetulus* that were close to settlement frequently rested on their sides on the bottom and swam with their bodies at an angle (Laroche et al., 1982). This behavior may be related to decreased buoyancy as a result of the ossification of bony structures and to the large increase in otolith size (Laroche et al., 1982). In addition, the gas bladder is lost during metamorphosis in some species of flatfish, including the related Atlantic species *Citharichthys arctifrons* (Richardson and Joseph, 1973; Ahlstrom et al., 1984). Laidig[2] observed that the gas bladder was reduced in stage-4 Pacific sanddabs and absent in 90% of stage-5 specimens.

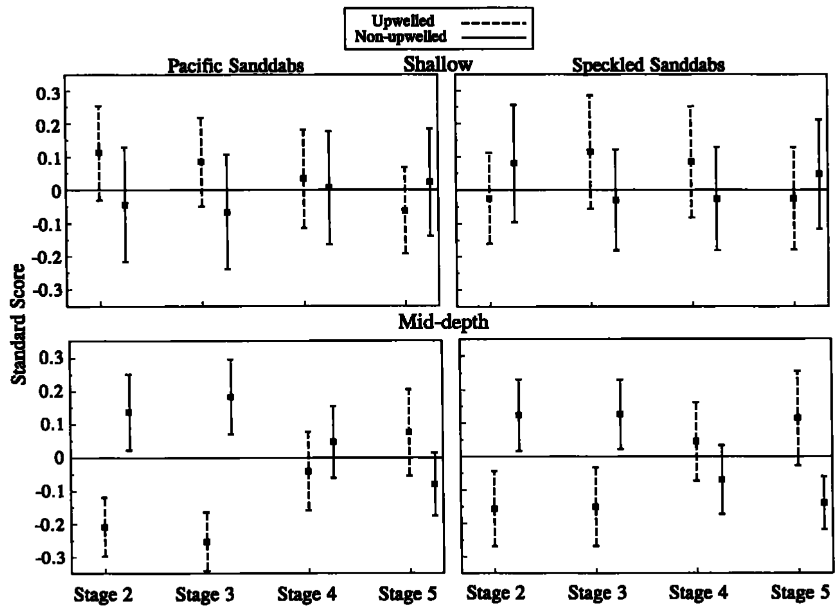

Figure 10

Mean standard scores and standard errors of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in shallow and mid-depth trawls during 1990 and 1991 in upwelling and non-upwelling areas (upwelling=surface salinity >33.6 ppt and surface temperature <11°C).

[2] Laidig, T. E. Tiburon Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Drive, Tiburon, CA 94920. Personal commun., 1994.

The decrease in buoyancy due to increased otolith size, the ossification of other bony structures, and the loss of the gas bladder may account for the deeper bathymetric distribution of later metamorphic stages in both sanddab species (Tables 3 and 4; Fig. 6). The greater water density at deeper depths may reduce the energy expenditure required for less buoyant fish to remain pelagic; however, beyond a given range of SL and otolith size, individuals may sink more rapidly. Therefore, the decrease in buoyancy may account directly for the deeper bathymetric distribution of later-stage pelagic sanddabs, although fish may behaviorally seek deeper water as well.

Lenarz et al. (1991) reported that younger, smaller juveniles of the shortbelly rockfish, *Sebastes jordani*, were found deeper in the water column than larger individuals during May–June. It was suggested that the smaller individuals were adapted to seeking deeper water as a method of avoiding offshore advection due to upwelling (Lenarz et al., 1991). In contrast, the early stages of both sanddab species showed a shallower distribution than the later stages (Tables 3 and 4; Fig. 6). The shallow distribution of early stages may explain the comparisons of abundance in upwelling and non-upwelling areas for the 30-m depth trawls, which suggest that early stages are subject to offshore advection due to coastal upwelling (Table 6; Figs. 6, 8, 9, and 10). The offshore advection of early stages may also explain their predominantly offshore distribution (Figs. 8 and 9).

The lack of significant differences in abundance between upwelling and non-upwelling areas for the shallow depth trawls observed in both sanddab species might be explained by the fact that the majority of these trawls were conducted nearshore where early stages were generally less abundant and that later stages were generally less abundant at the shallow trawl depth (Tables 3, 4, and 6; Figs. 6, 8, 9, and 10). In contrast, the 30-m mid-depth trawls, in which most metamorphic stages occurred, were more widely distributed and probably indicated better the relation between upwelling and the distribution of metamorphic stages (Tables 3, 4, and 6; Fig. 6). Figure 10 shows a change in distribution of metamorphic stages in the 30-m mid-depth trawls; earlier stages tended to be more abundant in water that had not been upwelled recently, whereas later stages were more abundant in recently upwelled water.

The reduction in abundance of early stages in trawls within upwelling areas may have been due to the fact that these stages were present predominantly offshore while upwelling events occurred nearshore (Figs. 8 and 9). However, the large abundances of stage-2 individuals of both species observed nearshore north of Point Reyes during sweep 1 of 1990 associated with an extension of oceanic waters toward shore (Fig. 8) and the large abundances of stage-2 individuals occurring within the transitional areas between offshore oceanic waters and nearshore coastal waters (Figs. 8 and 9) suggest that these early stages were subject to transport by ocean currents. Analysis of California Cooperative Oceanic Fisheries Investigations (CalCOFI) data by Ahlstrom and Moser (1975) and Loeb et al. (1983) indicated that the larvae of both sanddab species were collected both nearshore and well offshore. Therefore, sanddabs of both species are probably passive drifters during their early life history stages as evidenced by the predominantly offshore distribution of their early metamorphic stages (Figs. 8 and 9) and the somewhat dispersed distribution of their larvae (Ahlstrom and Moser, 1975; Loeb et al., 1983).

In contrast to the distributional patterns of early stage metamorphic sanddabs, the tendency for later stages of both species to be more abundant in upwelling areas was probably due to the fact that later stage individuals occurred predominantly nearshore (Figs. 8 and 9). Although large numbers of stage-5 individuals of both species occurred within upwelling plumes (Figs. 8 and 9), large abundances of stage-5 individuals could also be found nearshore in areas outside of the upwelling plumes (Figs. 8 and 9). Because later-stage individuals were more abundant at deeper depths, they were probably less susceptible to offshore advection by upwelling. The deeper and more shoreward distribution of later-stage sanddabs parallels the observations of Barnett et al. (1984) on later stages of northern anchovy, *Engraulis mordax*, white croaker, *Genyonemus lineatus*, and queenfish, *Seriphus politus*, off southern California. Larson et al. (1994) also found that late-stage pelagic juvenile rockfish (*Sebastes* spp.) off central California had a more shoreward distribution, although there was no evidence that later-stage fish were distributed at greater depths (Lenarz et al., 1991).

In summary, it appears that physical changes in metamorphosing sanddabs are correlated with changes in their depth distributions; more developed, less buoyant individuals occur deeper in the water column (Fig. 6). This may influence the horizontal distributions of pelagic sanddabs in the upwelling regions off central California. Early-stage sanddabs present within the upper mixed layer would be subject to offshore advection associated with coastal upwelling or to onshore advection associated with downwelling (Table 6; Figs. 8–10). In contrast, the deeper distribution of later-stage sanddabs decreases their susceptibility to upwelling-associated offshore advection and could potentially lead to onshore advection facilitated by the shoreward movement of deeper water (Tables 3 and 4; Fig. 6). In addition, the vertical and horizontal distributions of both early and late-stage sanddabs may have a substantial behavioral component; however, the means to resolve such behavioral patterns is beyond the scope of this study.

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