

Abstract.—Morphological changes during metamorphosis of Dover sole *Microstomus pacificus* are described from 2220 larvae and juveniles. Unlike most flounders, initiation of eye migration is uncoupled from metamorphosis and from the habitat change from planktonic to benthic. Dover sole larvae are optically asymmetrical during most of their planktonic life. Major features associated with metamorphosis are reduction in body depth with associated reductions in lengths of neural and hemal spines, increase in relative eye diameter, loss of canine-like teeth coincidental with acquisition of incisor-like teeth, resorption of posterior process of coracoid, development of body scales, change in body pigmentation, and development of the gut loop in the secondary body cavity. From initiation to completion, metamorphosis appears to take about 9 months, during which time there is little increase in body length.

Available evidence indicates that most spawning off Oregon occurs in spring, with April and May as peak hatching months. Settlement from the plankton occurs in winter, with January to March as peak settlement months. Duration of planktonic life appears to be about 2 years, with a minimum duration of about 18 months. Metamorphosing larvae settle over a broad "landing" zone (55–377 m), quantitatively distinct from, but overlapping, the narrower spring nursery zone (40–170 m). As yet, there is no evidence of delayed metamorphosis. Metamorphosis is protracted, seems to be seasonally-triggered, and may involve a significant period during which larvae switch between midwater and bottom habitats.

Metamorphosis and an overview of early-life-history stages in Dover sole *Microstomus pacificus**

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There is uncertainty about the length of the pelagic life of Dover sole *Microstomus pacificus*. Hagerman (1952) noted that the "pelagic life is prolonged for several months and metamorphosis is delayed." Allen and Mearns (1977) thought a 9-month planktonic stage was "probably not unusual." Percy et al. (1977a) examined the early life history in greater detail and concluded that "Dover sole larvae are pelagic for at least a year." Hayman and Tyler (1980), although citing Percy et al. (1977a), constructed a time-line indicating a 9-month pelagic larval stage.

There is also little agreement on estimated body length at the end of the first year of life. Percy et al. (1977a) estimated growth to be 20–30 mm standard length (SL) during the first year, but also concluded that metamorphosis took place after about 1 year at 30–50 mm SL (the extra 10–30 mm of growth was not explained). Hagerman (1952) and Demory (1972), both limited by small sample sizes, mention lengths of 66–75 mm total length (TL) for nominal 1-year-old specimens.

Uncertainty about duration and growth in the pelagic phase has important implications for age estimates. Whether based on scales or otolith sections, no researcher has

documented the age or size at which the first nominal annulus forms (Demory 1972, Chilton and Beamish 1982, Pikitch and Demory 1988, Hunter et al. 1990).

From the large midwater trawl collections made by W.G. Percy and colleagues (OSU) from 1961 to 1982, and juvenile bottom-trawl surveys conducted off Oregon from 1988 to 1990, we describe metamorphosis and other stages in the early life history of Dover sole and address questions relating to the duration and timing of these stages.

Materials and methods

Midwater trawl collections

A total of 796 Dover sole larvae were obtained from 425 midwater trawl stations off Oregon. Details of sampling methods are given in Percy (1976, 1980) and Percy et al. (1977 a,b). Because the midwater trawls were made for a variety of reasons, there are constraints on interpretation of these data. The most important constraints are seasonal, diel, depth, and gear. Seasonal coverage was best from June to September, and poorest in May and October (Table 1). There was a pronounced diel bias. Relatively few samples were collected between 0600 and 2000 hours (Table 2). Most samples were collected at night between 2200 and 0500 hours. The range of collec-

Table 1

Distribution of midwater trawl stations by month, 1961-82.

Month	No. of stations	Percent of total
January	94	3.8
February	127	5.1
March	157	6.4
April	174	7.0
May	85	3.4
June	306	12.4
July	397	16.1
August	237	9.6
September	479	19.4
October	74	3.0
November	165	6.7
December	173	7.0
Total	2468	99.9

tion depths was 0-6000 m, but 81.8% of the samples were from depths <500 m. Eleven different gear types were used: Tucker trawl, Cobb trawl, 0.9 m Isaacs-Kidd midwater trawl (IKMT), 1.8 m IKMT, 2.4 m IKMT, 3.0 m IKMT, 2.4 m rectangular midwater trawl (RMT), 2.7 m RMT, 1 m² multiple plankton sampler, 65 m² midwater trawl, and 100 m² midwater trawl. Some gears were operated with and without opening-closing devices (Pearcy 1980). Eighty-eight percent of the collections were made with either a 1.8 m or 2.4 m Isaacs-Kidd midwater trawl (IKMT). All specimens were preserved in 10% formalin and transferred to 50% isopropanol.

Juvenile bottom-trawl collections

A bottom-trawl survey of juvenile Dover sole was conducted bimonthly, January to November 1989, in three areas off Oregon (Fig. 1). In March 1988 and 1990, a more limited survey was conducted in the central (Foulweather) area. Each area was 10 miles wide and oriented to the coast such that the depth range of 50-400 m could be covered in the shortest distance. Each area was subdivided into six strata bounded by isobaths at 50, 80, 100, 120, 160, 220 and 400 m. Trawl stations were randomly chosen such that a minimum of three 5-minute trawls were attempted in each stratum. When time permitted, additional stations were added in strata with highest concentrations of Dover sole (100-119 and 120-159 m). All trawling was conducted from the FV *Olympic* during daylight hours. The gear was a commercial, 34.9 mm mesh, two-seam shrimp trawl with a 27.4 m headrope, rigged with a 28.5 m footrope and tickler chain. The posterior 3/4 of

Table 2

Distribution of midwater trawl stations by time of day, 1961-82.

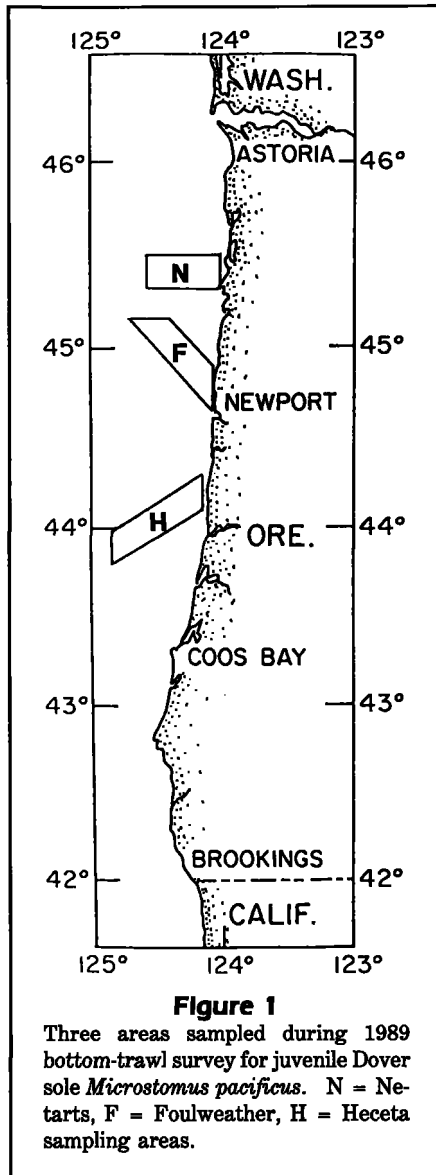
Hour of set	No. of stations	Percent	Hour of set	No. of stations	Percent
0100	192	7.8	1300	51	2.1
0200	158	6.4	1400	60	2.4
0300	177	7.2	1500	60	2.4
0400	184	7.4	1600	65	2.6
0500	154	6.2	1700	52	2.1
0600	82	3.3	1800	60	2.4
0700	68	2.8	1900	65	2.6
0800	61	2.5	2000	78	3.2
0900	61	2.5	2100	95	3.8
1000	69	2.8	2200	119	4.8
1100	45	1.8	2300	133	5.4
1200	55	2.2	2400	167	6.8

the codend had a 6.4 mm liner. The catch was sorted on board, all fish species were counted and measured, and all Dover sole <200 mm SL were frozen or fixed in 10% formalin and returned to the laboratory for morphological analysis. All formalin-fixed specimens were preserved in 50% isopropanol before measurement.

Morphological analysis

All measurements reported herein were made in the laboratory on defrosted or formalin-fixed, isopropanol-preserved specimens. We found no significant differences ($P > 0.05$) between measurements of 39 defrosted juvenile Dover sole (46.9-71.0 mm SL) when remeasured over a year after fixation and preservation.

Measurements were taken on 2220 larvae, juveniles, and adults. Using the staging system developed herein, the numbers examined in each stage were: Stage 1, 811; Stage 2, 29; Stage 3, pelagic captures, 12; Stage 3, benthic captures, 409; Stage 4, pelagic captures, 1; Stage 4, benthic captures, 461; and Stage 5, 497. On all specimens returned to the laboratory, we measured TL, SL, body depth at anus (BD1A), maximum body depth, snout to posterior extent of intestine length (SINT), and body weight. Length measurements were taken to the nearest 0.1 mm using an ocular micrometer on specimens <20 mm SL and dial calipers on larger specimens. Body weight was determined to the nearest 0.001 g for Stages 1 and 2 and to the nearest 0.1 g for Stages 3, 4, and 5 (see staging description below). Weights were taken from undamaged, pat-dried individuals. Weight loss in isopropanol-preserved larvae was as great as 10% after 2 minutes of air exposure due to alcohol evaporation. Although specimens were exposed for less time before weighing, a 10% weighing error was



assumed for this study. Considering the change in weight of three orders of magnitude between 10 and 50 mm SL, the weighing error was considered acceptable for this study.

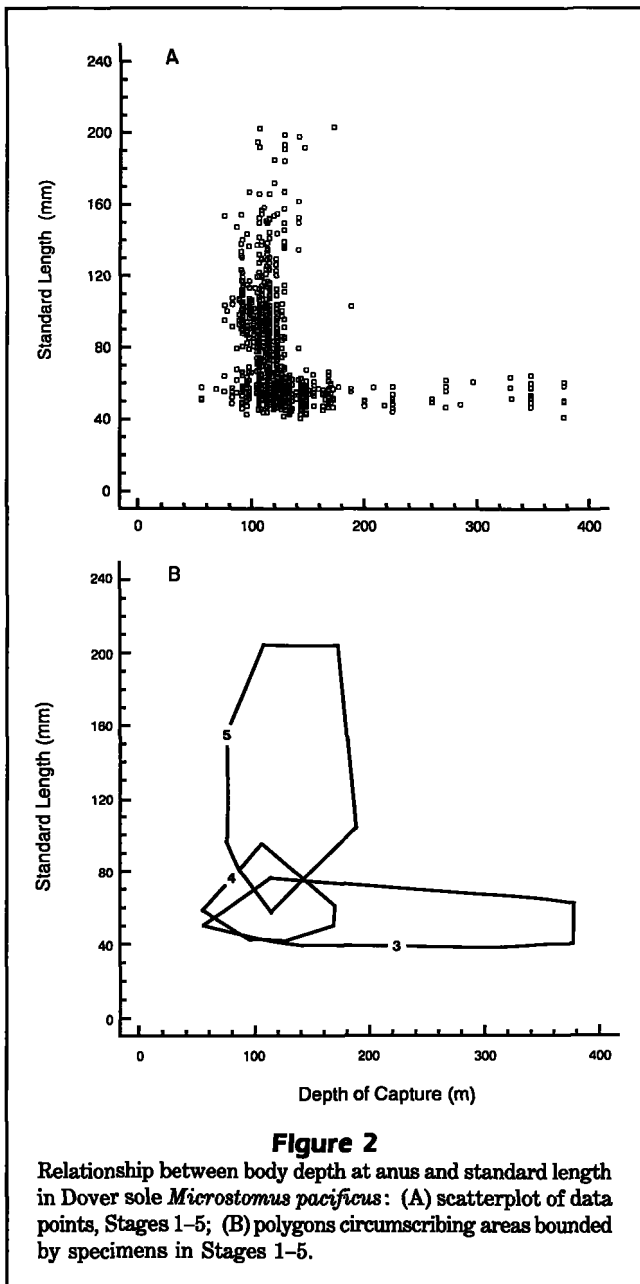
A smaller subset of 201 specimens was examined to describe metamorphosis in greater detail, and all were deposited in the Oregon State University Fish Collection (OS). These specimens were either cleared and differentially stained with alizarin red S and alcian blue (Potthoff 1984), radiographed, or both. This subset included only postflexion Stage-1, most Stage-2, and representatives of Stages 3-5 larvae. In addition to routine measurements listed above, we measured right eye diameter, interorbital width, right upper jaw length, length of gastrointestinal tract as measured

from anus to most posterior part of intestinal loop, length of first caudal neural spine, length of dorsal fin pterygiophore anterior to first caudal neural spine, length of dorsal fin pterygiophore posterior to first caudal neural spine, length of first hemal spine, length of anal fin pterygiophore anterior to first caudal hemal spine, and length of anal fin pterygiophore posterior to caudal hemal spine. Counts of vertebrae and rays of dorsal, anal, caudal, pectoral, and pelvic fins also were made.

A staging system describing Dover sole ontogeny was developed following the suggestions of Youson (1988). Our terminology deviates from Balon (1979, 1984) and Youson (1988) in our use of five numbered stages for early development, rather than numbered stages for metamorphosis only. Dover sole have a protracted metamorphosis, and our stages can be related, generally, to flatfish metamorphosis. We suggest terminology for each stage that incorporates traditional concepts of larval and juvenile periods as well as the metamorphic phase of the larval period. Metamorphosis occurs in Stages 2-4.

We were especially concerned with describing the beginning of metamorphosis, the initiation event, and the completion of metamorphosis, the climax event (Youson 1988). The initiation event was described based on six characters that reach the adult state during the plankton-to-benthos transition (see Results below). Another character, body scale formation, could be documented only in cleared and stained specimens and was concordant with completion of the six initiation-event characters. Development of the intestinal loop in the secondary body cavity, quantified by SINT, is the last character to change in Dover sole metamorphosis. The climax event was described based on the rate of change of the ratio of natural logarithms of two measurements (SINT and SL). Both initiation and climax events are further corroborated by body shape changes.

We use the concept of competency, as developed in the marine invertebrate developmental literature, as part of our definition of stages. The term regrettably has become a synonym for metamorphosis, as in the phrase "competent to metamorphose" (Pechenik 1986). Doyle (1975), using the term "delay" stage, noted that the onset of competency included both developmental criteria (strict metamorphosis as used herein) and a behavioral criterion, the ability to settle. In some invertebrates, attachment to a substrate is a prerequisite to metamorphosis; thus settlement must occur prior to metamorphosis. In fishes there is not necessarily a connection between metamorphosis (Youson 1988) and competence. However, Cowen (1991) applied the terms to fish and kept the marine invertebrate connection intact. Competency has been defined more narrowly



as the ability to settle (Jackson and Strathmann 1981), a conceptual improvement that removes predefined connections to metamorphosis. We identify precompetent, competent, and postcompetent stages during metamorphosis of Dover sole.

Time-series analysis

Two approaches were used to construct a time-line of early development: modal progression analysis (MPA, Bhattacharya 1967) and an analysis of seasonality of stages. MPA was facilitated using the computer pro-

Table 3

Characters used to quantify metamorphosis in Dover sole *Microstomus pacificus*.

Character	Character state
Teeth	0 Canines
	1 Canines, incisors developing
	2 Incisors
Eye position	0 Left side of head or dorsal ridge
	1 Right side of head, adult position
Position of dorsal fin	0 First ray posterior to left eye
	1 First ray equal with posterior margin or anterior to left eye
Posterior process of coracoid	0 Straight, angled posteriorly
	1 Resorption beginning, tip curled into hook
	2 Resorption complete, process absent
Pectoral fin shape	0 Round, paddlelike shape, < adult shape complement of rays, no radials formed
	1 Intermediate shape, adult complement of rays, cartilaginous radials
	2 Adult morphology
Pigmentation	0 Planktonic coloration
	1 Benthic coloration

gram ELEFAN (Pauly 1987), but its utility was limited by sample sizes. Analysis of seasonality of stages was corroborated partly by monitoring growth of a single metamorphosing individual held in the laboratory at 13°C. The Stage-3 specimen was 57.7 mm SL when captured on 20 March 1989. It was measured regularly and progressed completely through Stage 4 to an early Stage 5, when it was sacrificed on 15 June 1989.

Results

Morphology and development

Stage 1 (premetamorphic larvae), 6.1–58.5 mm SL

For convenience and because of our emphasis on metamorphosis, all premetamorphic planktonic specimens are referred to as Stage 1. However, the premetamorphic phase of the larval period could be usefully divided into two intervals, the first approximating Stage I of Percy et al. (1977a). A transition from the first interval to the second occurs around 10–15 mm SL, during which eye migration begins, body depth increases (Fig. 2), the first dorsal and anal fin rays form, and caudal fin flexion begins. During the second interval, specimens acquire the adult numbers of vertebrae, and dorsal, anal, caudal, and pelvic fin rays; the stomach and intestine coil; 3–4 pyloric caecae develop; and a pigmentation pattern of dashes develops into a solid

Figure 3

Jaw dentition during metamorphosis in Dover sole *Microstomus pacificus*, left lateral views: (A) OS12578, Stage 1 with canine teeth; (B) OS11377, Stage 2 with canine and developing incisor teeth; and (C) OS11288, Stage 5 with developed incisor teeth.

outline at the base of the dorsal and anal fins around 35–40 mm SL (Pearcy et al. 1977a).

Stage 2 (metamorphic precompetent larvae), 42.3–60.4 mm SL Six morphological characters that define the initiation event of metamorphosis are, in their approximate order of development: jaw dentition, completion of eye migration, position of anterior margin of dorsal fin, position or presence of posterior process of the coracoid, pectoral fin morphology, and beginning of asymmetrical coloration. Numerical scores given to the two or three states of each character are shown in Table 3. A metamorphosing presettlement individual can have a metamorphic score of 1 to 8. A score of 9 defines Stage 3, metamorphic competent larvae.

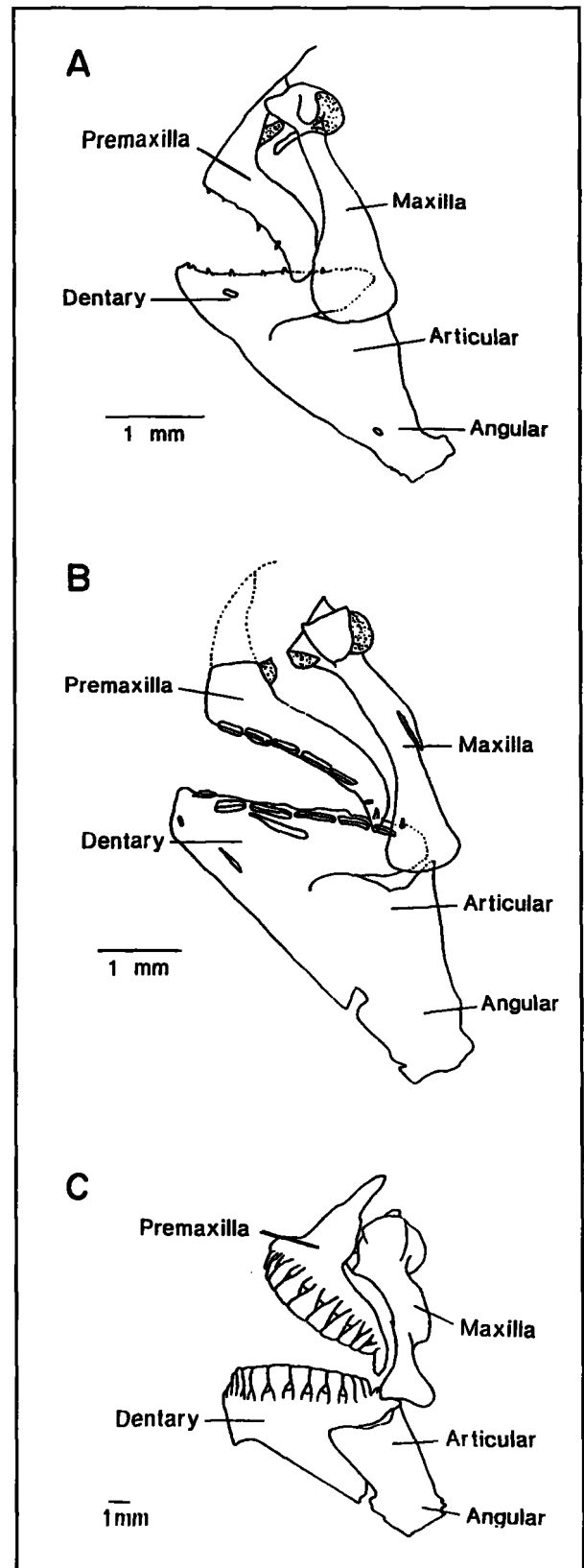
Dover sole larvae have canine-like teeth on left and right jaws (Fig. 3A). During Stage 2, incisor-like teeth develop on the left premaxilla and dentary (Fig. 3B). The canine-like teeth are lost from both jaws coincident with eruption of incisors in the left jaw (Fig. 3C).

In Stage 1 larvae, anterior dorsal-fin pterygiophores and fin rays are posterior to the orbit of the left eye which is located on the dorsal ridge of the cranium (Fig. 4A). During Stage 2, these pterygiophores move anterior to the orbit of the left eye (Fig. 4B).

The posterior process of the coracoid in larvae is a long, slender element that projects posteriorly above the visceral cavity, underneath the skin (Fig. 5A). During metamorphosis the process is resorbed. At the beginning of resorption, during Stage 2, the distal end of the process curls anteriorly into a hook (Fig. 5B). In our samples there is some indication that the process deteriorates (poor staining with alcian blue), but there is no gradual reduction in length or thickness of the process. Specimens either have the process or have lost it (Fig. 5C).

The pectoral fin in Stage-1 larvae is a paddle-shaped membrane with a thin, fleshy base and without radials. During Stage 2, a fleshy rectangular base, cartilaginous radials, and the adult complement of fin rays form (Fig. 5).

The Stage-1 larval color pattern consists of little or no pigment on the midlateral areas. A transitional pattern, in which melanophores aggregate along myosepta, is followed by the first indication of melanophores aggregating in two approximately circular groups anteriorly and posteriorly along the lateral line (Fig. 6). We score larval



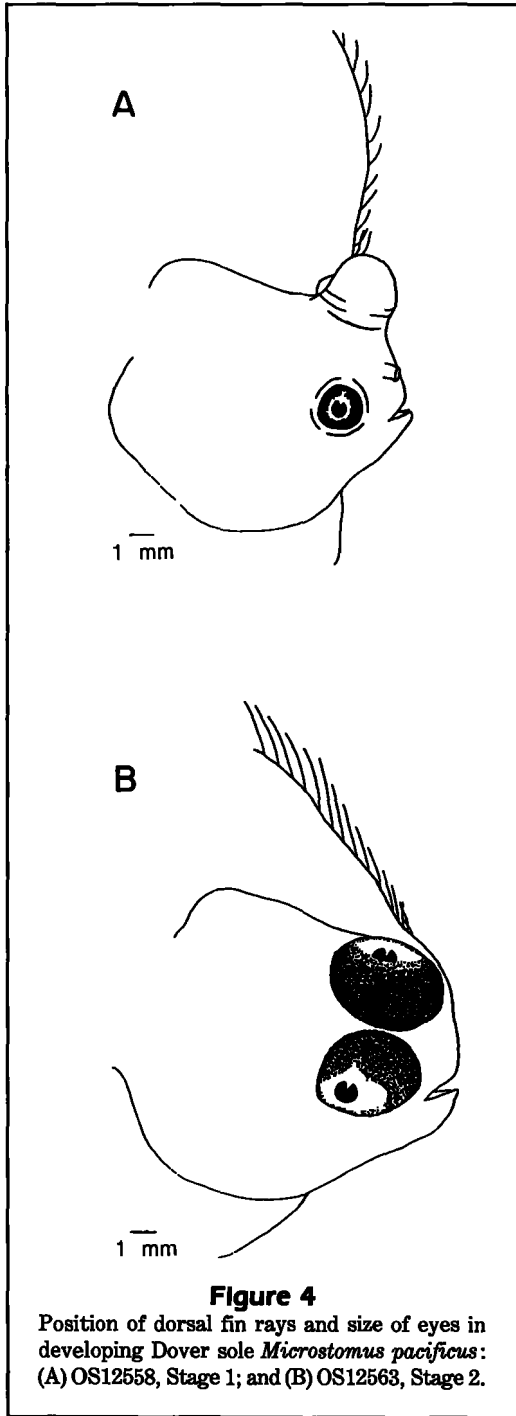


Figure 4

Position of dorsal fin rays and size of eyes in developing Dover sole *Microstomus pacificus*: (A) OS12558, Stage 1; and (B) OS12563, Stage 2.

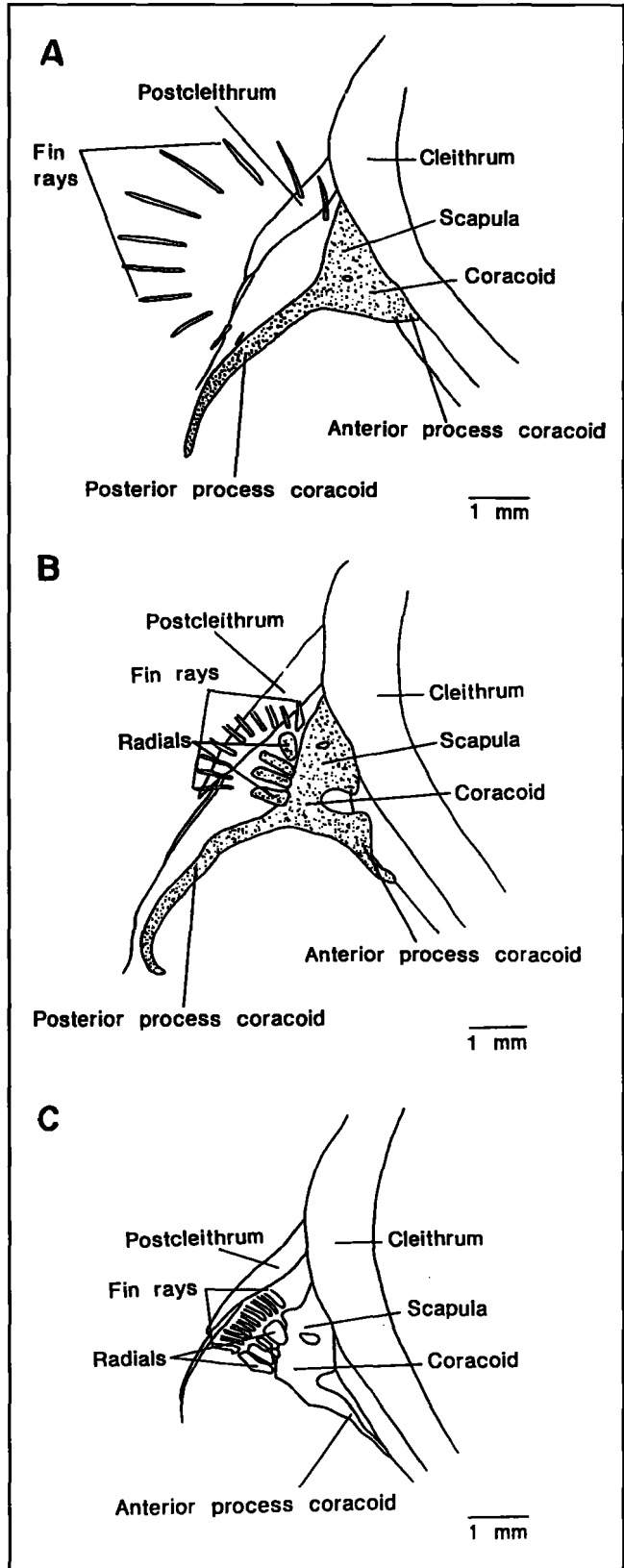
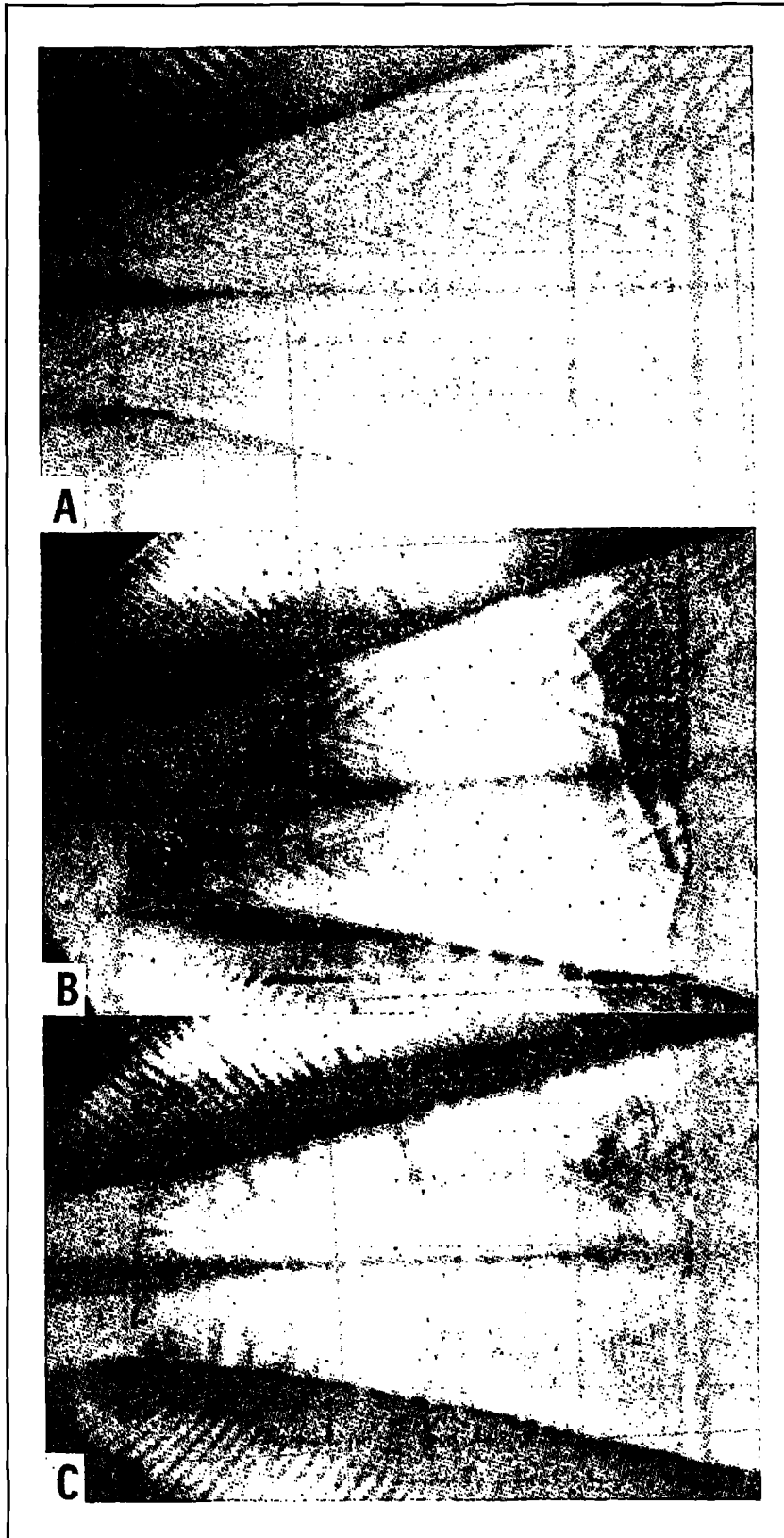


Figure 5

Pectoral fin development in Dover sole *Microstomus pacificus*: (A) OS12558, Stage 1 with straight ventral process of coracoid; (B) OS11377, Stage 2 with hooked tip on ventral process of coracoid; and (C) OS12563, Stage 3 after resorption of ventral process of coracoid.

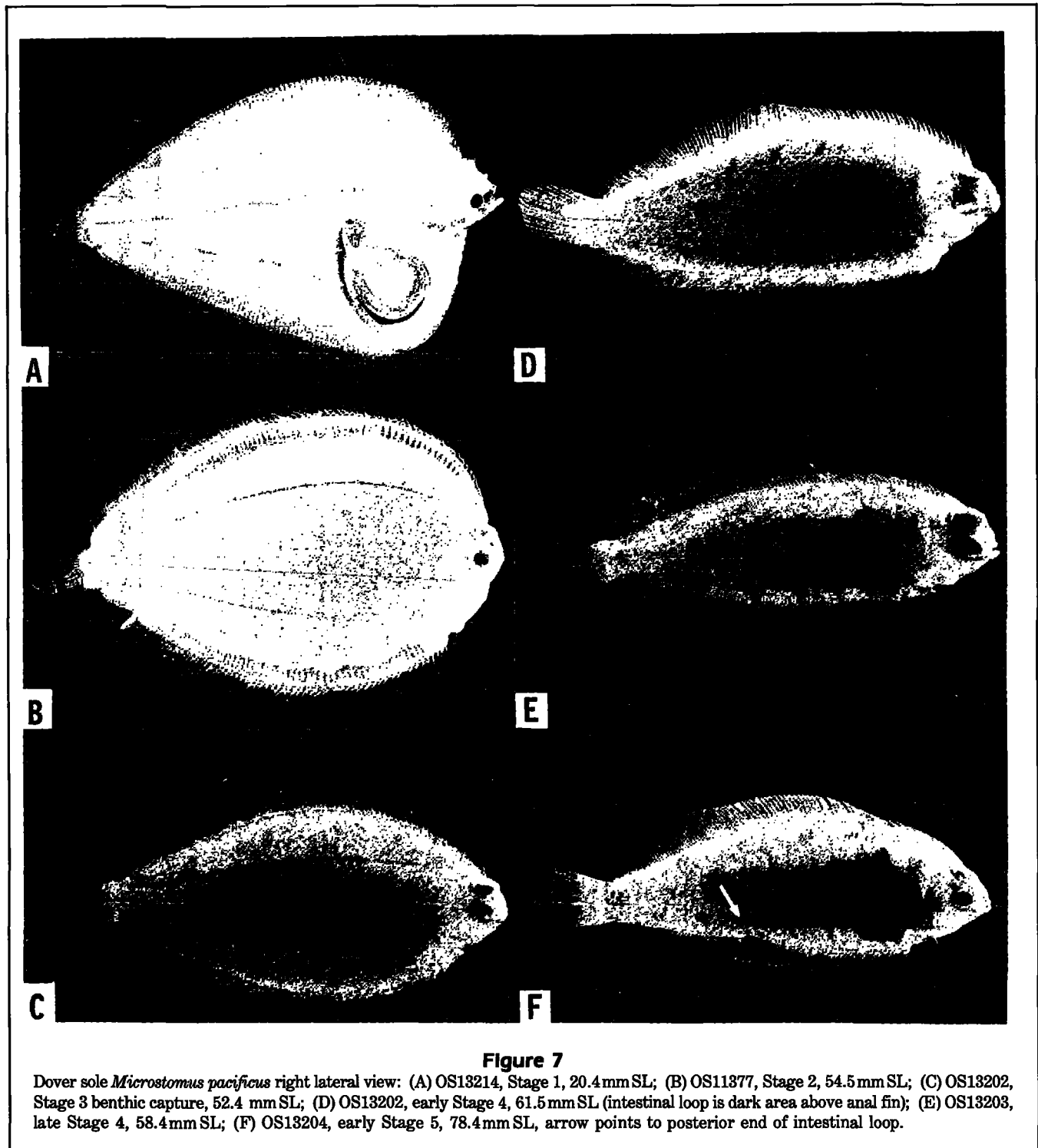
**Figure 6**

Right-side midlateral pigmentation patterns during development in Dover sole *Microstomus pacificus*: (A) OS13115, Stage 2, developmental score 5, larval pattern of no melanophores on myomeres; (B) OS13118, Stage 2, developmental score 8, transitional pattern of melanophores on myosepta; and (C) OS13117, Stage 3, aggregated pattern of melanophores in circular area on caudal peduncle and anterior trunk.

and transitional patterns equally and consider the circular aggregations as the first indication of asymmetrical coloration.

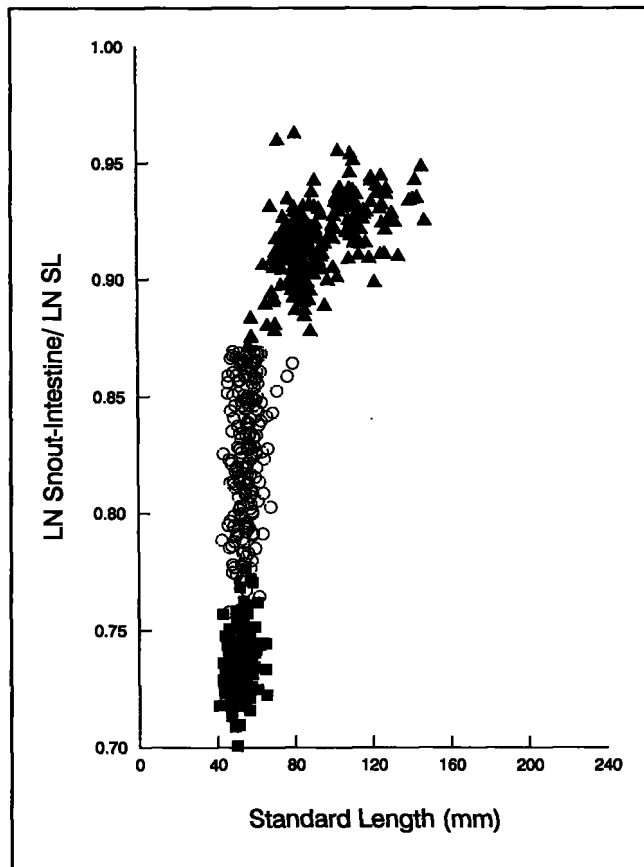
Coincident with changes in these six features are changes in features that are not easily coded: gradual loss of otic spines, reduction in body depth (Figs. 3 and 8), reduction in interorbital width (Fig. 7), increase in right eye diameter (Fig. 7), and increase in right upper jaw length (Fig. 3). Development of body scales also begins in Stage-2 specimens with metamorphic scores of 7 or 8. Body scales first form above and below the lateral line, anteriorly near the pectoral fin base, and on the caudal peduncle.

Stage 3 (metamorphic competent larvae), 40.7–74.9 mm SL Stage-3 specimens have a metamorphic score of 9, indicating that all six initiation-event features have either begun or reached the adult state. These specimens have a translucent appearance, intermediate between the earlier transparent stages and later opaque stages. Stage-3 specimens have asymmetrical coloration, retain the coiled, larval gut configuration, and have resorbed the posterior process of the coracoid. Some morphometric features initiated in Stage 2, such as increasing right eye diameter and shrinkage in body depth, continue in Stage 3 (Fig. 2). Ossification of pelvic-fin rays and radials is initiated in Stage 3, apparently after settlement (1 of 10 pelagic specimens and 4 of 4 benthic Stage-3 specimens have ossified pelvic fin rays and radials).



Stage 4 (metamorphic postcompetent larvae), 41.7–79.3 mm SL Adult Dover sole have a long intestinal loop in the secondary body cavity above anal fin pterygophores (Hagerman 1952). This intestinal loop (Fig.

7) forms after settlement, and its initiation is the defining feature of Stage 4. Continuous metamorphic changes in morphology, such as shrinkage in body depth, are completed during Stage 4 (Fig. 2).

**Figure 8**

Relationship between the \ln SINT/ \ln SL ratio and standard length during development of Dover sole *Microstomus pacificus*. Symbols represent Stage 3 (■), Stage 4 (○), and Stage 5 (▲).

as 9.5 mm SL (Pearcy et al. 1977a). Eye migration in Dover sole is arrested during planktonic growth, with the left eye stopping at the dorsal margin of the cranium at 15–20 mm SL (Fig. 4A). It remains in this position until metamorphosis. Thus, during most of their planktonic life, the eyes of Dover sole are asymmetrical.

There is a complex relationship between body depth and SL (Fig. 2), including (1) an interval of rapid increase from about 10 mm to at least 60.4 mm SL in some individuals, (2) a compensatory shrinkage phase over the size range 40.7–74.9 mm SL, and (3) a more typical linear growth phase that may begin in specimens as small as 41.7 mm SL. Body depth reduction is a regressive process (Youson 1988) in which lengths of neural and hemal spines and pterygiophores are reduced (Fig. 9). Two- and three-fold reductions occur in lengths of first caudal neural and hemal spines and their immediate anterior and posterior pterygiophores. Consequently, metamorphosing Stage-3 specimens 40–50 mm SL have neural and hemal elements comparable in length to those of 20–30 mm SL Stage-1 larvae. Neural and hemal elements and dorsal and anal pterygiophores in Stage-1 larvae are cartilaginous or weakly ossified, and vertebral centra lack zygapophyses. Complete ossification of neural and hemal elements and formation of zygapophyses occurs in Stages 2 and 3.

During most of metamorphosis, especially in Stages 2 and 3, body length appears to be arrested (Fig. 10). Although the sample size of Stage-2 larvae limits our confidence in further analysis, the data show little indication of growth between Stages 2 and 3 (Fig. 10). Because metamorphosis occurs over a broad range of sizes, similarity in size minima and maxima between stages also suggests little or no growth in body length. For example, the minimum sizes for Stages 2, 3, and 4 are almost identical (42.3, 40.7 and 41.7 mm SL, respectively). During Stage 4 there is finally some indication of growth because the smallest Stage-5 juvenile is 48.9 mm SL, more than 7 mm larger than the smallest Stage-4 larva. Yet, even this juvenile is 26 mm smaller than the largest metamorphosing Stage-3 larva.

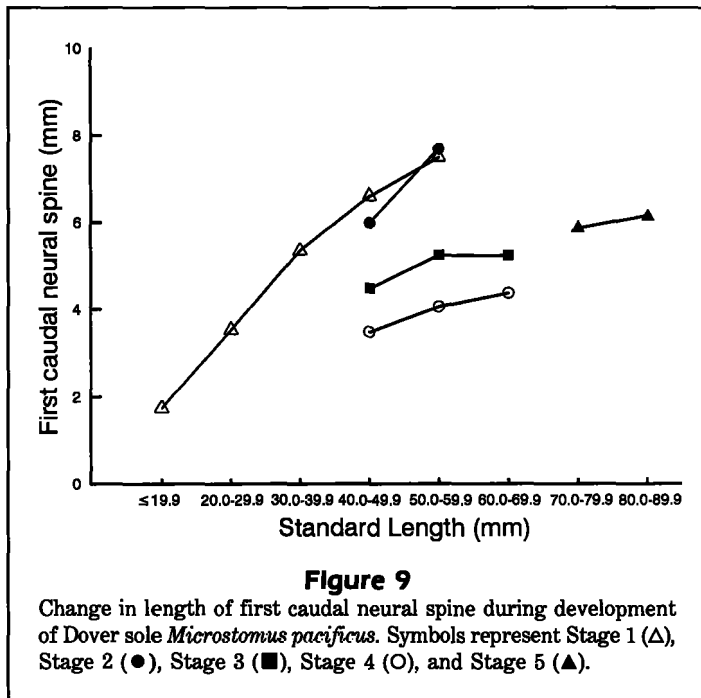
There is an apparent loss in body weight during metamorphosis because of a decrease in mean weight from 2.6 to 2.4 g from Stage 2 to Stage 4 (Fig. 11). However, the small sample size of Stage 2 and our measuring error preclude attaching significance to the

Stage 5 (Juvenile), 48.9 mm SL to sexual maturity

We define the climax event, and Stage 5, as the point at which length of the intestinal loop attains adult proportions. The continuous nature of this process is illustrated in the logarithm ratios of SINT/SL (Fig. 8). We chose a cut-off ratio by calculating the ratio for 2 mm SL increments and examining the rate at which the ratio changes over length. The greatest rate of change occurs between 67 and 69 mm SL, during which the mean ratio changes from 0.85 to 0.89. We chose the midpoint of these ratios and therefore define Stage 5 as those individuals with a ratio of \ln (SINT)/ \ln (SL) > 0.87. Coincident with this change is an overall darkening of body color such that Stage 5 specimens look like small adults.

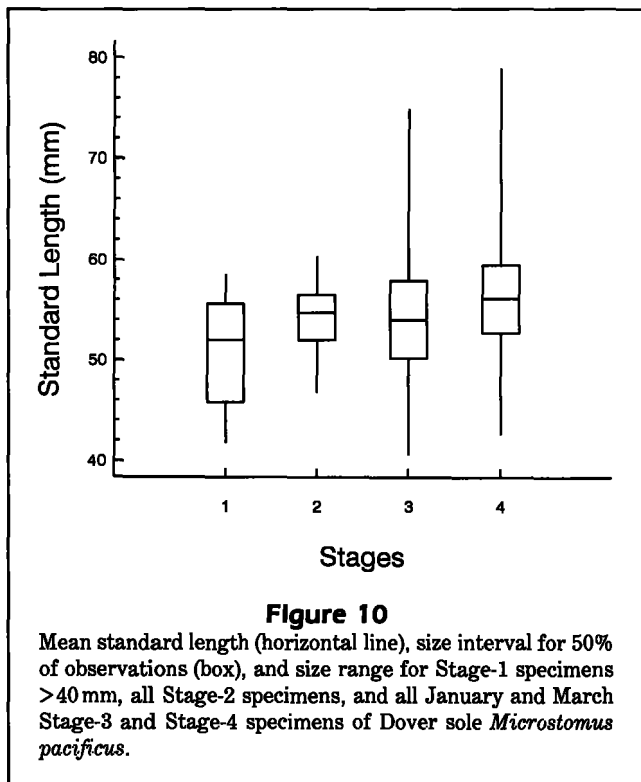
General features of early development and metamorphosis

Unlike most flounders, initiation of eye migration in Dover sole is uncoupled from the change in habitat from planktonic to benthic, as well as from the process of metamorphosis (as defined herein). Eyes are symmetrical up to a maximum size of only 13.4 mm SL, and the left eye can be on the midline in specimens as small



apparent loss. During the second year of life in the plankton (see next section), body weight increases an order of magnitude from a mean of about 0.30 g for Stage 1 in February to 2.0–4.0 g for Stage 2. All individuals that reach a size of 40 mm SL are at least 0.74 g; Stage-2 specimens are at least 1.39 g; Stage 3, at least 0.80 g; and Stage 4, at least 1.0 g. Because our sample size for Stage 3 is relatively large, our best estimate of a weight threshold for metamorphosis is ~0.8 g. However, if the suggestion of weight loss during metamorphosis is not an artifact (Fig. 11), the weight threshold may be closer to the minimum weight of Stage 2. Further complicating an estimate of that threshold is the observation that our lightest Stage-2 specimen (42.6 mm SL and 1.39 g) was caught in January with a developmental score of 7, and presumably may already have lost weight.

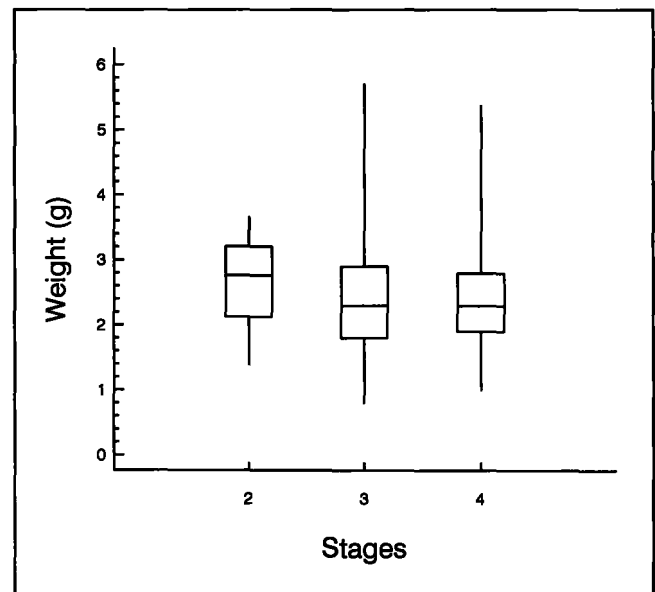
Because SINT increases during metamorphosis and BD1A decreases, the SINT/BD1A ratio provides an additional means of visualizing the relationship between the metamorphic process and developmental stages (Fig. 12).



Timing and duration of stages

Temporal change in size of Stage-1 larvae <40 mm SL was analyzed using MPA (Fig. 13). Small larvae, about 6–8 mm, were found from February to June. The smallest identifiable mode was in April, and from November to March modes were level around 22–25 mm. Two notable features of these data are apparent accelerated growth in June and reduced availability of larger

Figure 11
Mean weight (horizontal line), weight interval for 50% of observations (box), and weight range for Stages 2–4 in Dover sole *Microstomus pacificus*.



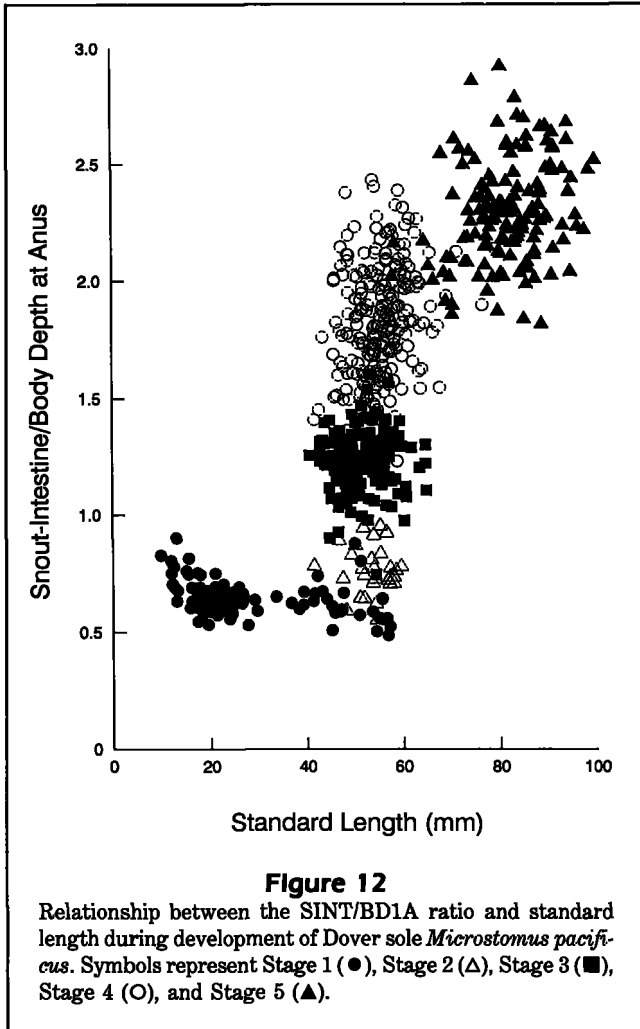


Figure 12

Relationship between the SINT/BD1A ratio and standard length during development of Dover sole *Microstomus pacificus*. Symbols represent Stage 1 (●), Stage 2 (△), Stage 3 (■), Stage 4 (○), and Stage 5 (▲).

specimens after March (Fig. 13). All small larvae (<10 mm SL) were collected on one day, 12 June 1971, between 50 and 67 km offshore, whereas larger larvae from June were collected considerably further offshore, 108–275 km on various dates. There appears to be little or no coherent size progression after the 24.5 mm mode in March. Specimens >30 mm are found in every month, and weakly-defined modes can be visualized around 50 mm in June, July, and September. Accelerated growth in April and May would seem to be required if the modal size were to double from about 25 mm in March to 50 mm in the second summer of life. Paradoxically, April is a time when micronekton biomass is normally low (Pearcy 1976).

Stage-2 specimens were caught from June to February (Table 4). The coherent progression of metamorphic scores for Stage-2 larvae indicates that metamorphosis begins as early as June; Stage-3 larvae are present as early as December and as late as March. About 6 months seems to be required to progress

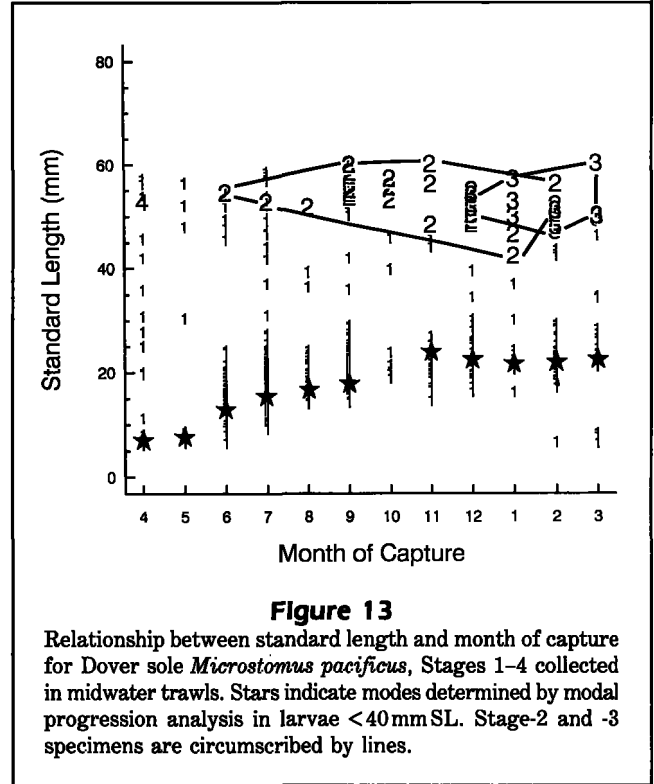


Figure 13

Relationship between standard length and month of capture for Dover sole *Microstomus pacificus*, Stages 1–4 collected in midwater trawls. Stars indicate modes determined by modal progression analysis in larvae <40 mm SL. Stage-2 and -3 specimens are circumscribed by lines.

Table 4

Seasonal catch-per-effort for planktonic Stage-2 and Stage-3 Dover sole *Microstomus pacificus* larvae off Oregon. N = number of trawls.

Month of collection	N	No. of Stage 2 based on metamorphic score								No. of Stage 3	
		1	2	3	4	5	6	7	8		
January	128	—	—	—	—	—	—	—	2	—	2
February	167	—	—	—	—	—	—	—	—	2	4
March	147	—	—	—	—	—	—	—	—	—	2
April	201	—	—	—	—	—	—	—	—	—	0
May	106	—	—	—	—	—	—	—	—	—	0
June	278	1	—	—	—	—	—	—	—	—	0
July	291	—	—	—	—	—	1	—	—	—	0
August	303	1	1	—	—	—	—	—	—	—	0
September	217	—	1	—	4	2	1	—	—	—	0
October	129	—	—	—	—	1	1	—	1	—	0
November	217	—	—	—	—	—	—	2	1	—	0
December	126	—	—	—	—	—	—	—	2	6	2

through Stage 2.

The seasonal distribution of Stage-3 larvae in benthic samples was consistent with their planktonic distribution (Table 5). During bimonthly sampling in 1989, 98.5% of Stage-3 specimens were caught in January or March. Five Stage-3 specimens were caught in May, and most new settlers appear to be in Stage 5 by July

Table 5

Seasonal distribution of Dover sole *Microstomus pacificus* stages in bottom-trawl samples off Oregon, 1989.

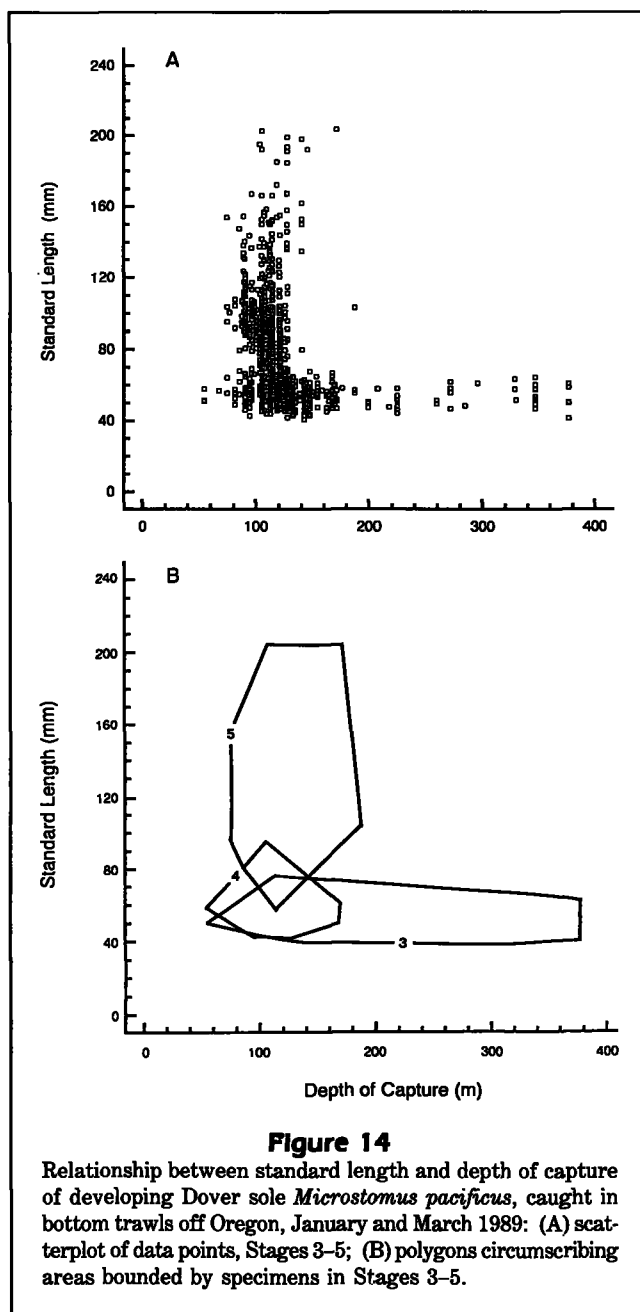
Month of collection	N	Number (%)		
		Stage 3	Stage 4	Stage 5
January	371	177 (48)	12 (3)	182 (49)
March	655	155 (24)	347 (53)	153 (23)
May	222	5 (2)	113 (51)	104 (47)
July	60	0	11 (18)	49 (82)
September	154	0	5 (3)	149 (97)
November	267	0	3 (1)	264 (99)

(Table 5). Individuals appear to require about 45 days to progress through Stage 3. Our laboratory-held specimen progressed through Stage 4 in 43 days. Overall, the progression through Stages 2–4 appears to require about 1 year for the population as a whole and about 9 months for an individual.

The length and weight of benthic Stage 3 larvae were compared between January and March 1989. Mean length in March (51.5 mm SL) was significantly smaller than the mean length in January (56.3 mm SL, $P < 0.00001$). March specimens were also significantly lighter (2.0 g) than January specimens (2.7 g, $P < 0.0001$). A similar pattern (earliest individuals in a stage being largest) was seen in Stage-2 larvae. The mean length of Stage-2 larvae captured between January and March (late in the season, Table 4) was smaller (53.0 mm vs. 54.3 mm SL) and lighter (2.4 vs. 2.8 g) than Stage-2 larvae captured between June and December (early in the season, Table 4), but the differences were not significant (length $P < 0.4642$; weight $P < 0.1227$).

Habitat of stages

On average, Stage-1 specimens were caught in nets fished to a maximum depth of 338 m, Stage-2 specimens in nets fished to 538 m, and planktonic Stage-3 specimens in nets fished to 293 m. All planktonic Stage-3 larvae were caught at night, between 1835 and 0544 hours, and 93% of Stage-2 larvae were caught at night, between 1802 and 0748 hours. Sampling effort was also greatest at night (Table 1; opening-closing nets collected 516 Dover sole but most (509) were Stage 1). The minimum depth of capture in the discrete depth samples was < 100 m for 82%, and < 300 m for 95%, of Stage-1 specimens. Only six Stage-2 specimens were caught in discrete depth samples, and only two of these in nets not fishing the surface. One Stage-2 larva was caught at 100–150 m and the other at 400–500 m. The

**Figure 14**

Relationship between standard length and depth of capture of developing Dover sole *Microstomus pacificus*, caught in bottom trawls off Oregon, January and March 1989: (A) scatterplot of data points, Stages 3–5; (B) polygons circumscribing areas bounded by specimens in Stages 3–5.

single Stage-3 larva collected in a discrete depth sample was collected at 0–330 m.

Benthic specimens were caught at depths shallower than the maximum depth fished by non-closing mid-water nets. Based on our stratified sampling, a comparison of depth of capture of stages shows that Stage-3 specimens were caught at an average depth of 146 m (SE 2.65, range 55–377 m), Stage-4 specimens in January and March at an average depth of 118 m (SE 0.68, range 40–170 m), and Stage-5 specimens in January and March at an average depth of 110 m (SE

0.48, range 75–188 m). Compared with Stages 4 and 5, the greater average depth and variance of benthic Stage-3 larvae indicate a much broader depth distribution (Fig. 14).

Stage-3 larvae occupy a transitional “landing” zone quantitatively distinct from, but overlapping, the later larval and juvenile nurserygrounds. Although Stage-3 larvae caught in bottom trawls quickly take to the bottom when placed in aquaria (pers. observ.), their nighttime capture in midwater trawls and daytime capture in bottom trawls suggest they may be eurybenthic (nearbottom) or benthopelagic, rather than exclusively benthic.

Behavior associated with metamorphosis presumably includes some short-term (hours to days) switching between midwater and bottom habitats. In one individual in our data set, the behavior continued into Stage 4. A 53.0 mm Stage-4 specimen was caught 19 April 1963 off the mouth of the Columbia River at 0411 hours in a midwater trawl fished to 73 m over a bottom depth of about 125 m. Its gut loop was well developed and contained sand grains. Additional evidence is provided by midwater Cobb trawl samples collected by W. Lenarz and colleagues (NMFS Southwest Fish. Sci. Cent., Tiburon, CA 94920) between Monterey and San Francisco, California, from 28 March to 2 April 1990. In eight nighttime (2235–0447 hour) samples, fished at 0–110 m (most 0–30 m) over bottom depths of 33–1462 m, they collected 14 Stage-3 larvae (40.4–51.2 mm SL) and 16 Stage-4 larvae (42.4–53.4 mm SL). Stage-3 larvae were collected over bottom depths of 73–1462 m, and Stage-4 larvae were collected over bottom depths of 33–91 m. Thus, settling Stage-3 larvae were found in a “landing” zone at 55–377 m and in a wedge of the water column above and seaward of that zone.

Discussion

Time-line

Dover sole spawn in deep water in winter, December to February, according to Hagerman (1952), and November to April according to the circumstantial evidence of Harry (1959). Yoklavich and Pikitch (1989) provide evidence that smaller Dover sole have an earlier, shorter spawning season than larger fish, and that Dover sole now mature at significantly smaller sizes than reported by Hagerman (1952) or Harry (1959). These observations suggest the possibility that size-selective exploitation might have shifted the spawning season to earlier dates.

However, other observations suggest that peak hatching of Dover sole off Oregon is later, not earlier, than indicated by Hagerman (1952) or Harry (1959). Results of sampling the commercial Dover sole catch

off southern Oregon (43°N) from March 1990 to September 1991 indicate running ripe females were caught from February through July with a peak in April (Mike Hosie, Oreg. Dep. Fish Wildl., Charleston, OR 97420, pers. commun.). Spent females increased from less than 10% of all females in April to 100% by early August. However, these observations may be biased towards later-spawning fish because the commercial catch is culled of small fish (Yoklavich and Pikitch 1989). Experiments performed in 1972 by S. Williams at Newport, Oregon, showed that hatching took 18 days at 12.5°C, 27 days at 10.0°C, and 38 days at 7.5°C (Mike Hosie, pers. commun.). In agreement with these observations, small larvae (<10 mm SL) in this study were collected from February to July, with most caught in April and May (Fig. 13, Percy et al. 1977a). In ten NMFS ichthyoplankton cruises conducted at 40–48°N from 1980 to 1987, high densities of Dover sole eggs were found in each of six cruises conducted in March, April, or May; none or trace amounts were found in four cruises conducted in August, November, or January (Urena 1989; M. Doyle, NMFS Alaska Fish. Sci. Cent., Seattle, WA 98115, pers. commun.). Finally, “spawning” adults off Alaska have been collected primarily in May and June (Hirschberger and Smith 1983), and eggs are collected in June (Kendall and Dunn 1985). Thus, the weight of evidence seems to indicate that most Dover sole off Oregon hatch from February (Fig. 13) to August (Urena 1989), with a peak in April and May (see also the time-line in Hayman and Tyler 1980).

Settlement is restricted to the period from January to March or April (Table 5), whereas metamorphosis requires a protracted period of up to one year, occurs at sizes >40 mm SL (Fig. 3), includes little growth in body length, and may include loss of weight. Cessation in growth of body length before and during metamorphosis has been documented in other flounders (Fukuhara 1986, 1988). If the modal size of Stage-1 larvae is ~25 mm in March, then the average duration of the planktonic period of Dover sole is about 21 months (Fig. 15). However, the timing of settlement has a size component; larger larvae tend to settle before smaller larvae. It seems reasonable that larger larvae are those that grow faster, but it is also possible that they are slow growers or have otherwise delayed metamorphosis and, therefore, are more than 2 years old (see Discussion below).

Distribution and relative abundance of metamorphic planktonic stages provide additional insight. Larger planktonic specimens were generally rare in midwater trawl collections (Fig. 13). However, Stage-2 larvae, with developmental scores of 7 and 8, and Stage-3 larvae were the most abundant of all metamorphic stages found in midwater (Table 4), even though they

were collected in months with few samples (Table 1). Planktonic Stage-2 larvae were caught in nets fished deeper than either Stage-1 or planktonic Stage-3 larvae. The rarity of larger planktonic and early metamorphic stages may reflect movement deeper into the mesopelagic zone and lower relative sampling effort in deeper water. Late in Stage 2 (developmental scores 7 and 8) and in Stage 3 this trend appears to be reversed, as these stages were caught more frequently. If metamorphosis is a time of increased vulnerability, deeper water may provide a predation refuge. Alternatively, the behavior may place metamorphosing specimens in a water mass that facilitates late larval transport.

Settlement seems remarkably gradual, coincides with the downwelling season, ends with the spring transition in the oceanographic regime (Huyer et al. 1979), and occurs over a very broad "landing" zone (Fig. 14). Stage-3 larvae settling outside the nursery zone may experience differential mortality, or their broad depth distribution may reflect a process of testing the habitat in search of the preferred nurseryground. Capture of Stage-3 and -4 specimens in both nighttime midwater and daytime bottom trawls suggests a diel vertical search pattern.

Egg and larval drift

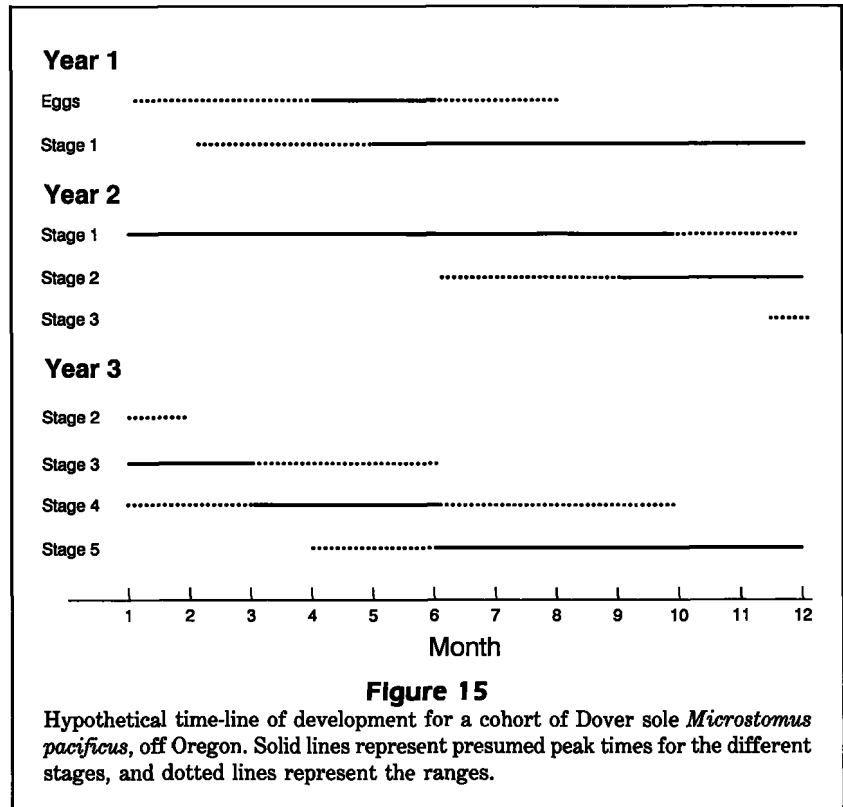
A proposed recruitment mechanism for Dover sole (Hayman and Tyler 1980, Parrish et al. 1981) focuses on inshore-offshore transport. The long planktonic period of Dover sole implies that alongshore transport also may be important. Our data allow some first-order generalizations about the distribution of early-life-history stages and may give further insight into the recruitment mechanism.

Urena (1989) found that greatest abundances of Dover sole eggs were in neuston samples collected beyond the 200m isobath. In April and May in the upper 50m, the current flows southward at about 10–15cm/second at the 200m isobath (Huyer 1977, fig. 9; Huyer et al. 1979) and is even weaker further offshore (Huyer and Smith 1978). At 10cm/second, eggs could be transported 260km southward in 30 days, assuming that their transport was not interrupted by offshore jets or gyres. Onshore-offshore transport of eggs should be variable. During upwell-

ing, the upper 20m may experience an average offshore velocity of 2–5cm/second (Huyer 1983), and the upper 5m may experience an average offshore velocity of 15cm/second (Peterson et al. 1979). The short duration of the egg stage, restricted area of high offshore velocity, and the return inshore of water masses during relaxation after upwelling (Peterson et al. 1979) suggest that average offshore transport of eggs should be slow, but nontrivial. Deepwater spawning may help reduce both alongshore and onshore-offshore transport.

Stage-1 larvae also are found beyond the 200m isobath (Pearcy et al. 1977a) and, like eggs, would be vulnerable to the southward flow of the California Current. In fact, the large surface area of the body of Dover sole larvae might facilitate such transport. Although there are important seasonal changes in direction (Huyer et al. 1979), on an annual basis the average surface current around 100km offshore is ~0.5–1.0cm/second to the south (Hickey 1979, fig. 8b). If Stage 1 lasts an average of 15 months, and assuming a mean flow of 0.75cm/second, these larvae would travel an additional 295km southward.

We suggest that early Stage-2 larvae move into deeper water. The California Undercurrent is a northward-flowing countercurrent located below 200m and



influencing an area up to 500 km off the shelf (McLain and Thomas 1983). Its velocity is <10 cm/second over the continental slope north of Cape Mendocino (Hickey 1979) and weaker seaward of the slope. Somewhat further south, between Pt. Arena and Pt. Reyes, the current is 3–10 cm/second from July to October and <1 cm/second from October to January (Huyer et al. 1989). If eggs and Stage-1 larvae are displaced, on average, 555 km (260 + 295) southward of their spawning site, a northward-flowing undercurrent of 3.25 cm/second would be sufficient to return Stage-2 larvae to the vicinity of their spawning site in 6 months. This does not seem to be an unreasonable average velocity for the undercurrent from July to January.

The depth range of the Stage 3 “landing” zone (55–377 m) corresponds with the northward undercurrent located at 200–300 m (Huyer and Smith 1985). However, these larvae appear to need a mechanism to bring them shoreward. The surface Ekman layer, 0–20 m, within which wind-driven transport occurs (Huyer 1983), could be reached if larvae moved up in the water column during storms. Diel offbottom migrations could be part of this mechanism. Alternatively, as the body surface area is reduced during this stage, larvae may become less passive and move actively inshore.

Delayed metamorphosis and settlement

The protracted process of metamorphosis in Dover sole is contrary to expectations based on the ideas of saltatory ontogeny (Balon 1981). In general, ontogenetic transformations are expected to occur rapidly because intermediate forms are presumed to be maladapted. For example, loss of teeth from the right side of the jaw and development of incisors on the left side seem to hold no advantage for a planktonic larva, yet this is the situation in Dover sole for several months during the precompetent Stage 2. Delayed metamorphosis is also related to the concept of saltatory ontogeny; because the transition is assumed to be quick, an organism without the proper cues simply delays metamorphosis and settlement. In other words, it keeps the morphology appropriate for the habitat. Typically, field researchers identify a minimum threshold size or developmental stage for metamorphosis and assume that planktonic specimens greater than the threshold size or in the threshold stage have delayed metamorphosis (Pechenik 1986). Others have used a minimum age as a threshold (Cowen 1991).

Pearcy et al. (1977a) suggested that larger “hold-over” Dover sole larvae (>50 mm SL) delayed metamorphosis and few successfully recruited to the benthic juvenile stage. Delayed metamorphosis is predicted for coastal organisms subjected to offshore transport

(Jackson and Strathmann 1981) and there is some evidence for delayed metamorphosis in fishes (Victor 1986, Cowen 1991). An advantage of delayed metamorphosis is extension of the settlement season beyond what would be expected based on the spawning season (Victor 1986). Contrary to this expectation, the duration of Dover sole settlement is seasonally restricted and, off Oregon, no greater than the duration of the spawning season. Because precompetent larvae are probably a great distance from their settlement site, cues for metamorphosis are likely to be seasonal rather than site-related.

Experimental studies focusing on flounders have shown (1) fast-growing individuals metamorphose at smaller sizes, (2) fast-growing individuals retain their faster growth rate for at least several weeks after metamorphosis, (3) age at metamorphosis (defined by eye migration) is more variable than size at metamorphosis, and (4) a target size or threshold must be reached prior to metamorphosis (Policansky 1982, Chambers and Leggett 1987, Chambers et al. 1988). Other fishes and organisms may have age-triggered, size-triggered, or age- and size-triggered metamorphosis (Policansky 1983). Policansky (1983) points out that a size threshold would be expected when there is a size difference in available food between different habitats or a minimum energy requirement to successfully function at a certain stage.

We suggest two contrasting interpretations of the early life history of Dover sole. If size and age at metamorphosis are positively correlated, as is the case in winter flounder (Chambers et al. 1988), then larger, earlier settlers are older and slower-growing than smaller, later settlers. The difference in age could be the difference between early and late spawners or between different years of spawning. Alternatively, variation in size at metamorphosis may simply reflect differential growth rates operating for a long time, probably at least 2 years. As a consequence, larger, earlier settlers would be the faster growers rather than slower growers. One could distinguish between these alternatives and demonstrate delayed metamorphosis by documenting different year-classes among settlers.

In terms of life-history strategies, delayed metamorphosis and protracted metamorphosis may confer similar advantages. Extension of settlement through delayed metamorphosis allows for adaptive responses to short-term oceanographic variability and avoidance of settling during unfavorable conditions. If metamorphosis and settlement are cued to favorable seasons, protracted metamorphosis and the ability of competent metamorphosing individuals (Stage-3 larvae) to spend several months moving between midwater and bottom habitats should also compensate for any short-term unfavorable oceanographic conditions.

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