Timing of parturition, planktonic duration, and settlement patterns of the black rockfish, *Sebastes inermis*

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Synopsis

The microstructure of otoliths was used to examine the relationship among timing of parturition, duration of planktonic stage, and temporal patterns of settlement in young-of-the-year (YOY) *Sebastes inermis* collected during the settlement seasons of 1998–2001 in a seagrass bed at the northwestern coast of Japan. Parturition occurred in winter, predominantly around the new and full moons, and parturition dates were distributed mainly from early January to late February. In the 4 years YOY *S. inermis* settled into distinctive groups at early spring, synchronized mainly to a semi-lunar cycle at new and full moon phases; except for 1998, in which settlement occurred around the first and third quarter moons. In all years settlers extruded earlier in the parturition season encompassed the first settlement groups that appeared in the bed and vice versa. Planktonic period ranged from 53 to 113 days, and its mean values varied significantly among settlement groups and years. Mean size at settlement showed less variability among settled groups and between years (range: 18–26 mm total length), which suggested an ideal size for settling and active migration. On the basis of our findings we discuss the extent to which the 'tidal control', 'settlement linkage', and 'competent size' hypotheses explain the temporal pattern of settlement.

Introduction

Understanding the factors that affect the patterns of settlement of young fish from their pelagic habitat to their nursery habitat has become an important goal in studies of the early life history of fishes. Great attention has been focused on tropical reef fishes, which has allowed researchers to test broad hypotheses concerning the relationship between temporal patterns of settlement and both timing of spawning and duration of the larval stage. In general, it appears that benthic spawners show a semi-lunar spawning cycle, whereas pelagic spawners spawn either monthly or asynchronously relative to the lunar cycle (Sponaugle & Cowen 1994). Lunar synchrony at spawning encompasses moonlight spawning, in which moonlight facilitates migration to spawning sites and helps adults guard their eggs; and tidal spawning, in which reproduction occurs during ebbing spring tides to maximize the offshore tidal transport of the eggs so as to avoid benthic predators (Johannes 1978). Information to date indicates a significant variability in larval duration. Whereas a fixed larval duration has been associated with synchrony between timing of spawning and subsequent settlement (settlement linkage hypothesis; see Robertson et al. 1990), a variable larval duration seems to allow flexibility in settling whenever a specific environmental condition occurs (e.g. lunar or tidal period) or an appropriate stimulus is found, such as habitat or nearshore flow (Cowen & Sponaugle 1997).

Rockfishes of the genus *Sebastes* are viviparous. They represent an important component of shelf and slope fish faunas of temperate and subarctic regions (Boehlert & Yamada 1991). Most *Sebastes* spp. have

reproductive modes and early life history traits that are still poorly understood (Bohehlert & Yamada 1991); in particular, those factors enhancing juvenile survival and allowing young fish to find suitable habitat to settle (Boehlert & Yamada 1991, Boehlert et al. 1991). *Sebastes* larvae are born at an advanced stage of development, in which organogenesis is essentially complete; hence they are active swimmers and predators (Wourms 1991). Furthermore, *Sebastes* larvae metamorphose into pelagic juveniles, which occupy the pelagic habitat for several months to a year (Moser & Boehlert 1991, Wourms 1991, Webb 1999). Some young-of-the-year (YOY) *Sebastes* young migrate into nearshore areas (e.g. seagrass beds, Sargassum beds, or kelp canopy habitats) as larvae or very early juveniles after completing their planktonic stage offshore (Moser & Boehlert 1991, Love et al. 1991). Although this kind of ontogenetic movement has been described as an adaptive strategy to allow these nearshore rockfishes to maximize settlement and avoid offshore dispersal (Moser & Boehlert 1991), it raises several questions: Do larvae and/or young juveniles move actively or passively into the nearshore zone? How do they synchronize migration with timing of settlement? What role might the planktonic duration play in this adaptive strategy? These questions might be linked to the settlement linkage, lunar or tidal control hypotheses pointed above; however, it remains untested for rockfishes yet.

The black rockfish *Sebastes inermis* is a commercially important demersal species in coastal waters of Japan and southern Korea (Kido 1984). Planktonic *S. inermis* larvae and small juveniles initially recruit in shallow *Zostera* beds. As they increase in size (ca. 60 mm total length (TL)), they move to deeper Sargassum covered reefs (Harada 1962, Hatanaka & Iizuka 1962a,b, Love et al. 1991). We selected this species to examine the relationship among timing of parturition, duration of the planktonic stage and subsequent settlement. Thus, we attempted to understand the adaptive strategy that allows this rockfish to settle to its nearshore nursery ground.

Materials and methods

Study area and sampling methods

Matsushima Bay is a shallow enclosed embayment (<2.5 m depth) at the northwestern coast of Japan (Figure 1). The submerged vegetation is mainly
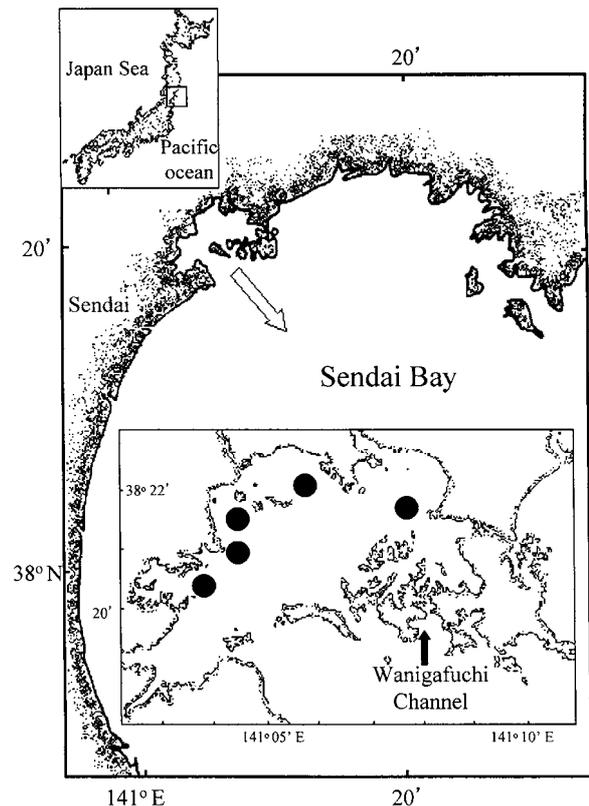

Figure 1. Map of Matsushima Bay, northern Japan, showing the location of sampling sites (filled circles). Arrow indicates the Wanigafuchi channel where the channel nets were set.

Z. marina, which grows on sandy and muddy bottoms forming continuous or patchy covers around the bay. Sampling were carried out from March to November at five stations from 1998 to 2001, forming part of a research program to study the early life history of *S. inermis* in this nursery ground. All samples were collected in the daytime with a small trawl net, which had 14 m of total wing length, 1.5 m in height, 5 mm mesh at wing, and 3 mm mesh at codend. Two 5 m ropes were attached to each end of the wings and tied to two long poles fixed to the front and rear on the right side of a small-engine boat. A 150 m rope was mounted in a rotator device equipped with a cylindrical part and a crank. A bamboo stick, at which the end of the 150 m rope was tied, was sunk in the mud bottom. The whole rope was released as the boat was driven covering the 150 m long rope, and then the boat was turned perpendicular to the rope. At this time, the net was deployed from the left side and was then pulled by turning the crank manually across the 150 m long rope (see Plaza et al. 2002 for a

schematic diagram of the sampling procedures). Due to the fragile nature of seagrass bed samplings were carried out twice a month in the early-spring (March–April) and monthly hereafter. Overall, 356 individuals of YOY *S. inermis* were caught in 1998, 1952 in 1999, 1637 in 2000, and 1113 in 2001. Juveniles were preserved in 95% ethanol so that the otoliths could be removed later. The TL was measured to the nearest 0.01 mm without correcting for shrinkage. Water temperature during the study period ranged from 6.45°C to 27.25°C in 1998, from 11.4°C to 29.3°C in 1999, from 8.65°C to 27°C in 2000, and from 12.35°C to 29.8°C in 2001.

Otolith analysis

In Sendai Bay northern Japan, *S. inermis* mates in early December and extrude their larvae from mid-December to early March in rocky areas. After a planktonic stage off Sendai Bay post-flexion and transforming larvae (ca. 12 mm SL) move to benthic habitats in mid-March at 10-m depth zone. Thereafter, by mid-April most benthic larval or juvenile fish move into *Zostera* belts in Sendai Bay (Nagasawa et al. 2000, Plaza et al. 2002). Increment widths of otolith change from narrow increment (before settlement) to wide increments (after settlement) in YOY *S. inermis* (Plaza et al. 2001). Settlement was interpreted to occur at the point where increment width changed drastically. This approach, first developed by Victor (1982), has been used in a number of studies to characterize settlement patterns (Victor 1986a–c, Kingsford & Milicich 1987, Wellington & Victor 1989, Sponaugle & Cowen 1994, Hamer & Jenkins 1996, Jenkins et al. 1996, Jenkins et al. 1997, Wilson & McCormick 1997, Reventós 2001). For the purpose of this paper random subsamples of juveniles collected from late spring to summer regardless location were taken in each year for otolith analysis because otoliths in these juveniles showed a clear shift in increment width from pre-settlement to post-settlement increments. Counting and measuring of growth increments were carried out using an image analysis system (Quantimet 600, Leica) at magnifications of 400–1000×. All counts were made twice across the area of distinctive increments. Increment widths and otolith radius were measured from the core along the posterior axis of the sagittae. More detailed information on otolith preparation and age validation for this species were given by Plaza et al. (2001).

To determine if the transition zone in otolith was linked reliably to settlement we examined the otolith microstructure (increment width) of non-settled juveniles collected by channel nets during the immigration season in March and April 1999. Nets were suspended and remained continuously in tidal passes in the Wanigafishi channel during flood tides of the new and full moon period. The transition-centered method described by Wilson & McCormick (1997) was used. This method consists in comparing increment widths from the settlement mark to avoid the masking effect of different age at settlement on the increment width profile. A repeated measure ANOVA (Sokal & Rohlf 1995, Zar 1999) was used to compare the widths of the 20 consecutive growth increments prior to the otolith margin of immigrating juveniles with the widths of the 10 consecutive growth increments before and after the settlement mark of juveniles caught in *Zostera* belts.

Daily patterns of settlement and extrusion dates were calculated by subtracting the post-settlement age (days after settlement mark) and the total age, respectively, from the collection date. Periodicity of settlement and extrusion dates over the lunar cycle was tested by using the Rayleight test (Batschelet 1981, Zar 1999). New moon was set as the first day of the lunar calendar. Maximal tidal heights for day and night were plotted to determine whether tidal times synchronized with lunar phases. The Kolmogorov–Smirnov test was used to compare parturition dates between years and between settlement groups.

'Planktonic duration' was defined as the number of days after the extrusions check to the settlement mark. This term was used instead of larval duration, because transformed juvenile *Sebastes* remain planktonic beyond the larval interval. Since a linear relationship between otolith size and fish size has been described for this species after settlement into seagrass beds (Plaza et al. 2001), we were able to back-calculate size at settlement (SAS). The biological intercept method (Campana 1990, Campana & Jones 1992) was used to the back-calculations as follow:

$$SAS = L_c + (R - R_c)(L_c - 6.63)(R_c - R_i)^{-1}$$

The mean TL of newly extruded larvae of *S. inermis* measured under rearing conditions was 6.63 mm (Plaza et al. 2001). R_i is the otolith radius at this biological intercept, L_c is the fish size, R is the otolith radius at settlement mark, and R_c is the otolith radius at time of capture.

One-way ANOVA (Sokal and Rohlf 1995, Zar 1999) was used to test for significant differences in both planktonic duration and SAS. The Shapiro–Wilks and Bartlett tests were used to test for normality and homogeneity of variance in the ANOVA procedures, and log-transformations were made when it was necessary. Tukey's HSD was used for multiple comparisons.

Results

Transition zone

The transition-centered method clearly separated the narrower increments formed before settlement mark (mean range, 3.79 ± 0.97 to $5.35 \pm 0.71\,\mu m$) from the wider increments (mean range, 12.74 ± 2.08–$17.48 \pm 146\,\mu m$) (Figures 2a and 3a) formed after
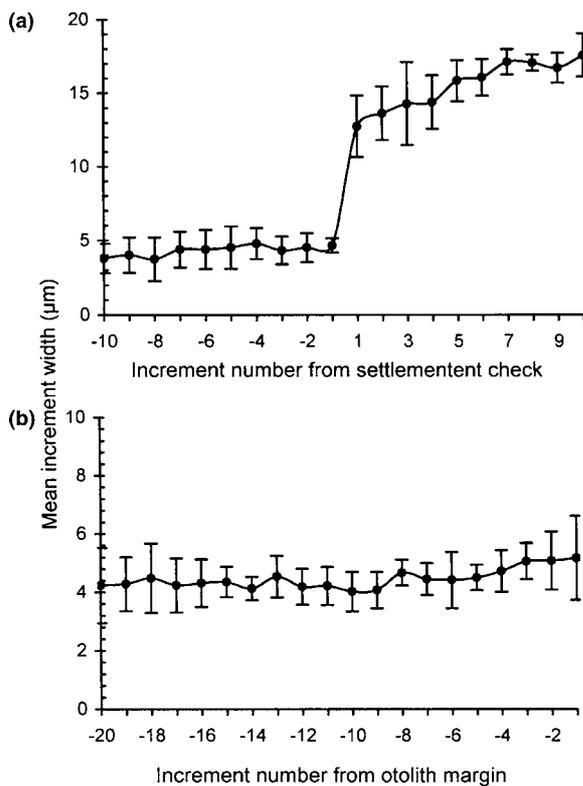

Figure 2. Comparison between (a) 10 increment widths prior to and from the transition zone of newly settled juveniles caught in seagrass beds (n = 10) and (b) the first 20 increment widths before otolith margin of pre-settlement *Sebastes inermis* juveniles collected by channel net (n = 10). Vertical bars indicate standard deviations.

the settlement mark. By contrast, juveniles collected by channel nets did not show the settlement mark or a dramatic shift in increment width (mean range, 3.77 ± 0.69 to $5.47 \pm 0.51\,\mu m$) (Figures 2b and 3b). Furthermore, repeated measures ANOVA showed significant differences on increment width over time ($F_{(19,342)} = 81.57$, $p < 0.001$) and between immigrating and newly settled juveniles $F(1,18) = 265.29$, $p < 0.001$). Therefore, the transition zone was linked to settlement.

Temporal pattern of settlement

Settlement season of YOY *S. inermis* into Matsushima-*Zostera* bed ranged from late March to late May, with the major occurrence in April. In all years, the daily pattern of settlement showed distinct groups that coincided with a semilunar cycle (Table 1, Figure 4). The first settled groups were arbitrarily designated as A, the second as B, and so on, in order of date. In 1998, the first group (A) arrived in late March in a new-moon phase, whereas the remaining groups – B, C, and D – settled near the first- and third-quarter moons. By contrast, all groups synchronized closely with new and full moons in 1999–2001, except for a few YOY arriving in the first-quarter moon in April of 2001, which for convenience were included in group B (Figure 4). In all years, timing of tides corresponded to the respective lunar phases. Group A for 1999 and 2001 were excluded from subsequent analyses due to their low frequency.

Timing of parturition

Distributions of parturition dates showed a similar pattern in all years; groups A and B, which settled earlier, corresponded mainly to January cohort, whereas groups D and E, which settled later were extruded mainly in February (Figure 5). Parturition dates of group C ranged from January to February. In the comparison of histograms among years, there were no significant differences among groups for 1998 and 1999 (Kolmogorov–Smirnov, $p > 0.05$). Conversely settlers in 2001 and 2001 were mainly extruded in January and February, respectively. Parturition dates were uniform over the lunar cycle in almost settlement groups within years. (Rayleigh's test, Table 1). When data were for all settlement groups combined, parturition dates peaked around the new and full moons in almost years (Figure 6, Table 1).
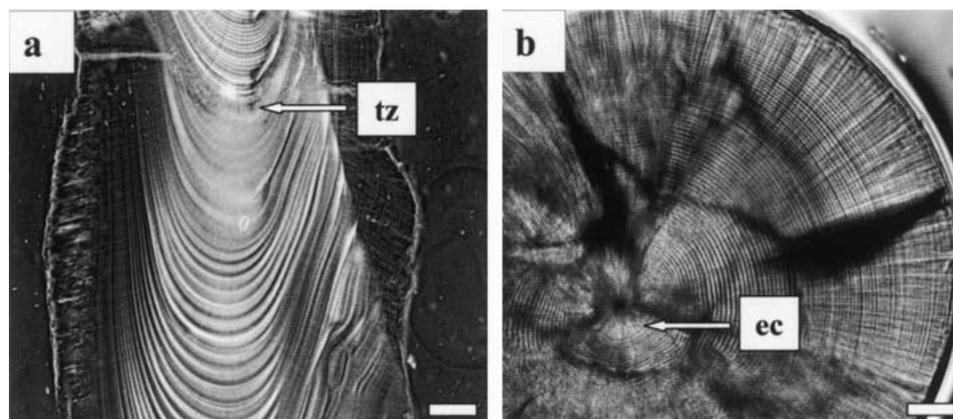
Figure 3. Light microphotograph of a: (a) sagitta from a 20 mm TL pre-settlement *Sebastes inermis* juvenile collected by channel nets; (b) sagitta (frontal view) from a 45 mm TL post-settlement juvenile collected in Matsushima Bay. tz: transition zone; ec: extrusion check; scale bar = 30 μm.
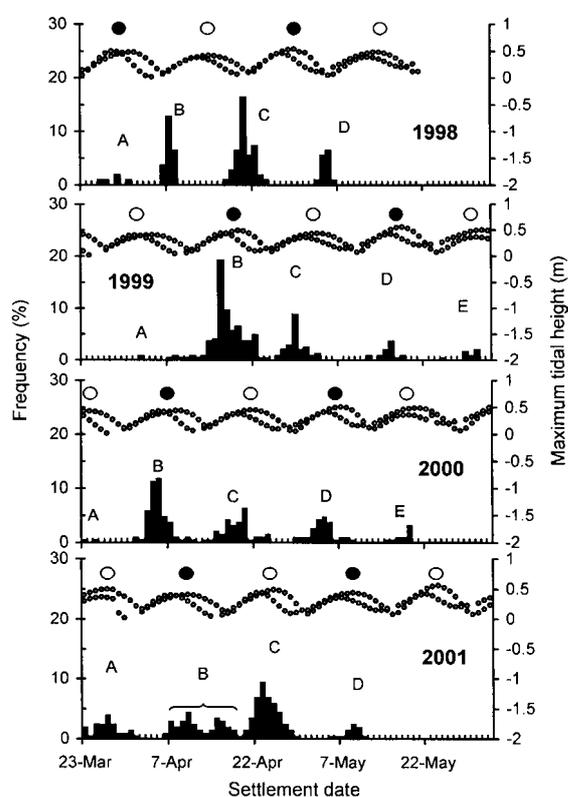

Figure 4. Daily patterns of settlement of *Sebastes inermis* in a *Zostera marina* belts at the northwestern coast of Japan from early March to late May of 1998–2001. Filled circles denote new moon; open circles denote full moon. Maximal tidal heights are plotted for each day. Capital letters over the histograms denote settled groups (see text).

Planktonic duration

To reduce the high number of multi-comparisons, one-way ANOVA was used to test for significant differences in planktonic durations among settlement groups within each year, and log-transformations were enough to correct for violations of normality and homogeneity of variance (Table 2). Planktonic durations ranged from 53 to 113 days, varying significantly among settlement groups within each year (Table 2). Planktonic durations also varied significantly among years (ANOVA, $F_{(3,745)} = 202.96$, $p < 0.001$) and the widespread range of the planktonic stage was more evident in the data combined (Figure 7). However, mean minimal and maximal values, were not significantly different among the 4 years (ANOVA, $F_{(3,12)} = 1.91$, $p > 0.01$).

Size at settlement

Back-calculated SASs ranged from 16 to 28 mm TL during the 4 years. Log-transformations were not needed previous to the ANOVA analysis. There were not significant differences in mean SAS within (ANOVA $p > 0.05$) settled groups in almost years, except for some juveniles that arrived to significantly shorter sizes in group B in 1998 and longer sizes in group D in 2001 (Table 3). However, there were significant differences in mean SAS among years (1998: mean = 23.41 ± 4.41; 1999: mean = 24.03 ± 2.79; 2000: mean =

Table 1. Statistics of Rayleigh's test (Z) for distributions of settlement dates and parturition dates in 1998 and 1999.

Year	Group	n	Settlement date			Birth date		
			Z	a[a]	s	Z	a[a]	s
1998	A	10	4.36*	1	1.73	2.17		
	B	35	24.53**	10	0.65	0.96		
	C	62	42.03**	23	1.42	1.35		
	D	43	14.66**	9	0.72	0.53		
Pooled		150				17.57**	2–17[b]	4.53
1999	B	145	107.5**	2	1.79	9.25**	3	0.9
	C	60	28.68**	14	0.65	0.15		
	D	27	18.79**	28	0.52	0.67		
	E	21	11.56**	13	0.17	3.74*	13	0.94
Pooled		253				15.45**	1–15[b]	4.12
2000	B	80	64.46**	0	0.44	1.53		
	C	49	37.82**	15	0.47	3.43*	13	3.12
	D	41	32.68**	1	0.46	1.16		
	E	15	10.3**	14	0.59	5.41*	2	3.37
Pooled		185				13.23**	2–14[b]	5.23
2001	A	25	51.55**	2	0.93	0.82		
	B	46	17.72**	2	0.89	1.82		
	C	76	58.81**	0	0.47	8.29**	12	2.37
	D	14	5.39*	14	0.9	5.36*	4	4.32
Pooled		161				1.53		

Mean vector angle 'a' transformed into a lunar calendar scale in days, and mean angular deviation 's' are given when the hypothesis of randomness over lunar cycle was rejected;
*p < 0.05, **p < 0.001.
[a]new moon = day 1.
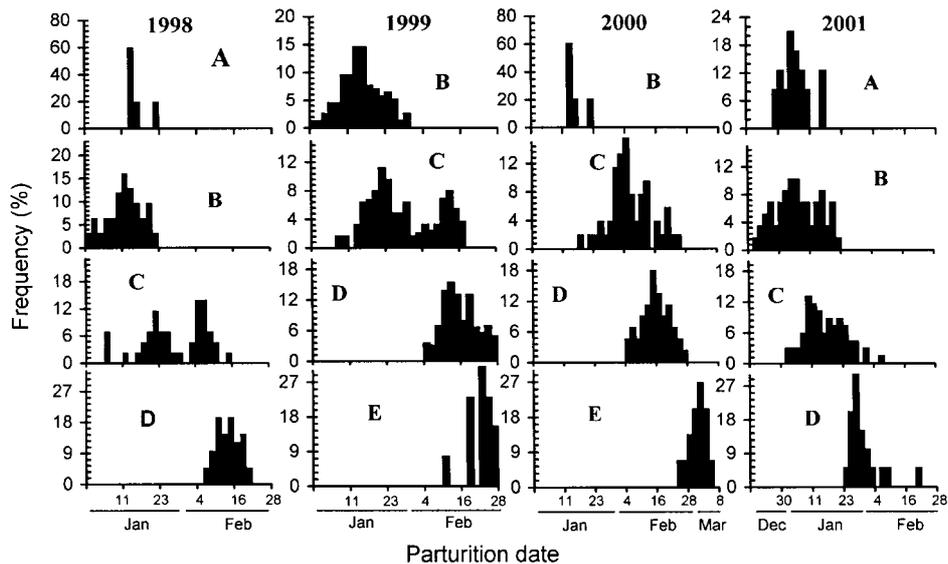[b]axially data transformed into unimodal data to apply Rayleigh's test (Z).

Figure 5. Frequency distributions of parturition date of *Sebastes inermis* by settlement group for 1998–2001. Capital letters denote settled groups (see text). Sample sizes are given in the Table 1. Group A for 1999 and 2001 were excluded due to their low frequency.
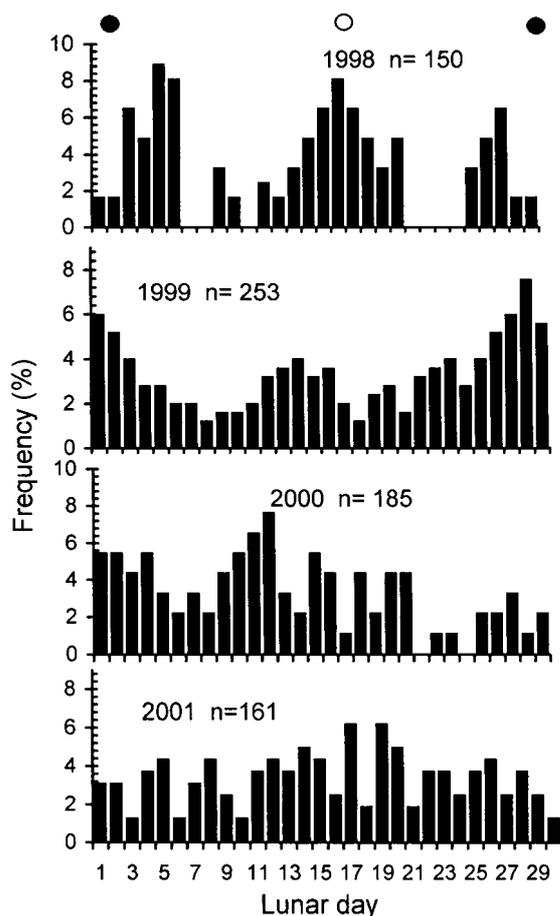
Figure 6. Distribution of parturition dates over the lunar month. Data are for all settlement groups combined in each year. New moon was set as the first day of the moon calendar. Filled circles denote new moon; open circles denote full moon.

17.92 ± 2.01; 2001: mean = 21.08 ± 2.51; ANOVA, $F_{(3,745)} = 146.44$; $p < 0.001$), although the Tukey multi-comparison test showed that only juveniles in 2000 settled to a significantly lower size ($p < 0.05$).

Discussion

It has been suggested that the synchrony between the temporal pattern of settlement and a semi lunar cycle found in a number of reef fishes would be related to the tidal cycle, because neap tides generally are coupled to quarter moons, and spring tides are coupled to new and full moons (Victor 1986b, Sponaugle & Cowen 1994). These arguments suggest that the settlement of *S. inermis* into seagrass belts was governed by selective
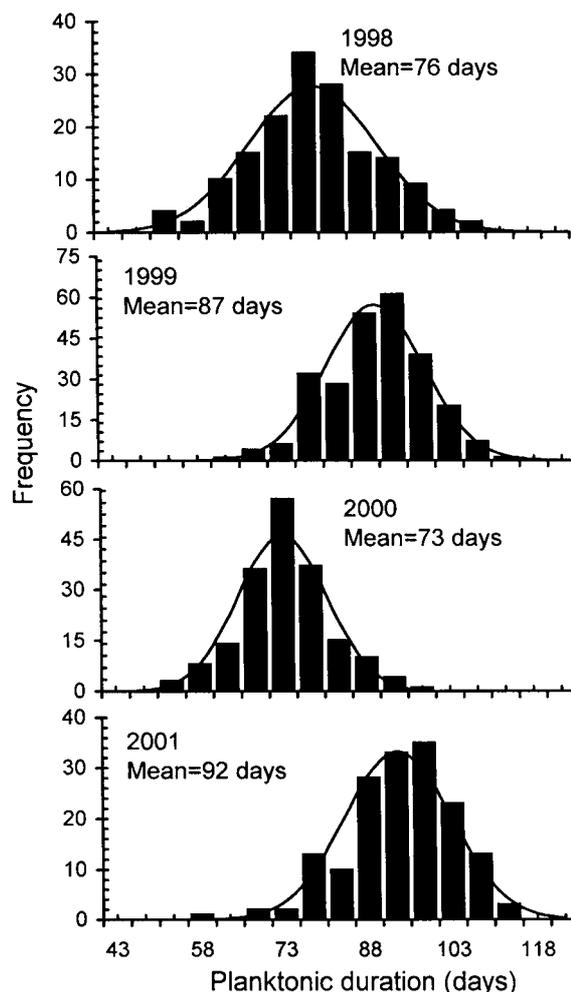

Figure 7. Distribution of planktonic durations of *Sebastes inermis* for 1998–2001. Data are for all settlement groups combined in each year.

tidal currents, such as has been described for a number of fishes (Gibson 1973, McCleave & Kleckner 1982, Yamashita 1996, Boss 1999). However, this assumption should be considered carefully, because synchrony was quite different between years – neap tides in 1998 and spring tides in 1999–2001. Settlement at quarter moon, with a high synchrony with neap tide, has been reported for a number of demersal fishes (Victor 1986b, Robertson 1992, Sponaugle & Cowen 1994). Sponaugle & Cowen (1994) suggested that neap tides would provide optimal conditions for settlement and survival of larvae and juveniles, because of slower currents and lower predation pressure. However, this situation might be advantageous when the settlement area is not so far

Table 2. Mean planktonic duration PD (days) of *Sebastes inermis* in Matsushima-*Zostera marina* bed, northern Japan.

Year	SG	Mean ± SD	Range	W; p	T	F & χ^2
1998	A	84.6 ± 8.5	76–99	0.88; <0.34	a	$F_{(3,147)} = 9.42$
	B	90.2 ± 10.3	61–102	0.93; <0.19	a	<0.001
	C	76.2 ± 10.6	53–97	0.94; <0.02	b	
	D	76.3 ± 5.9	63–84	0.86; <0.001	b	$\chi^2_{(3)} = 4.12$
1999	B	91.6 ± 8.0	65–103	0.96; <0.16	c	$F_{(3,249)} = 16.55$
	C	92.3 ± 9.2	72–113	0.97; <0.26	c	<0.001
	D	82.5 ± 8.4	63–84	0.91; <0.06	d	
	E	83.2 ± 5.1	69–90	0.88; <0.18	d	$\chi^2_{(3)} = 6.39$
2000	B	70.6 ± 7.1	54–92	0.98; <0.68	e	$F_{(3,181)} = 17.37$
	C	71.0 ± 7.0	55–84	0.71; <0.07	e	<0.001
	D	78.5 ± 6.5	67–93	0.94; <0.08	f	
	E	79.8 ± 8.5	66–100	0.95; <0.55	f	$\chi^2_{(3)} = 1.70$
2001	A	78.3 ± 8.0	60–86	0.92; <0.07	h	$F_{(3,157)} = 45.35$
	B	95.1 ± 7.5	80–112	0.96; <0.26	i	<0.001
	C	97.2 ± 6.8	77–111	0.97; <0.48	i	
	D	95.2 ± 8.1	72–111	0.91; <0.18	i	$\chi^2_{(3)} = 3.16$

SG: Settlement group; W: Shapiro-Wilks' test for normality; $p < 0.05$ were log transformed; F: One-way ANOVA for each year; χ^2: Chi-squared from Bartlett's test for homogeneity of variance; T: HSD Tukey's test $p < 0.05$, different letters shows significant differences in PDs among settled groups within years. Fish analyzed are given in Table 1.

Table 3. Mean size at settlement (SAS) of *Sebastes inermis* in Matsushima-*Zostera marina* bed, northern Japan.

Year	SG	Mean ± SD	Range	W; p	T	F & χ^2
1998	A	23.89 ± 2.51	19–24	0.98; <0.76	f	$F_{(3,147)} = 8.48$
	B	26.59 ± 2.61	23–28	0.91; <0.12	f	p<0.001
	C	23.39 ± 2.43	19–26	0.88; <0.75	fg	
	D	20.36 ± 2.44	18–27	0.96; <0.67	g	$\chi^2_{(3)} = 1.83$
1999	B	24.46 ± 2.89	18–28	0.98; <0.72		$F_{(3,249)} = 1.81$
	C	23.21 ± 2.67	20–28	0.94; <0.21		p > 0.05
	D	24.03 ± 2.56	19–28	0.94; <0.14		
	E	23.89 ± 2.49	20–27	0.96; <0.94		$\chi^2_{(3)} = 0.78$
2000	B	17.82 ± 1.83	17–26	0.94; <0.09	pq	$F_{(3,181)} = 3.95$
	C	17.59 ± 1.86	16–22	0.98; <0.76	p	p = 0.009
	D	18.27 ± 1.93	17–23	0.97; <0.60	pq	
	E	20.36 ± 2.81	18–24	0.89; <0.07	q	$\chi^2_{(3)} = 5.81$
2001	A	20.61 ± 2.31	16–26	0.96; <0.34		$F_{(3,157)} = 2.33$
	B	21.49 ± 2.95	17–22	0.96; <0.16		p = 0.072
	C	21.22 ± 2.18	17–23	0.97; <0.20		
	D	22.18 ± 2.03	18–24	0.97; <0.84		$\chi^2_{(3)} = 3.50$

SG: Settlement group; W: Shapiro-Wilks' test for normality; F: One-way ANOVA for each year; χ^2: Chi-squared from Bartlett's test for homogeneity of variance; T: HSD Tukey's test $p < 0.05$, different letters shows significant differences in SASs among settled groups within years. Fish analyzed are given in Table 1.

from the area of larval distribution and when larvae have a well-developed swimming ability. On the other hand, spring tides also seem to play an important role in the settlement of planktonic larvae. If larvae use tidal currents to move into nearshore areas, or actively migrate into onshore currents, spring tides would lead to larger inshore migration owing to their greater flux (Johannes 1978, Victor 1986b). Moreover, spring tides may provide a selective advantage, allowing the fish to keep the greatest distance between themselves and the bottom and thus minimizing their exposure to benthic predators (Johannes 1978).

Besides tidal control, the effects of topography and local oceanographic conditions might play some role in explaining the existence of distinctive settlement groups. Some authors have suggested that wind-driven currents and storms are the predominant factors in onshore movements (Winant & Olson 1976, Shank 1983, Kingsford & Milicich 1987, Shenker et al. 1993, Jenkins et al. 1997). Further, it has been suggested that many of the settlement pulses shown by some species may be explained by the frequency of occurrence of these events (Black et al. 1993, Jenkins et al. 1997). Although direct measurements of oceanographic variables are needed to test these influences, we believe that far less periodicity than we found would be expected if settlement were governed mainly by oceanographic conditions. In consequence, a synchronism of settlement with spring tides seems to be the consistent pattern of settlement of this rockfish to move faster into nearshore nursery grounds. Synchronism of settlement to first and third quarter moon phases seemed to be exceptional.

Extrusion and settlement seemed to be synchronized, because individuals extruded earlier in the parturition season tended to settle earlier than those extruded later. This suggests that in addition to tidal control of settlement, as discussed previously, other mechanisms could be involved. Christy (1978) proposed 'the settlement linkage hypothesis', which suggests that a lunar spawning cycle may occur in species that settle at a relatively fixed age associated with a preferred lunar period. More specifically, this hypothesis proposes that the synchrony of larval production with a lunar cycle is an adaptation to maximize settlement of planktonic juveniles (Robertson et al. 1990). The synchronism to a new and full moon phases in both extrusion and settlement found in almost years, supports partially this hypothesis, if it is assumed that the variability found in the planktonic period might be a result of the major variance associated to the misreading of otolith increments before settlement. We propose a new hypothesis as an extension of the settlement linkage that includes active migration. These arguments are supported because in each year, mean SAS is consistent within settlement groups and years (except for 2001), ranging from 18 to 26 mm TL, and is larger than the size (17 mm TL) at which this species complete morphologically the transformation from larvae to juveniles (Suzuki & Aida 1999). Although juveniles in 2001 settled at both shorter size and ages, they were extruded mainly in February, suggesting that SAS could not be fully represented by an enhanced survival of individuals extruded

later. The 'competent size' hypothesis comes closer to the idea that a flexible planktonic period is needed to maximize competent size, because environmental conditions may change within a season and among years. A flexible planktonic period was made evident by the differences found in planktonic duration among settled groups and years. In addition, planktonic period might vary with larval growth rate. Nagasawa (2001) reported growth rates during the planktonic period, using the slope of the relationship of daily age on TL, in five species of *Sebastes* occurring around the Japan coast: *S. thompsoni*, *S. schlegeli*, *S. vulpes*, and *S. inermis*. The highest growth rate was 0.66 mm day^{-1} for *S. schlegeli*, whereas the lowest was 0.13 mm day^{-1} for *S. inermis* (the five *Sebastes* species, except for *S. inermis* are non-winter spawners). In consequence, it appears that the adaptation of extruding in winter months for *S. inermis* is advantageous when settlement occurs in pulses and at a consistent body size, because a variable planktonic period does not affect largely the settlement size when growth rate is low. Further research analyzing the relationship between larval growth and water temperature by settlement group and years could help test this inference.

In conclusion, our results show that settlements of *S. inermis* occurred in patches, independent of age, and were hence under active behavioral control. Settlers arrived mainly at new and full moon phases suggesting either settlers used the spring tidal currents to move shoreward actively and faster, or extrusion and settlement were synchronized, or both. The synchrony with first and third quarter moon found in 1998 seemed to be exceptional and governed by unknown mechanisms. It could be argued that such extreme differences in settlement pattern might be a result of either a misinterpretation of the otolith transition zone or a misclassification of otolith increment. However, the transition zone was distinctive and the post-settlement increments were very easy to count, which facilitated the back-calculation of settlement dates. These facts suggest that still more complex mechanisms controlling the settlement pulses may be involved, such as spatio-temporal variability in the onset of migration. The synchrony of settlement pulses with spring tides in almost years supports the idea that juveniles migrated from a more offshore eastward position to the seagrass beds, which a spring tide would help, but not in 1998, when migration predominated at neap tides. The longer planktonic periods in 1999 and 2001 suggest that juveniles remain in the plankton until they reach the competent size, perhaps in response to environmental

conditions. The three hypotheses examined (control tidal, settlement linkage, and competent size) are not necessarily mutually exclusive and suggest that settlement of YOY *S. inermis* into its nearshore nursery grounds encompass an adaptive strategy to ensure the survival of its offspring.

Acknowledgements

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