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Lunar cycles of otolith growth in the juvenile starry flounder *Platichthys stellatus*

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Abstract

The otolith microstructure of juvenile starry flounders (*Platichthys stellatus*) sampled from a monitored environment was examined for evidence of lunar periodicity. Three types of biweekly cycles were observed in all of the flounder otoliths; two of the cycles were correlated with a tidal modulation of the environment. Through a multiple regression model, much of the day-to-day variability in increment width could be related to daily variations in temperature, salinity and tidal mixing. My results suggest that a 15-d increment width cycle was entrained by the interaction of a 15-d tidal cycle with temperature and salinity. The same tidal cycle/temperature interaction probably produced a biweekly pattern of increment contrast. However, the presence of otolith checks formed at weekly and/or biweekly intervals could not be so explained, although checks were consistently formed on the new and full moons.

Introduction

Deposition on the otoliths of young fishes occurs with a circadian periodicity, resulting in the formation of a continuous series of structures known as daily growth increments (Pannella, 1971; Brothers *et al.*, 1976; Mugiya *et al.*, 1981). Examination of the otolith microstructure thus provides a dated record of past fish growth, and has been used for the detailed determination of age, growth rate and life history information (Pannella, 1980; Brothers and McFarland, 1981; Methot, 1981; Rosenberg and Haugen, 1982). Such data are often difficult to obtain by other means.

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In addition to daily growth patterns, "lunar" cycles of otolith growth have been reported in some marine fishes (Pannella, 1971, 1974, 1980; Brothers *et al.*, 1976; Rosenberg, 1982). Periodic patterns of 14 to 15 or 28 to 30 daily increments, occasionally delimited by checks (discontinuities), were recognizable through cyclical differences in width and/or visual contrast. Despite the implication of tidal influence, no processes have yet been offered to explain these cycles of otolith growth.

Although lunar patterns in otoliths are poorly understood, plausible mechanisms for daily increment formation have been developed. A diel light cycle apparently entrains an endogenous circadian rhythm of otolith deposition (Taubert and Coble, 1977; Tanaka *et al.*, 1981; Radtke and Dean, 1982), with the need for entrainment reduced with increased age (Campana, 1983c). Temperature influences both increment width and appearance (Brothers, 1981; Neilson and Geen, 1982; Campana, 1983c), but does not act as a zeitgeber (Campana and Neilson, 1982; Neilson and Geen, 1982; Campana, 1983c). Feeding rate also affects increment width (Struhsaker and Uchiyama, 1976; Neilson and Geen, 1982).

Daily increment production has been verified in the juvenile starry flounder *Platichthys stellatus*, (Campana and Neilson, 1982). In this paper, I present evidence for the existence of lunar patterns in the otoliths of this marine fish. I suggest that such patterns are explicable in terms of variables that are known to influence deposition on the otolith. Development of a simple model of otolith growth consistent with the observed patterns supports this suggestion.

Material and methods

Juvenile starry flounders (mean standard length = 4.5 cm) were sampled from Spanish Banks, Vancouver, Canada, a region with a low gradient intertidal zone and mixed tides of up to 3.3-m range. Collections were made at 2- to 7-d

intervals between 2 September 1981 and 2 October 1981, on or near low tide. A minimum of 20 flounders were collected on each sampling date with a 10-m beach seine of 1.2-cm (stretched) mesh. Daytime samples were the norm, but night collections were occasionally made on the same date for food consumption comparisons.

Water temperature and salinity readings were recorded at 2- to 5-d intervals at the sampling site on both high and low tides. However, since these values were highly correlated with mean daily air temperature and rainfall respectively, the latter values were used in all analyses (as reported in Environment Canada, 1981 for Pt. Grey).

Sagittal otoliths were removed from the first ten flounders of each sample and prepared as described below. Food consumption was assessed through dry weights of recently-ingested food ($n \cong 20$ per sample). Stomach contents (between the pyloris and the anterior end of the intestine) were emptied onto tared filter papers, dried at 95 °C for 24 h, and weighed to the nearest mg. Since the food consumption index of stomach content/body weight was constant over a range of body weights, the mean food consumption index was calculated for each sampling date.

Otoliths were prepared for photography as per Campana (1983 b), with the modification that otoliths were ground from both sides to a thin section. Thin sections of otoliths can be clearly photographed in a single focal plane, unlike single-ground preparations. Since increment width always exceeded 2 μm, light microscopic examinations were considered reliable (Campana, 1983 b). Increment widths were measured to a precision of $\pm 5\%$, from photographs taken at 500×. The date of formation of all checks was determined microscopically at magnifications of 400 to 500×. No differentiation was made between lunar and stress-induced checks. If the latter were correlated to the lunar cycle, no differentiation would be necessary. Otherwise, stress-induced checks should be randomly distributed by date and would not affect the

results reported here. Note also that otolith sample size varied among the examination procedures depending upon the length, clarity and preparative quality of the required growth record.

To determine the mean width of daily increments formed on a given date, increment series of 31 otoliths were measured and assigned as to date of formation. Individual otoliths differed among themselves with respect to overall growth rates and the location of the axis of measurement. To eliminate the effect of these differences, the length of the entire increment sequence was multiplied by the standardization factor necessary to bring it to a common, among-otolith value: each increment within a sequence was multiplied by the same standardization factor, thereby retaining relative width differences among dates for a given otolith. Mean width was calculated for each date from the combined, standardized otolith data.

The daily increment sequence appeared to cycle between regions of high and low visual contrast. The locations of such regions were determined visually from photographs, and subsequently assigned dates of occurrence. To ensure that there was an objective basis to the visual determinations of contrast, negatives from randomly-selected, "blind-labelled" photographs ($n = 8$) were scanned with a Beckman R-112 scanning densitometer. Peak heights were quantified and assessments of contrast in the photographs were made before the two were matched up and compared.

Results

Lunar checks

The otolith microstructure of wild starry flounders was characterized by a sequence of daily growth increments punctuated by prominent checks (discontinuities) (Fig. 1). The distinct appearance of these structures at a variety of
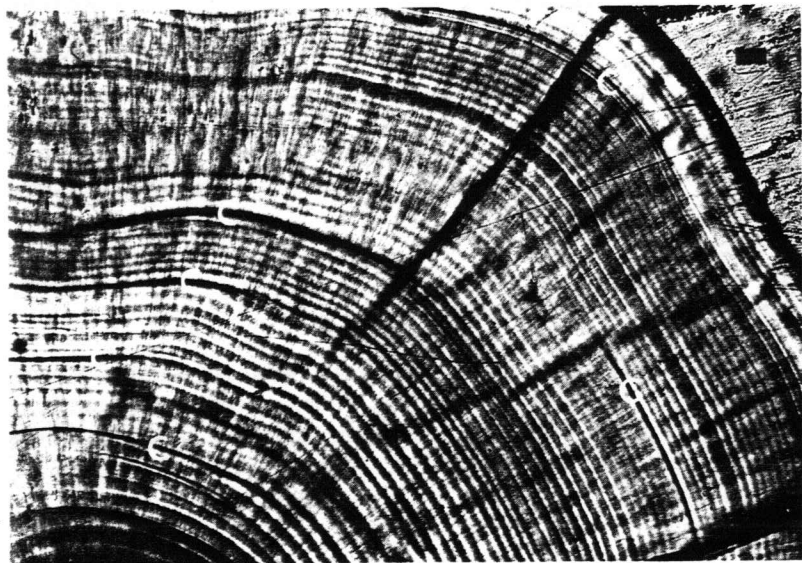

Fig. 1. Otolith microstructure of a wild starry flounder. The regular daily growth record is punctuated by prominent checks (C) at irregular intervals. Bar = 20 μm

focal lengths ensured that their presence was always unambiguous. Checks on the postrostrum were the most frequent, but were not often continuous around the otolith, suggesting the presence of localized growth interruptions. Rostral checks appeared to be more representative of the sagitta as a whole, since they were generally observed in all quadrants.

Check periodicity was not random; when the postlarval growth record of a random sample ($n = 19$) of otoliths was examined, checks were most commonly separated by 7- to 8- or 14- to 15-d periods (Fig. 2). Other multiples of weekly intervals were also evident.

By counting the number of daily increments between the most recently formed check and the otolith periphery (representing the sampling date), the date of check formation can be calculated. My calculations were consistent with the periodicity results of Fig. 2; in addition, the dates of formation were closely correlated with the phases of the moon (Fig. 3). The date corresponding to the most commonly observed check (August 31) was very close to the date of the new moon (August 29), while the second most frequent check (September 13) occurred on a full moon. Such similarities are probably not coincidental, since checks in the otoliths of starry flounders sampled from Bellingham Bay, Washington on 13 August 1980 ($n = 7$) and 19 June 1981 ($n = 9$) occurred within 1 d of a new moon. Therefore, my results suggest that lunar checks are produced in phase with the lunar cycle.

Lunar patterns

A biweekly cycle of daily increment contrast was evident throughout the post-larval growth region in all flounder otoliths. At intervals of 14 to 15 d, visual contrast between the opaque portion of each increment and its adjacent
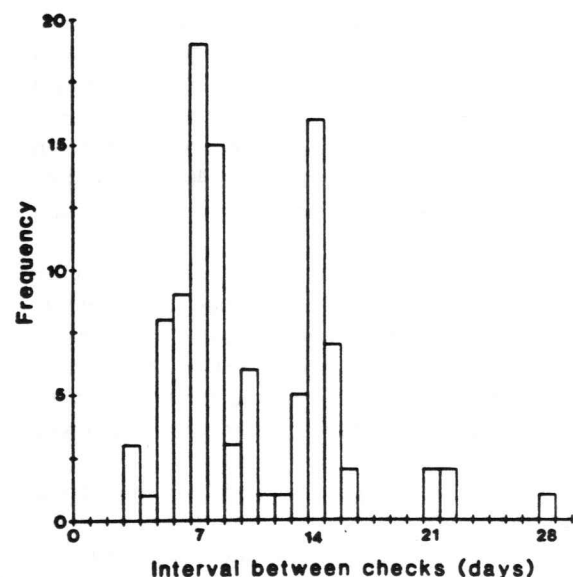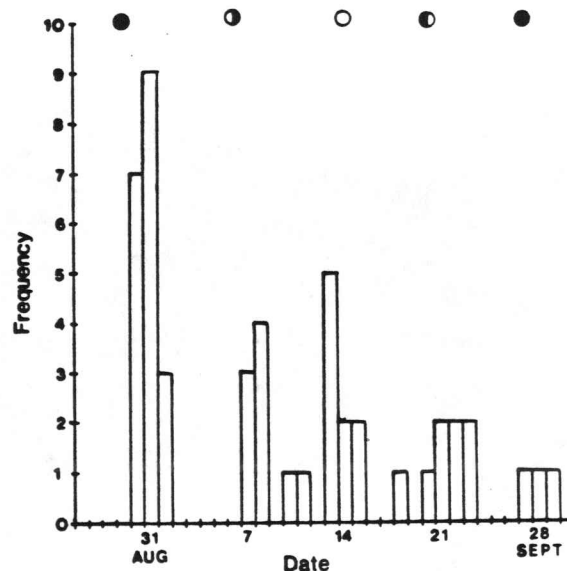

Fig. 3. Date of formation of the most recent check in otoliths of juvenile flounders sampled at ca 5-d intervals between 2 Sept and 2 Oct. The sequential sampling regime tends to emphasize check frequency at earlier dates at the expense of the later dates. Phases of the moon are indicated. (● = new moon) ($n = 48$)

translucent region, peaked, decreasing to a minimum a week later. These visual assessments were confirmed with the densitometer; the scans were characterized by a "sawtooth" pattern whose small-scale peaks corresponded closely to the daily increments visible in the photographs (Fig. 4). After the removal of long-term trends (those spanning more than one day), regions of high visual contrast were represented in the scan by peaks that were significantly greater in amplitude than those in low contrast regions (Student's t-test, $P < 0.01$). A plot of peak amplitude vs time (after trend removal) resulted in a wave form whose periodicity, maxima and minima matched those of contrast cycles determined visually. Maximal contrast occurred September 13–14 and September 26–27 during the sampling period. These dates coincide with the full and new moon respectively, and a period when daily tidal range had reached a maximum. One prominent subdaily increment was evident within each day of the high contrast region. If subdaily increments were produced in the low contrast region, they were not apparent.

Lunar correlates of feeding

Little is known of the feeding habits of juvenile starry flounders. Many flatfish feed intertidally on incoming and/or outgoing tides (Tyler, 1971; Lockwood, 1980; Toole, 1980), and starry flounders probably do the same (Orcutt, 1950). To test whether feeding occurs both day and night, flounders were collected on the two low tides of September 15 (one at noon, the second at midnight), a date when the tidal heights and ranges of both pairs of
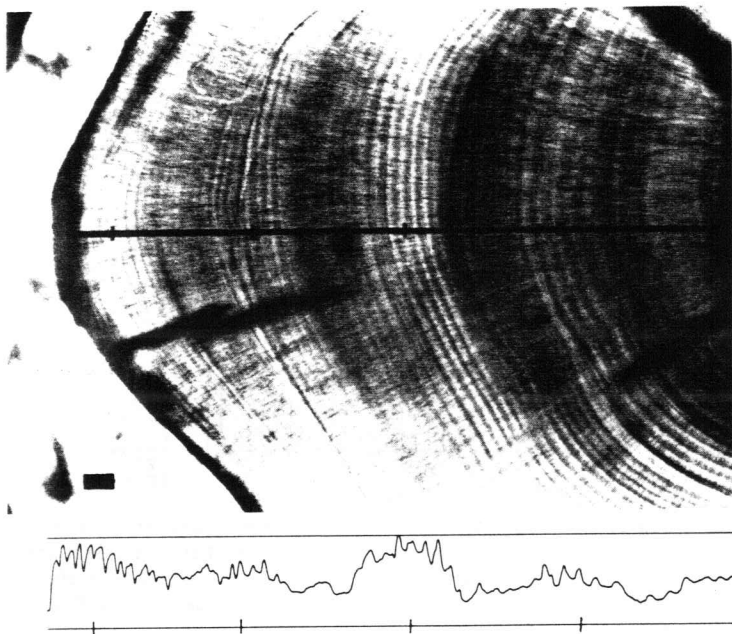

Fig. 2. Histogram depicting the time interval between checks in otoliths of juvenile flounders ($n = 19$)

Fig. 4. (Top) The daily growth sequence in the otolith of a wild starry flounder. Vertical bars denote regions of high increment contrast that occur at approximately biweekly intervals. Bar = 20 μm. (Bottom) Densitometer scan along horizontal line in (Top) view. Vertical bars correspond to those apparent in (Top) view. Note the difference in small-scale peak amplitudes between the high and low contrast regions
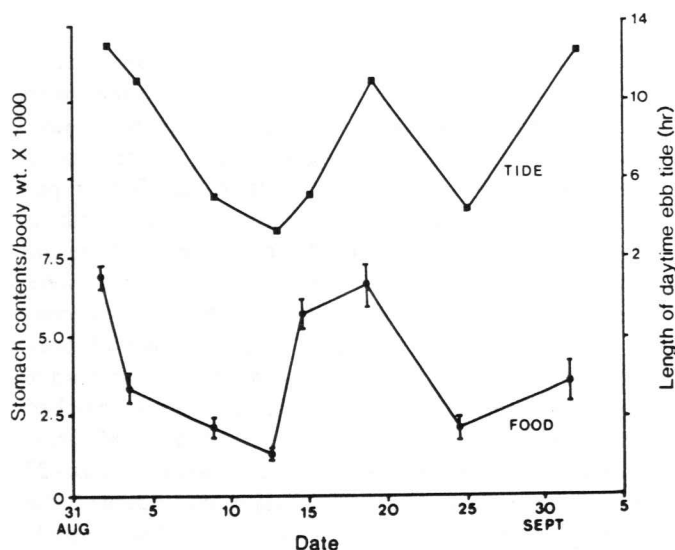

Fig. 5. Food consumption as a function of time for starry flounders sampled between 2 Sept and 2 Oct. $n = 20$ for each date. Consumption was highly correlated with available feeding time (= duration of daytime ebb tide)

tides were similar. Flounders collected at night ($n = 21$) contained significantly less food in their stomachs than did day-caught fish ($n = 19$) (Student's t-test, $P < 0.05$); little of the food in the night fish was freshly ingested. Therefore, the data support the view that juvenile flounders are daytime feeders.

Mean food consumption varied significantly over the sampling period. At approximately 2-wk intervals, the quantity of ingested food peaked (Fig. 5). Food intake was apparently related to the tidal cycle; since flounders feed at high tide during the daytime, little feeding time should be available on days when the high tides occur at night or

are of short duration. Available feeding time cycled with the tides (a 2-wk period) and was highly correlated with food consumption (Fig. 5).

Daily increment width

To determine if increment widths reflected a lunar cycle, a sample of otoliths ($n = 5$) with long (60 to 120 d), uninterrupted daily increment sequences was analyzed with periodogram analysis. Periodograms among the otoliths were similar. All increment width sequences were significantly different from white noise ($P < 0.0005$) indicating that cycles were present. No individual cycles were significant at $P = 0.05$; however, a combination of cycles with periods of 28 to 30 d and 14 to 15 d was significant ($P < 0.05$). In addition, cycles of 14–15, 20–21 and 28–30 d were always the three most important rhythms in the data series, together explaining 30 to 40% of the data variance. Weekly periods (7 to 8 d) were generally not prominent in the periodogram.

The variables that might be expected to influence increment width include temperature, food consumption, salinity (through a change in the ambient Ca concentration) and tidal mixing (through its effect on temperature and salinity). These data were collected for the sampling period in preparation for incorporation into a stepwise multiple regression model.

For a multiple regression model to be interpreted causally, a small number of relevant variables must be selected a priori, and then inserted into the model in a stepwise manner depending on significance. Such an approach was followed in this study, where only the aforementioned variables were considered for forward stepwise inclusion. However, two lagged variables were also ex-

Table 1. Partial correlations of potential regression model variables with daily increment width in flounder otoliths

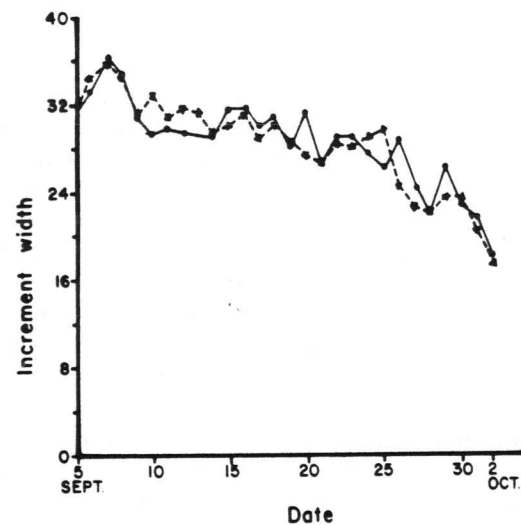| Controlled variables	Partial correlation with daily increment width						
	Temp	Rain	Lag-rain	Food[1]	Lag-food	Tidal range	Tidal ratio
None	0.618*	−0.563*	−0.746*	−0.030	0.411*	−0.202	0.295*
Temp	–	−0.455*	−0.684*	−0.006	0.512*	−0.068	0.143
Temp, lag-rain	–	NA	–	0.224	0.547	−0.392*	0.213
Temp, lag-rain, lag-food	–	NA	–	NA	–	−0.260	−0.329

NA = not applicable
* $P < 0.05$
[1] correlate of food consumption (from Fig. 5)

Table 2. Multiple regression model of daily increment width in starry flounder otoliths. Variables were added in a forward stepwise fashion

$$Y = 0.655 \ \text{Temp} - 0.309 \ \text{Lag-rain} + 0.439 \ \text{Lag-food} + 17.341^{1}$$

$F = 41.81$	$P < 0.000$	$R^2 = 0.84$	$n = 28$

Variable	B	Partial F Value	Significance
Temp	0.655	22.83	0.000
Lag-Rain	−0.309	26.20	0.000
Lag-Food	0.439	14.85	0.001
Constant	17.341	23.59	0.000

[1] Y = daily increment width (in arbitrary units, since the data were standardized). Temp = mean air temperature. Lag-rain = rainfall lagged 1 d and Lag-food = food consumption lagged 3 d – see text for justification of lag times

Fig. 6. Time series of mean daily increment width (solid line) ($n = 31$ fish). Expected increment width (dotted line), as predicted from a multiple regression model, is also plotted

amined: rainfall data were lagged 1 d to allow runoff to reach the estuary, and food consumption data (correlate from Fig. 5) were lagged 3 d due to the slow reaction of otolith deposition to feeding changes (Campana, 1983 b). Partial correlations of these variables with increment widths were then calculated (Table 1). Stepwise addition of the two most significant variables, temperature and rainfall (in mm, lagged 1 d) resulted in the model: Increment width = 0.625 Temp −0.346 rain-lag + 21.023 ($P < 0.001$, $R^2 = 0.74$). However, the residuals were significantly autocorrelated (Durbin-Watson test, $P < 0.05$) with a period of 14 d, suggesting the need for a tidally-modulated variable in the model. Inclusion of the next most significant variable, lagged food consumption (Table 1), eliminated the autocorrelation, as well as becoming the last significant variable to be added to the regression equation (Table 2).

Increment widths predicted from the regression model were similar to those actually observed (Fig. 6). Temperature was a dominant variable in the model, accounting for much of the decline in increment width through time. Since there was a strong serial correlation between temperature and date, it was conceivable that the variable time, not temperature, was responsible for the overall trend in width. However, the strong influence of temperature on increment width is well documented (Brothers, 1981; Marshall and Parker 1982; Neilson and Geen, 1982), while there is no evidence to suggest that the intrinsic growth rate of the flounders (or their otoliths) declined substantially through the relatively short time course of the study. Therefore, time was assumed to have been an opportunistic correlate of temperature and increment width.

Discussion

The lunar cycle was correlated with three aspects of otolith deposition in juvenile flounders. Both increment width and contrast cycle with a biweekly periodicity, apparently due to a tidal influence on those environmental variables that affect otolith growth. The existence of otolith checks with a weekly or biweekly periodicity cannot be so

explained, although check formation is closely correlated to the phases of the moon.

Check formation is normally associated with a stressful incident in the life history of a fish (Pannella, 1980). Stress reduces branchial uptake of calcium, resulting in a calcium-poor structure that is visually prominent relative to the surrounding daily increments (Campana, 1983 a). However, an analogous mechanism does not appear to exist during the formation of lunar checks. At its maximum, the two-week cycle of tidal mixing/turbulence might stress an intertidal fish sufficiently to form a check. Yet it is unlikely that such a cycle would result in weekly checks. Moreover, discontinuities seldom occur adjacent to one another, although such might be expected at the peak of a particularly high series of tides. Although my data do not suggest a weekly cue for check production, biweekly periods are likely entrained by the tidal cycle/lunar phases, with or without the existence of an endogenous lunar rhythm.

Visual contrast of otolith growth increments can be increased by two processes: a diel temperature shift (Brothers, 1981; Campana, 1983 c) and stress (Campana, 1983 a). Both processes apparently result in the same product – an increment with an increased protein:calcium carbonate ratio. Since contrast in the flounder otoliths varied with a 2-wk periodicity, I suggest that the lunar pattern was a consequence of the temperature regime induced by a biweekly tidal cycle. A biweekly temperature regime is known to exist in some intertidal zones (de Wilde and Berghuis, 1979). However, since flounders move in and out with the tides, the 15-d tidal cycle will also influence fish position relative to the sun-warmed inshore region (at high tide) and the cooler subtidal waters (at low tide). Maximum increment contrast occurred on dates when the tidal range was large, and consequently, the temperature difference between high and low tides was at its greatest (Vugts and Zimmerman, 1975). Falling nighttime temperatures increase the protein:calcium ratio in concert with an endogenous circadian rhythm, resulting in the formation of the opaque region of a daily increment (Brothers, 1981; Mugiya et al., 1981; Campana, 1983 c). A daytime temperature shift, as would occur during tidal migration, should also result in the formation of an opaque zone. The presence of a single subdaily increment in the high contrast region of the otolith is consistent with this hypothesis.

Much of the day-to-day variance in increment width was accounted for by a small number of environmental variables. Variation of the mean daily air temperature accounted for the largest proportion of the observed width variability. It is likely that water temperature would have provided an even closer correspondence, although the collection of such data would have required continuous monitoring of the flounder through its inshore/offshore migrations. The air temperature data were limited in that they exhibited more severe fluctuations than did the water. In addition, any biweekly cycles in water temperature due to tidal mixing would not be reflected in the air tem-

perature data. The proposed tidal mixing terms were developed in an attempt to compensate for the absence of this effect. However, the inclusion of the food consumption variable, with its attendant biweekly rhythm apparently eliminated the need for an additional mixing term. The change in the residual pattern from one of autocorrelation with a 14-d cycle, to one of random distribution after addition of the food variable, supports this view. Unfortunately it also confounds the relative significances of food and tidal mixing to the regression model, since the effect of the two factors could not be separated. Since an earlier study demonstrated that there is a poor correspondence between food consumption and short-term otolith growth (Campana, 1983 b), it is likely that the food variable was influential through its correlation to tidal mixing, and not its food:fish growth relationship. Temperature may strongly influence increment width in other species (Marshall and Parker, 1982; Neilson and Geen, 1982).

Salinity (a correlate of rainfall) had a significant ($P < 0.05$) but puzzling effect on increment width. Calcium deposited on the otolith is derived from the ambient water supply (Simkiss, 1974; Mugiya et al., 1981) where it exists as a salt in solution. Presumably, calcium concentration is proportional to salinity. If calcium uptake is proportional to available calcium supply, then a decrease in salinity could result in reduced calcium deposition on the otolith, i.e. a narrower increment. However, there is evidence against such a relationship (Irie, 1960). More likely, rainfall had a direct negative effect on water temperature.

Periodograms of long-term otolith growth records demonstrated the presence of a prominent "lunar" rhythm of growth. Food consumption displayed a similar periodicity, although its importance in the regression model was questionable. Neither air temperature nor rainfall varied over a lunar cycle. However, their correlates, water temperature and salinity, are under a large tidal influence. The tidal cycle induces a 14- to 15-d periodicity in the temperature of intertidal waters (Vugts and Zimmerman, 1975), and this probably accounts for the observed biweekly rhythm of otolith growth (but not the 21-d rhythm, whose presence remains unexplained). The significance of this observation may lie in the relationship between short-term otolith and fish growth. Wilson and Larkin (1982) demonstrated that the daily increment width:fish growth relationship was significant and linear for juvenile sockeye salmon Oncorhynchus nerka. Starry flounders have a similar relationship (Campana, unpublished data), suggesting that the lunar cycle of otolith growth is a reflection of a similar cycle in fish growth. To my knowledge, tidally-modulated growth cycles in fish have not been documented to date.

The few documented examples of lunar rhythms in fish are generally associated with spawning and/or migratory activities on the new or full moon (reviews by Gibson, 1978; Neumann, 1981). Causal mechanisms are poorly understood, but in at least some species, there appears to

be an endogenous lunar rhythm (Grau et al., 1981; Kavaliers, 1982). In this study, lunar cycles of otolith growth (increment width) and increment contrast appear to be explicable in terms of tidally-modulated environmental variables, particularly temperature. It was not necessary to postulate the existence of an endogenous lunar rhythm. Supporting this supposition was the absence of any observable lunar pattern in the otoliths of ten species of freshwater fishes. Biweekly contrast patterns were observed in juveniles of the following marine species: *Leptocottus armatus*, *Psettichthys melanostictus*, *Cymatogaster aggregata*, *Pholis ornata*, *Mallotus villosus*, *Apodichthys flavidus*, *Embiotoca lateralis*, *Clinocottus acuticeps* and *Parophrys vetulus*. Lunar checks were only observed in the pleuronectid species examined; thus, their significance is unclear.

Otolith microstructure examination can provide useful information on short-term growth trends in juvenile fishes; the lunar growth cycle of flounders would have been difficult to detect by other means. In addition, the clarity of the biweekly increment contrast patterns suggests their potential for rapid age determination of some marine fishes. Lunar checks are too variable for this purpose, although juvenile *Parophrys vetulus* from Oregon have been aged in this way (Rosenberg, 1982). Check periodicity may vary geographically, since young English sole in the Vancouver region produce both weekly and biweekly checks (Campana, personal observation). However, since the checks in starry flounder otoliths did not necessarily appear on both the rostrum and postrostrum, localized otolith growth interruptions may have contributed to the frequency of observed checks.

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