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Periodicity of Otolith Check Formation in the Juvenile Plaice *Pleuronectes platessa* L.

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ABSTRACT: Juvenile plaice (*Pleuronectes platessa* L.) were sampled in the intertidal zone of Port Erin Bay (Isle of Man, Irish Sea) by push-net in the summers of 1990 and 1992. Check formation on the sagittal otoliths was examined to test the hypothesis that tidal and light cycles periodically disrupt the growth of 0-group plaice. Otolith checks occurred mostly at weekly (7-8 d) intervals (range 3-21 d). This periodicity matched activity patterns that were lowest at both spring and neap tides. Check formation may reflect ontogenetic changes in feeding and activity, as measured by diurnal and seasonal variations in catches.

Introduction

Periodic checks, or prominent discontinuous zones, in fish otolith were first described by Pannella (1971). Juvenile flatfish otoliths in particular are distinguished by prominent checks at seemingly regular intervals. Environmental conditions that vary with a regular periodicity over lunar-tidal cycles coincide with checks on juvenile flatfish at 14-d intervals (Rosenberg 1982; Campana 1984). Seven-day intervals between checks have also been observed but remain unexplained (Campana 1984). Otolith checks have been linked to lunar cycles (English sole, *Parophrys vetulus*, (Rosenberg 1982)) and tidally controlled feeding rhythms (starry flounder, *Platichthys stellatus*, (Campana 1984)). The combined stress of high temperature and high solar radiation levels has been linked to variations in otolith deposition in juvenile plaice, *Pleuronectes platessa*, visible as hyaline zones when viewed using low-power light microscopy (Berghahn and Karakiri 1990; Berghahn et al. 1993). Similarities in the development, shape, and increment pattern have been noted for the otoliths of many juvenile flatfish species (Sogard 1991). However, the ultimate cause of check formation may differ between intertidal and subtidal species, and between areas with different tidal regimes, because of differences in the importance of various environmental cues.

It is particularly interesting to examine the relationship between environmental conditions and check formation in juvenile plaice. Plaice are tied closely to the intertidal zone during their first year of life. They are the first flatfish to appear on the beach in the spring. They occur in the shallowest

zones, and move generally with the edge of the tide during flow and ebb. Therefore, in plaice the tidal excursions are closely linked to tidal and lunar cycles, perhaps more so than in many other flatfish.

Feeding opportunities for juvenile flatfish are not always optimal, because the location of the fish on the beach is more closely related to the movement of the tide during ebb and flow than to the location of the prey species (Ansell and Gibson 1990). Temporally limited food resources could affect juvenile flatfish, and plaice in particular, in shallow-water nursery grounds such that adverse combinations of tidal height and light would occur during every lunar cycle, resulting in otolith checks at roughly 14-d intervals (Campana 1984). For example, if plaice feed primarily on the rising tide during daylight hours, mid-day low tides could interfere with feeding for up to 24 h.

We investigated the periodicity of check formation in the otoliths of juvenile plaice as a way of evaluating whether lunar tidal cycles present changing feeding opportunities. Our initial hypothesis was that changes in feeding would cause significant disruptions to fish and result in otolith checks. We also used the information derived from otolith analysis to examine activity patterns observed in the 0-group plaice population in relation to daily-tidal and lunar-tidal cycles.

Materials and Methods

All sampling was undertaken in Port Erin Bay, Isle of Man ($54^{\circ} 5.0'N$ $4^{\circ} 46.0'W$). This is a low-gradient, west-facing, sandy beach (450 m wide) with semidiurnal tides. In all experiments young plaice were sampled with a 1.5 m Riley push-net (Riley 1971) in 0.6-1 m water depth. The push-net is known to be size-selective when sampling the abundance of a whole population with a large size range. When sampling the intertidal stages of flatfish (15-90 mm) in shallow water (< 1 m depth), it is an appropriate sampling tool.

The height of low water at Port Erin Bay was obtained from the Admiralty Tide Tables (Hydrographic Office 1989). The changing height of low water in relation to chart datum was used to define the lunar-tidal cycle. Daily temperature data for Port Erin Bay was provided by D.J. Slinn (Port Erin Marine Laboratory, Port Erin, Isle of Man). The temperature anomaly was calculated as the difference in temperature between the day in question and the preceding day.

OTOLITH STUDY

Juvenile plaice were sampled over nine 13-h periods during the summer of 1990 (14 and 26 June; 4, 11, 16, and 19 July; 2, 9, and 22 August). A pair of samples was taken 1 h before low water (slack ebb-tide), at low water, at half-tide rising (mid-flood tide), at high water (slack flood tide), at half-tide falling (mid-ebb tide), and at low water again. All the individuals captured were counted and 10 individuals from each haul preserved in 95% alcohol for analysis of otolith check formation.

All preserved plaice were measured (total length) to the nearest 1 mm. The sagittal otoliths of 104 individuals from five sample dates (4 July 1990 - 22 August 1990) were ground and polished on both sides (Campana 1984) and then examined at 250X magnification. Increment counts and check identifications were made along the best axis for each otolith; since increment width was not being measured, standardization of the axis used was not necessary. Using a Hitachi video camera and Macintosh-computer-based software (Image 1.44, National Institute of Health), each increment

was labelled as either a normal primary increment or a check, beginning from the edge of the otolith and continuing in as far as possible up to the first accessory primordia. Check identification was subjective, based on the difference in contrast and width of the discontinuous zone (Fig. 1).

Primary increments on juvenile plaice otoliths are formed daily, an observation based on laboratory experiments that have included testing severe stress conditions (Berghahn and Karakiri 1990; Karakiri et al. 1991). The frequency of check formation for the population as a whole was analyzed by calculating what portion of the population formed checks on any day. To do this, the date of each check formation for each individual was estimated by counting back from the date of capture. The frequency of check formation for the whole population was calculated as the number of checks formed as a proportion of all increments formed on a particular date. These data form a time series of the occurrence of checks between 1 June 1990 and 22 August 1990. Periodogram analysis (Fourier series; Systat, Inc.) was performed on the time series. To examine whether the periodogram analysis for the population data accurately reflected the individual pattern, we also determined how often each individual fish formed checks, that is, the interval (number of primary increments) between checks on an individual basis. The number of increments between checks was counted on each individual between the ultimate and penultimate check. The ultimate check was at least two increments (range 2-11) from the otolith edge in all samples.

Linear relationships between the proportion of the population showing otolith checks on any one day and the corresponding physical parameters (temperature anomaly, lunar tidal height, number of daylight hours, etc.) were tested by standard regression analysis (MINITAB, Release 7).

ACTIVITY STUDY

Samples were taken at low water on 18 dates between 31 May and 22 August 1990. All plaice were counted, and subsamples were retained for further analysis. In addition, plaice were sampled on successive low tides (17 sample sets) over a 15-d period between 16 and 28 September 1992. Three pushes, 30 m long (measured between a series of stakes placed on the beach at the time of sampling), were made and all plaice counted. A mean catch was calculated for each sample time.

Results

The number of increments between checks in juvenile plaice from Port Erin Bay ranged from 3-21, but lunar weekly checks were most common (Fig. 2). The tidal cycle is 24.8 h, and thus the number of days between lunar phases (a lunar week) is close to eight solar days. Periodogram analysis revealed one major peak at 8 d, with a minor peak at 14 d and a minor peak at 3 d that is most likely an artifact of the Fourier process. At the population level, weekly check formation coincided with both spring and neap tides (Fig. 3a). Rapid changes in temperature could be a factor influencing check formation. Linear regression analysis showed that the relationship between the frequency of checks in the population and the daily change in temperature (temperature anomaly) was significant ($F = 3.85$; 1,81 df; $p < 0.05$), but the fit was very poor ($r^2 = 0.45$). Likewise, check formation was not related to the number of daylight hours of the ebbing tide as might be expected



Fig. 1. Otolith of juvenile plaice (approximately 40 mm TL). p = primary increments, c = check, a = accessory primordia. Magnification is 400X.

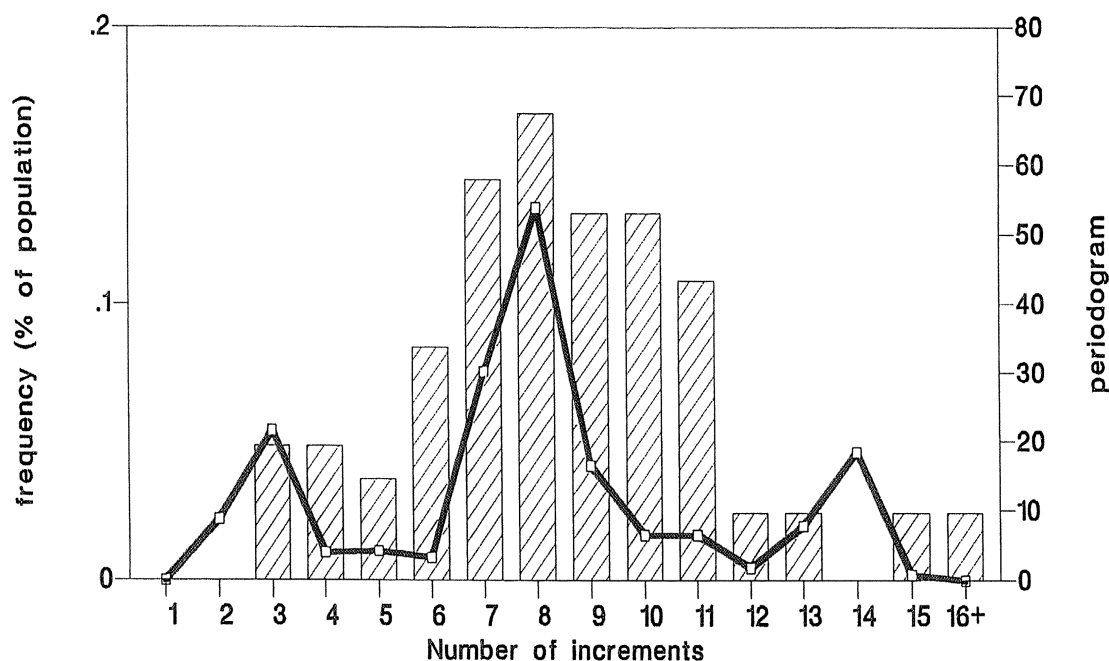


Fig. 2. The distribution of the number of increments between checks on the otoliths of individual juvenile plaice and the periodicity of check formation for the whole population. Histogram = number of increments between checks and solid line = Fourier periodogram.

if they only fed on the ebb tide and only during daylight hours ($F = 0.17$; 1,81 df; $p > 0.3$; $r^2 = 0.01$).

Over the late spring and summer (May to August) there was a pattern of elevated catches at mid-tide level (Fig. 3b) over the lunar-tidal cycle. In September, maximum catches of age 0 plaice sampled daily at low water also occurred halfway between spring and neap tides (i.e., strongly associated with mid-lunar-tide levels) (Fig. 4). Mean catches during spring tides were significantly less than the mean catches at mid-levels ($t = 1.89$; 10 df; $p < 0.05$) and neap levels ($t = 2.07$; 8 df; $p < 0.05$). The presence of peak catches at mid-tide levels coincides with a 7-d period in the lunar cycle. There was no peak in catches when the mid-tide level occurred after midnight (0300-0400 h), which introduces a 10-d rhythm into the population activity pattern.

Check formation was variable within the population when examined over the entire summer. Some of the breakdown in synchrony is due to cumulative errors in dating increments. However, some of the change in pattern could be related to ontogenetic and seasonal shifts in activity patterns. The number of increments between checks was analyzed separately by fish size and date of capture. If the checks are caused by disruption of feeding, larger fish might be expected to show fewer checks, with longer intervals between checks. Over time, as fish are on the beach longer, they may become entrained to the lunar cycle, and the number of increments between checks would be expected to become more uniform within the population and less dependent on fish size. The data collected were not sufficient to test conclusively for either of these trends (Table 1).

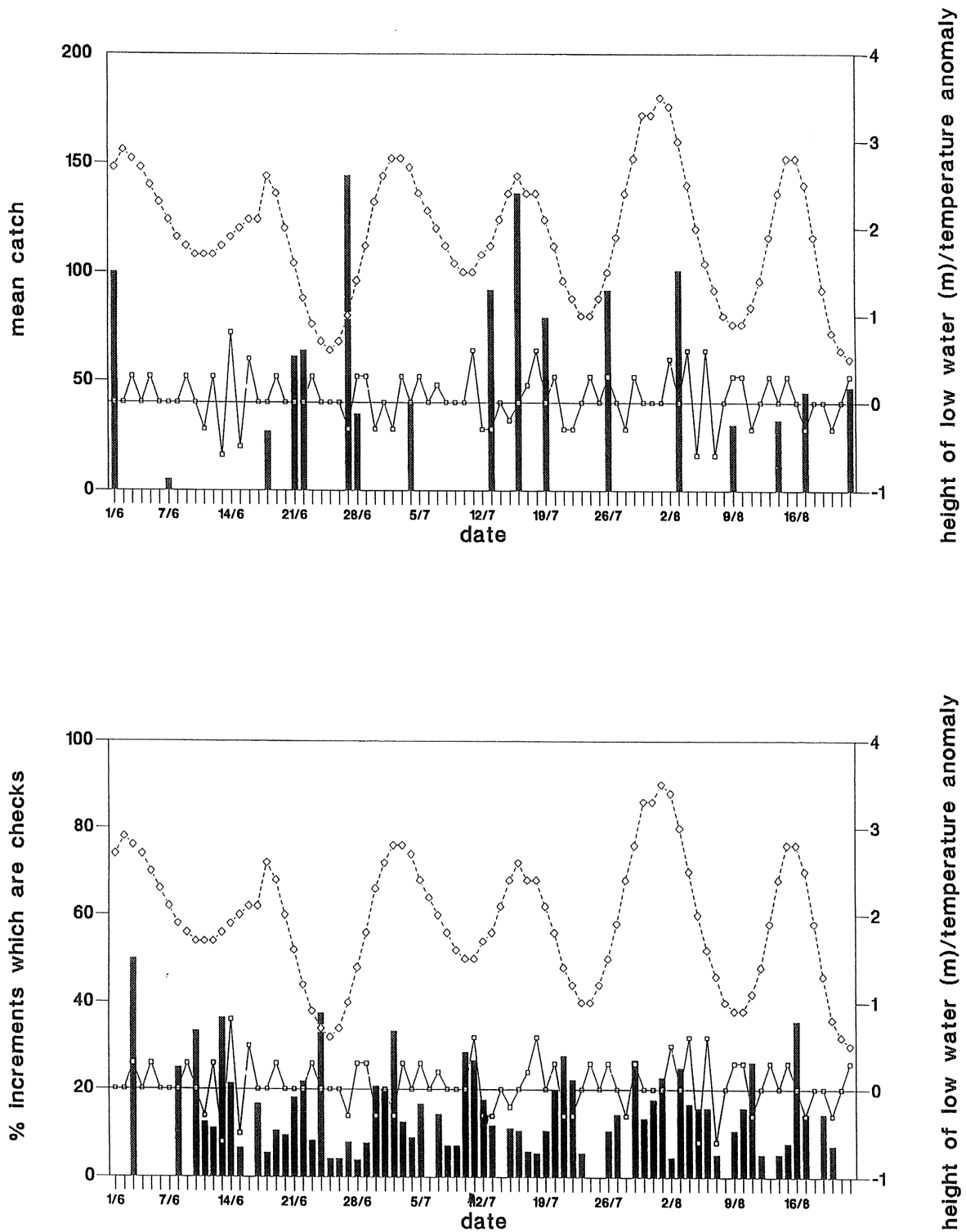


Fig. 3. The relationship between the date and (a) the percentage of all increments formed on each date that are checks on the otoliths of juvenile plaice (left axis) and (b) the mean catch of juvenile plaice in shallow water (left axis), with height of low water (dashed line, right axis) and temperature anomaly ($^{\circ}\text{C}$, solid line, right axis) between 1 June and 22 August 1990 in Port Erin Bay, Isle of Man.

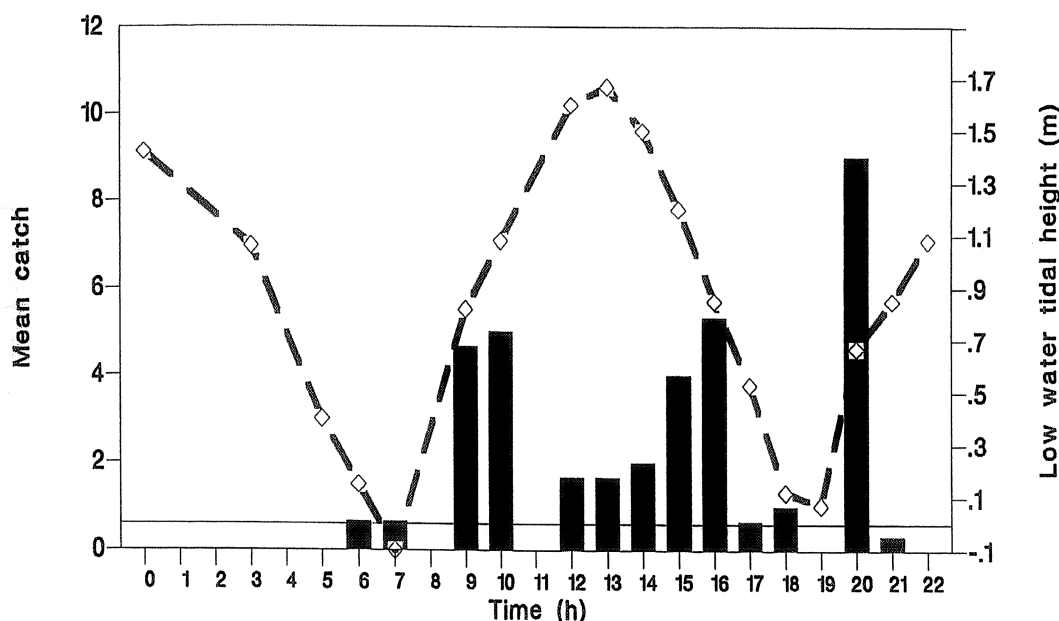


Fig. 4. Variation in mean numbers of juvenile plaice caught in Port Erin Bay, Isle of Man at low water in September 1992. Height of low water, in m above chart datum, is given as a dashed line.

Discussion

Spring tides (full and new moons) are obvious cues that could induce biweekly (14 d) checks on the otoliths of shallow-water fishes. These checks are presumed to be caused by the stress of large tidal excursions and large temperature fluctuations in shallow water, or by interference with feeding patterns (Campana 1984). When we matched the pattern of check formation in the plaice population with tidal cycles throughout the summer, it was clear that check formation was associated with both spring and neap tides. The pattern of check formation suggests that plaice in Port Erin Bay were exposed to stressful conditions at both extremes of the lunar tidal cycle.

The results of this study indicate that juvenile plaice in Port Erin Bay are not very active on spring and neap tides, and that there is a weekly rhythm to their activity. Berghahn and Karakiri (1990) suggest that plaice activity drops when the fish are stressed by starvation, high temperatures, or ultraviolet (UV) radiation, and that these stresses produce hyaline marks on the otoliths within 1-3 d. Hyaline zone formation did not disrupt daily increment formation under the conditions tested (Berghahn and Karakiri 1990).

Changing feeding behaviour and tidally controlled food availability could also act to interrupt otolith growth every 7 d. We expect that feeding patterns will match the activity cycles observed in this study and be higher at mid-tide levels of both daily and lunar-tidal cycles. During spring tides, juvenile plaice may be inactive and not feeding, or they may move up and down the beach beyond the range of habitats occupied by their preferred prey. During neaps, the fish may be relatively inactive or they may be prevented from reaching low subtidal or high intertidal prey.

Table 1. Relationships between number of increments between checks on the otoliths and fish length for juvenile plaice in Port Erin Bay, Isle of Man, over a number of different dates in 1990. All probabilities are greater than 0.10.

Date	n	Mean No. of Increments Between Checks	Range	SD	CV	r^2 , No. of Increments = Fish Length
4 July	30	7.70	3-11	2.32	0.30	-0.03
16-17 July	16	9.74	3-17	3.85	0.39	0.07
26 July & 2 August	14	7.92	3-11	2.46	0.31	-0.07
14 August	9	9.87	7-21	4.94	0.26	-0.14
22 August	12	8.69	4-12	2.17	0.25	0.12

because of the reduced tidal range. Lower activity at neap tides could also be caused by predation pressure, especially in Port Erin Bay where High Water Neap Tide (HWNT) occurs at dawn and dusk. This time period is often associated with influxes of predatory fish (e.g., gadoids) (Gibson 1973). These factors would reinforce the conditions producing otolith checks at both spring and neap extremes (i.e., weekly). These hypotheses can be tested by examining the distribution of prey and the distribution of juvenile plaice through the tidal cycle.

Check formation in Port Erin Bay plaice coincided with both peaks of the lunar-tidal cycle in an area with fairly even semidiurnal tides. Areas with small tidal ranges, or mixed tidal regimes, where lunar-tidal cycles are out of phase for morning and evening tides, might be expected to produce other patterns of check formation. Thus, starry flounder (Pacific Northwest) otoliths were found to have both 7-d and 14-d intervals between checks, though the biweekly pattern was dominant (Campana 1984).

The pattern of check formation was sometimes variable. The variation between individuals could be due to counting errors but equally to differential success in feeding. Therefore, the average values describe the population but not necessarily the individual. The number of increments between checks on the otolith may describe individual feeding success or activity pattern. Variations in check formation did not reflect the seasonal and ontogenetic changes in behaviour that were measured by beach seine experiments in Port Erin Bay (Nash et al. 1994). Juvenile plaice catches soon after settling (May) were not influenced by lunar cycles; however, by late summer (September) activity patterns were dominated by lunar-tidal cycles. The seasonal shift in activity may relate to changes in predator-prey relationships on the nursery grounds (increased numbers of predators—for example, gadoids—in the summer) or to increases in competition for food from other flatfish (Gibson 1973). The checks on the otoliths would suggest that an examination of the feeding activity and movements of juvenile plaice during the summer warrants further investigation.

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