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TIDAL MIGRATIONS IN THE FLOUNDER (*Platichthys flesus*)

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In estuaries, flounders move onto mudflats with the flood tide, feed extensively, and move off the flats as the tide recedes. Sizes of flounder visiting the mudflats of the Ythan estuary, Aberdeenshire, were estimated for a series of day and night high tides and it was found that smaller fish visited the flats more at night than during the day. Analysis of longer-term data sets of flounder catches on the Ythan revealed a regular cycle of feeding migrations at some times of the year, high catches alternating with low catches on consecutive tides. It is suggested that a combination of variation in tidal patterns and risk of avian predation may explain the observed patterns of feeding movements of flounders.

KEY WORDS Fish migrations, predation risk, tidal variation.

INTRODUCTION

Many species of fish undertake regular movements onto intertidal flats in strongly tidal areas, including the flounder (*Platichthys flesus*) and plaice (*Pleuronectes platessa*). The possible relationships between tidal migrations and feeding have been explored by Wolff *et al.* (1981) who suggested that flatfish in the estuarine Delta area of the Netherlands use at least two feeding strategies. The first, based on tidal migration, often involves swimming long distances from low tide channels onto the flats on the flood tide, returning to the channels on the ebb. The energy expenditure involved in these movements is presumably compensated for by the high abundance and biomass of invertebrate prey found on the flats compared to the channels. Fish leave the flats on the ebb tide because of the increased risks of desiccation, exposure to avian predators (Wolff *et al.* 1981) and a deteriorating physio-chemical environment (van der Veer and Bergman 1986). The second strategy is to remain in sublittoral areas and feed continuously. The costs of large-scale swimming are avoided, but the food resources in the estuarine sublittoral are usually meagre compared to those on the flats (Wolff and de Wolf 1977).

Different species of fish may adopt either strategy. For instance, migrations are well documented in plaice (e.g. Kuipers 1973, 1977, Gibson 1980, Wolff *et al.* 1981, van der Veer and Bergman 1986), and flounders (e.g. Summers 1980, Wirjoatmodjo and Pitcher 1984), but other flatfish such as dab (*Limanda limanda*) and sole (*Solea solea*) adopt the non-migratory strategy (Wolff *et al.* 1981). Tidal migrations also occur on more sandy beaches (Gibson 1972). The intertidal zone of such beaches may be relatively poor in invertebrate numbers and biomass compared to the shallow sublittoral and it seems unlikely that these onshore movements are driven purely by increased food availability. In such habitats increased risk of predation by other, larger fish may drive tidal migrations. Indeed, newly settled plaice in the Netherlands do not develop tidal rhythms until they are large enough to escape predation and they are restricted to the shallower areas of the flats (van der Veer and Berghman 1986).

An analysis of the relative costs and rewards of each of the strategies described above would prove rewarding, especially if the different behaviours occurred within the same population. Wolff *et al.* (1981) suggested that a study of the flounder (*P. flesus*) might be interesting in this respect, where non-migrating and migrating sections of the population might be found in the more brackish sections of estuaries, such as the Ythan estuary, Aberdeenshire, Scotland (Figure 1). The Ythan supports a large and well documented population of flounders (Summers 1979, 1980). Although there is no evidence of non-migratory individuals in the Ythan population there is some indication of intra-population differences in tidal movement patterns; different sizes of flounders may visit the mudflat depending on whether high tide occurs in darkness or daylight. Size specific costs of migration are unlikely to be related to energy demands for swimming in this population. Unlike the Netherlands, where fish may move several kilometres from the low water channel to the flats (Wolff *et al.* 1981) and swimming costs could be significant, the productive intertidal areas of the Ythan are only a few tens of metres from the channel. Although energy for swimming may not be a significant cost to the Ythan individuals, migrating flounders suffer increased exposure to piscivorous birds, such as herons (*Ardea cineraria*) and cormorants (*Phalacrocorax carbo*). Furthermore, the increased risk of predation associated with tidal migration is unlikely to be the same for all sizes of fish and will differ on night and day high tides, because herons and cormorants are diurnal predators on the Ythan. We therefore compared the size distributions of flounders visiting the intertidal areas of the Ythan on day and night high tides to test the hypothesis that any differences might be related to predation risk.

METHODS

Large numbers of flounders appear in the estuary in spring (April–May) and all year classes are present until late winter (December–January) when many fish move out of the estuary into the open sea. Fish feed extensively on the estuarine mudflats, especially in the section north of Waterside Bridge (Figure 1). The diet and feeding behaviour of the flounder has been described in detail by Summers (1980). Most of the prey (*Corophium volutator, Nereis diversicolor, Pygospio elegans* and *Hydrobia ulvae*) are infaunal and are taken by the fish biting the mudflat surface with its mouth, removing a volume of sediment and extracting food items by filtering the fine sediment particles through the gill rakes and out through the operculum. The holes created in the mudflat by this behaviour range

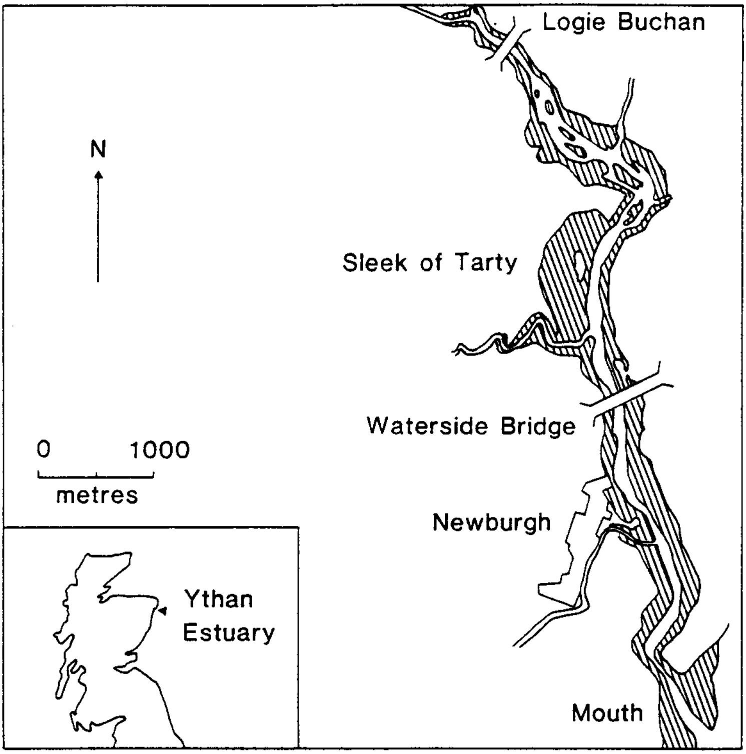

Figure 1 Location of the Ythan estuary and study sites.

from 1 to 4.5 cm in diameter and 0.5 to 1.5 cm deep and they remain visible at low tide. Sometimes the diamond-shaped outline of the fish accompanies the hole and this enabled us to determine the relationship between hole diameter and fish width, and hence fish length. By measuring hole diameters at low tide we could estimate the sizes of fish that visited the mudflat on the previous high tide. The number of holes is, of course, a function of both fish density and activity. We have assumed that activity is similar for all sizes of fish over the range examined and that hole density is a reasonable, if relative, estimate of fish density.

On each of the eight low tide periods between 3rd and 6th November 1983, eighteen 80 × 80 cm permanent quadrats were photographed on colour transparency film on the Sleek of Tarty mudflat (Figure 1). Predicted high tides over this period occurred from 1300 to 1500 h GMT (daylight) and 0100 to 0240 h GMT (night). The number and size of new holes formed after each high tide period were obtained for each quadrat by simultaneous projection of consecutive low tide photographs noting the appearance of new holes and the disappearance of others. Holes present on the first low tide period (3rd November) could have been formed on several high tides previously and they were omitted from the analyses. The frequency distribution of hole sizes was derived from the pooled data for the day and the night high tides and, knowing the relationship between hole size and fish length, the size frequency distribution of fish visiting the mudflats during the day and at night was determined.

The two most important piscivores on the Ythan, herons and cormorants, were censused by 35 surveys spread over different times of day and night between the 10th October and 14th November 1983 covering the entire estuary. Observations were also made of the feeding behaviour of herons, in particular the time taken to handle prey between catching and swallowing. This enabled an estimate of the most profitable sizes of flounders to herons. The size of flounders taken by herons was judged in relation to bill size. For fish size selection by cormorants we have relied on Ian Taylor's data for the Ythan reported in Summers (1979). Herons feed in shallow water and take only those fish moving on to the mudflats with the tide. Cormorants feed mainly in the channels and the deeper water covering the mudflats at high tide, but fish are likely to increase their risk of predation from cormorants by increasing their conspicuousness as they move through the deeper water to gain access to the shallower flats.

RESULTS

The relationship between flounder feeding hole diameter and fish width appears linear over the range examined (Figure 2). Measurements of flounder widths and lengths over this range indicated a ratio of 1:1.69. Our photographic data indicate a marked difference in the feeding activity of flounders during the day and night high tide periods (Figure 3). Almost five times as many holes were made at night ($n = 136$) as during the day ($n = 29$). There was also a difference in the size distribution of holes made during the night and in the day; smaller fish

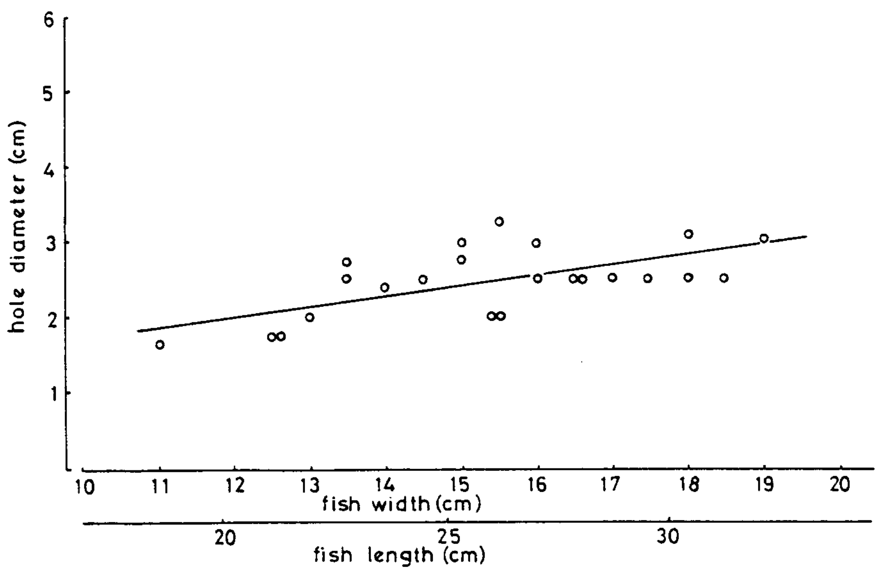

Figure 2 Relationship between flounder feeding hole diameter and fish size. Regression line: hole diameter = 0.67 + 0.21 fish width, $r = 0.57$, $n = 23$, $p < 0.01$.

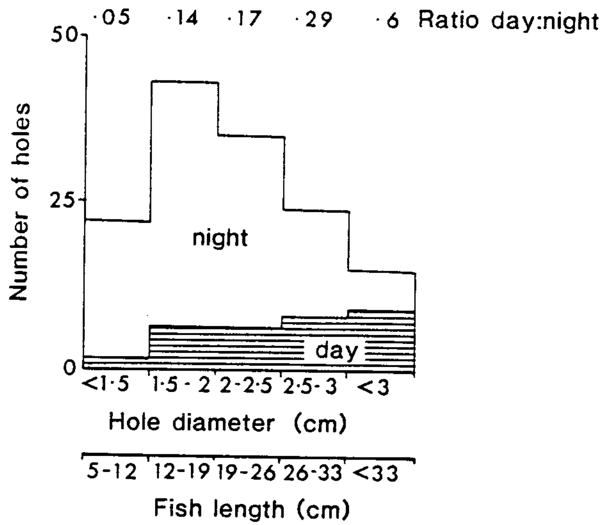

Figure 3 Size distribution of feeding holes created on night and day high tides, 3rd to 6th November 1983.

feeding more at night and larger fish predominating during the day ($X^2 = 13.11$, $p < 0.005$, Figure 3). The ratio of day holes to night holes progressively increases with fish size (Figure 3), indicating that the difference in feeding activity on day and night high tides becomes less pronounced in larger fish sizes.

Herons and cormorants were present on the estuary in all 27 day surveys but none was recorded on the 8 night surveys. An average of 3.8 (±0.65SE) herons and 36.5(±3.5SE) cormorants were recorded daily on the estuary over this period. The time taken for herons to handle flounders increased exponentially with fish size, fish larger than about 20 cm having very long handling times (Figure 4). Fish greater than about 25 cm in length could not be ingested and were rejected after a variable amount of time. Normally such large fish were not taken. Similarly, Summers (1979) estimated that cormorants could only ingest fish up to about 30 cm in length, with fish in the 25 to 30 cm class rarely taken (Figure

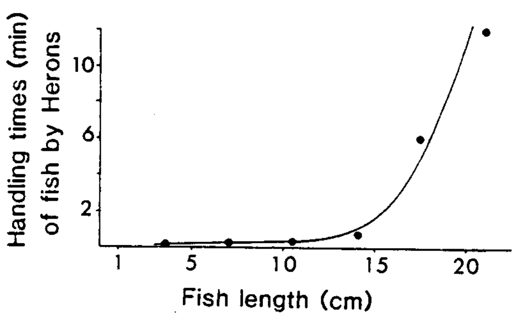

Figure 4 Time taken for herons to handle flounders of different sizes from the moment of capture to ingestion.

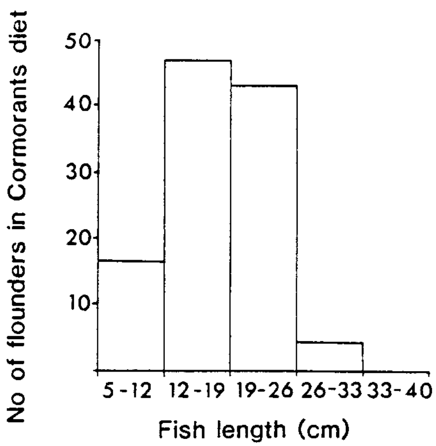

Figure 5 Size distribution of flounders caught by cormorants (after Summers, 1979).

5). Thus herons and cormorants probably select similar sizes of flounders, between 10 and 25 cm in length.

DISCUSSION

Our observations are consistent with the hypothesis that fish of the sizes most preferred by diurnal avian predators tended to visit the mudflats during the hours of darkness when they are least vulnerable. Herons and cormorants both select fish in the range 10 to 25 cm in length and it is these sizes that were common on the mudflat during the night high tides, whereas larger fish were recorded on both day and night high tides. In view of this close matching of flounder sizes most preferred by avian predators with the sizes of flounder visiting the flats it is unlikely that larger predatory fish could be responsible for these movements, since they would take smaller individuals than those recorded. As Wolff *et al.* (1981) predicted, the migratory behaviour of estuarine flounders seems to differ in different sections of the population.

Our observations were made over a relatively short period (5 days) during the winter when both herons and cormorants feed extensively in the estuary. It would be interesting to carry out a similar study in the summer when several consecutive high waters would occur in daylight at the latitude of the Ythan and smaller fish would be vulnerable to predators on every high tide during this period. This was outwith the scope of the present study, but we have been able to analyse a series of flounder catches from the early 1970's made by Summers. These data, which have not been previously published, were collected from stationary fish traps placed in the low intertidal that catch fish as they move off the flats with the ebb tide. Traps were visited on every consecutive tide for 16 days in April, 18 days in May and 18 days in June, and flounders counted. In April, the sizes of the fish were also measured.

Inspection of these data indicate that there is a marked alternating cycle of higher and lower fish catches over some periods consistent with our 1983 observations (Figures 6–8). This alternating cycle appears to break down briefly

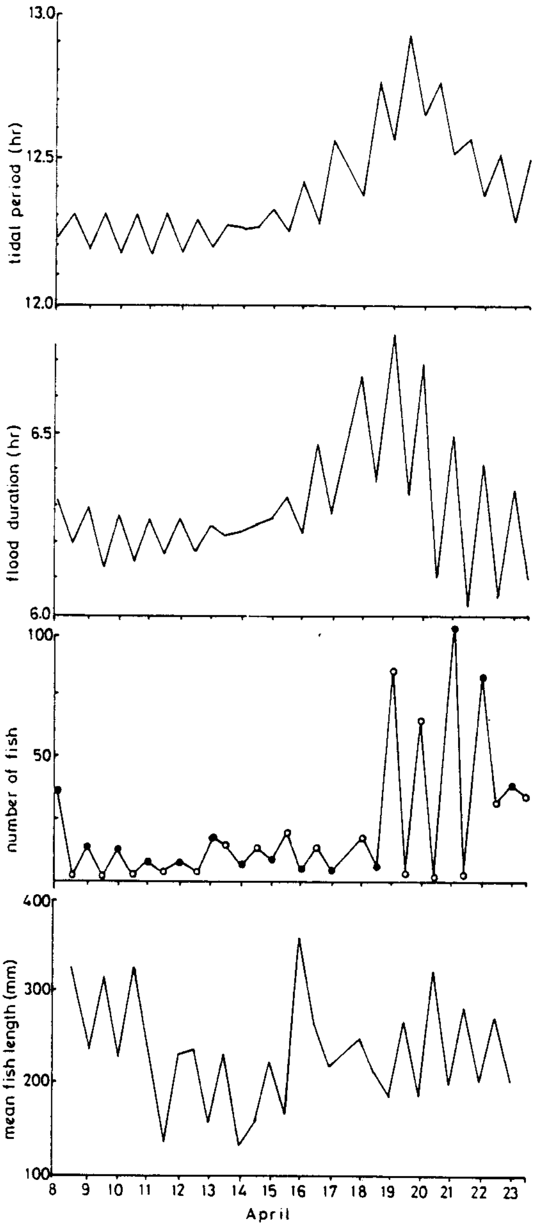

Figure 6 Tidal and fish catch data, Sleek of Tarty, April 1971. ● = night high tide; ○ = day high tide.

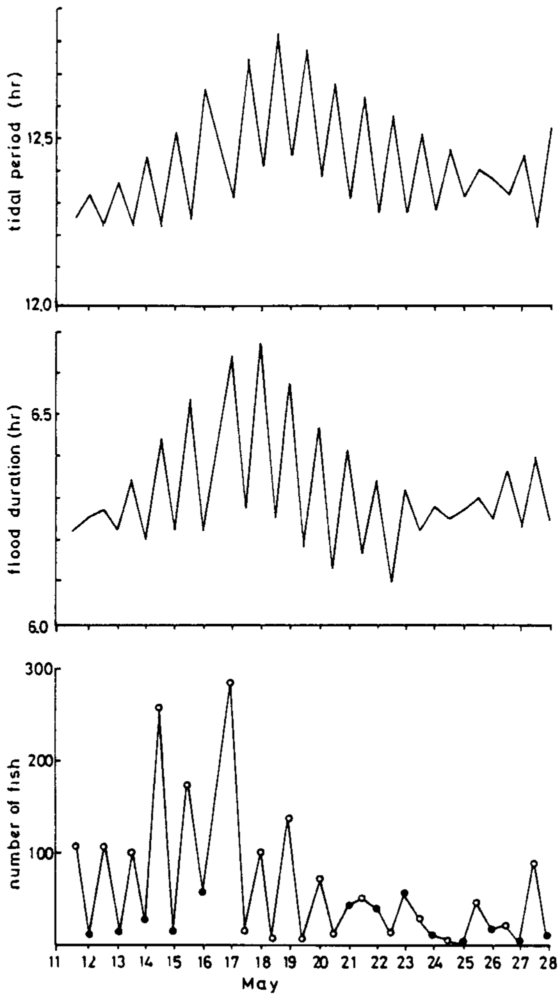

Figure 7 Tidal and fish catch data, Sleek of Tarty, May 1971.

on the 13th April (Figure 6), after the 20th May (Figure 7) and from 23rd June (Figure 8). We have further divided the catches into those where the previous high tide occurred mainly during the hours of darkness, or during the day. Since fish move onto the flats on the flood tide, our criterion for a "day" high tide was one where more than 3 hours of the flood tide period occurred before dusk and night high tides are defined as those where more than 3 hours of the flood tide period occurred before dawn. It can be seen that for some periods (e.g. 11th–17th May), considerably more fish were caught on daylight high tides, whilst in other periods (e.g. 18th–22nd April and 17–21st June) more were caught on night high tides (Figures 6–8). Moreover, high fish catches tend to be associated with a smaller mean size of individuals and low catches with larger fish, at least for April (Figure 6).

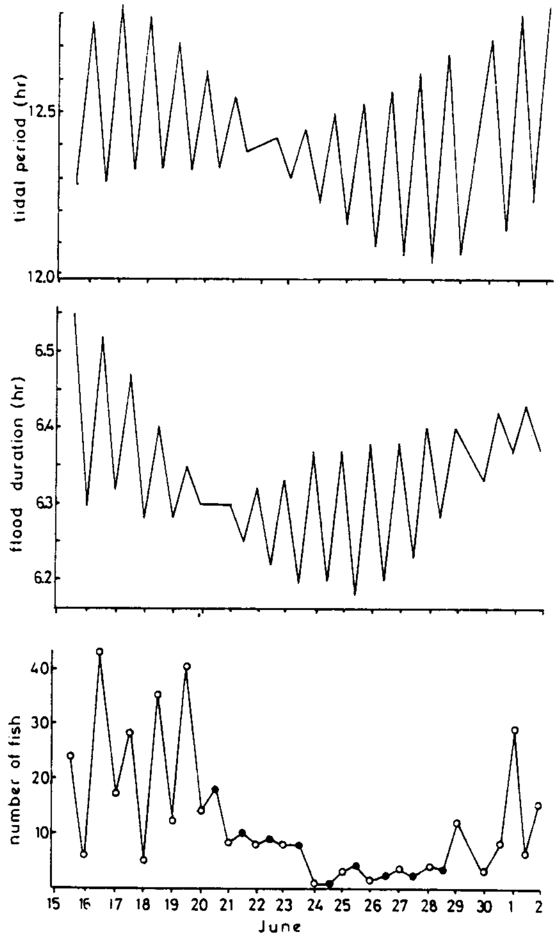

Figure 8 Tidal and fish catch data, Sleek of Tarty, June 1971.

This pattern of alternating high and low fish catches is intriguing and resembles that of the diurnal inequality of the tides. Tide tables for Aberdeen, the nearest standard port to the Ythan Estuary, were used to calculate the tidal period, as the time between successive low tides. This period is essentially that during which fish are visiting and leaving the mudflats. The tidal periods at Aberdeen are possibly altered within the estuary, but no accurate data were available for the Ythan itself. There is a pronounced daily alternation in tidal period (see Figures 6–8), the so-called "diurnal inequality" which results from the lunar declination cycle (see for example, Russell and Macmillan 1952). This cycle has a period of 13.66 days that produces greater and lesser ranges in the tidal period. The large diurnal inequalities observed, for example between 18th and 21st April 1971, are the result of the moon passing over the earth's tropics and will hence be referred to as the tropic tides whereas the small diurnal inequalities seen, for example between 13th and 16th April 1971, are the result of the moon passing over the equator and hence will be referred to as the equatorial tides (Barnwell 1976). These tropic tides are characterised by long tidal periods and asymmetrical tides, i.e. the ebb and flood durations are not equal. The flood duration is longer than the ebb duration during the shorter of the two daily tidal periods and vice versa. Equatorial tides are characterised by short tidal periods and symmetrical tides where ebb and flood durations are approximately equal.

Comparisons of the tropic/equatorial tidal cycle with the fish catch cycle reveals that the largest fluctuations in fish catches occur during tropic tides and the minimal or disrupted diurnal variation in fish catches occur during equatorial tides (Figures 6–8). Also larger fish catches occur when there are longer flood durations with especially high catches after a flood duration greater than about 6.4 hours (Figure 9). The relationship between ebb duration and fish catch is less clear (Figure 9) because both high and low catches occur after an ebb duration of less than about 6 hours.

It was noted earlier that a greater proportion of fish in high catches were small individuals (10–25 cm), implying that the risk of avian predation may be reduced during these tides with an unusually long flood duration, or perhaps that an increased availability of food to flounders during these tides overrides the risk of avian predation. The Ythan flounder feed predominantly on the amphipod

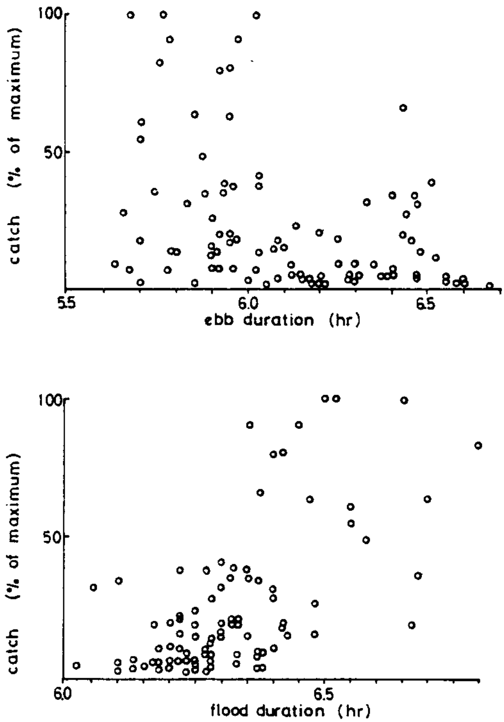

Figure 9 Relationship between fish catches and flood and ebb durations, Sleek of Tarty, 1971. Catches are expressed as a percentage of the maximum recorded in that month so that relative changes in catch during April, May and June are comparable.

Corophium volutator (Summers 1980) which, in the laboratory, displays an endogenous circatidal rhythm (Holmstrom and Morgan 1983, Harris and Morgan 1986). If the tidally synchronised activity of *Corophium* results in their increased availability during unusually long flood tides, this could explain the high abundance of flounders recorded on the mudflats at such times. In the absence of corroborative field data, however, such conclusions must be guarded.

The tidal hypothesis outlined above has considerable bearing on our 1983 observations. These were made during a period of equatorial tides when the alternation in tidal period is low and no unusually high fish catches would be expected. According to our tidal hypothesis, higher fish catches would be anticipated after longer flood durations, and during the 1983 experiments these were in daylight. In fact, the highest catches were at night, the result expected if risk of avian predation determines tidal migration.

Both the tidal and predation hypotheses could in fact be correct and may interact as follows. During equatorial tides, when flood an ebb durations do not vary greatly, fish catches would be expected to be greater after the longer flood durations *unless* these were in daylight in which case the risk of avian predation might override the tidal effect and lead to reduced fish catches. During tropic tides, the tidal influence overrides the risk of predation and high catches are expected after long flood durations *irrespective* of whether high tide occurs in daylight or darkness. According to the predation hypothesis, a greater proportion of smaller fish would be expected to visit the mudflat on night tides. This would be true during equatorial tides, but only true during tropic tides if the night tides were also those with the long flood duration. Examination of Figure 6 shows that smaller fish were caught during the night, both for equatorial and tropic tides, when the long duration floods were, coincidentally, at night. It is important to note, however, that during April's tropic tides smaller fish were captured on daylight tides at a time when all successive tides occured in daylight. This supports the view that the tidal influence outweighs the predation effect during the tropic tides. It would be of interest to further examine the interaction of these hypotheses by investigating fish movements when long flood durations coincide with daylight over a complete tropic/equatorial tidal cycle.

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