

Foraging time strategy of small juvenile plaice: a laboratory study of diel and tidal behaviour patterns with *Artemia* prey and shrimp predators

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ABSTRACT: The natural pattern over time of foraging and migration in juvenile plaice *Pleuronectes platessa* has evolved to enhance the survival of the fish. It is a product of endogenous rhythms and direct responses to biological and physical conditions, including their predators and prey. This study aimed to determine the relative roles of these influences through experimental manipulation of the physical and biological conditions. Infrared television cameras and illumination were used to observe freshly caught juvenile plaice in the light and dark over 24 h periods in arena tanks. Single *Crangon crangon* and *Artemia* nauplii were added to these tanks as predators and food respectively. The behaviour of juvenile plaice in the light was dominated by swimming on the sand surface, with little activity on the bottom during darkness. Most swimming on the bottom occurred 0 to 2 h after the expected time of high water. Activity in darkness largely comprised swimming in the water column or at the surface, with most swimming seen 2 to 4 h after high water. Off-bottom swimming was also seen at this time in the light. *Artemia* as prey reduced swimming on the bottom during the light period, but had no effect on off-bottom activity. The presence of single *C. crangon* in the tank had no discernible effect on behaviour. Different functions are proposed for pelagic and benthic swimming. Both may be used for migration while pelagic swimming may avoid predators on the bottom at night. Benthic swimming may be used for foraging.

KEY WORDS: *Pleuronectes platessa* · Endogenous rhythms · Feeding · Predation risk · *Crangon crangon*

INTRODUCTION

Juvenile plaice *Pleuronectes platessa* live in an environment dominated by tidal changes in habitat availability (Kuipers 1973). Changes in light levels between day and night strongly influence their ability, using vision, to detect and be detected by their predators (Ansell & Gibson 1993) and to detect and capture their prey (Blaxter 1968); juvenile plaice mostly feed in daylight (Edwards & Steele 1968, Thijssen et al. 1974, Lockwood 1980). Soon after settlement juvenile plaice develop patterns of migration (van der Veer & Bergman 1986), partly driven by endogenous rhythms (Gibson 1973a, 1975), which allow them to exploit their complex and variable habitat to best advantage (Burrows 1994).

The migration of juvenile plaice into the intertidal zone with rising tides is well documented (Edwards & Steele 1968, Berghahn 1983, Ansell & Gibson 1990) and apparently ubiquitous, occurring over a range of

habitats from sandy beaches on exposed coasts (Gibson 1973a) to sheltered intertidal sandflats (Kuipers 1973). There may also be a diurnal positional change. In some habitats plaice move into shallower water in the dark hours (Burrows et al. 1994a), while in others the extent of tidal migration is reduced in the dark (Berghahn 1986). Since migration is energetically costly, there are likely to be strong selective pressures for this activity. Among those factors suggested are: maintenance of position in a moving physiologically optimal zone (Rountree & Able 1992), avoidance of competition and replenishment of food resources, avoidance of predators (Ansell & Gibson 1990), the benefits of finding temporarily available food (Wolff et al. 1981, Berghahn 1987), or a combination of the last two (Burrows 1994).

Migration patterns of juvenile plaice have a direct parallel in the vertical migrations of pelagic fishes and zooplankton (e.g. Forward 1988, Frost & Bollens 1992). Current explanations of these migrations are based on

their utility as feeding and predator-avoidance strategies (Clark & Levy 1988) and in selective current transport (Hill 1991, Metcalfe et al. 1991).

When removed from their natural habitat and maintained in constant laboratory conditions, juvenile plaice continue to show cycles of activity similar to those seen in the field (Gibson 1973b, 1975), albeit without, as yet, a detectable directional component. The endogenous rhythm which produces these changes is at the centre of the mechanism which produces the appropriate patterns of feeding, migration and other behaviour.

The aim of this study is to elucidate the function of observed patterns of movement and behaviour in natural conditions (Gibson 1980, Burrows et al. 1994a). Since juvenile plaice normally range over many hundreds of metres in their natural habitat, observations are not possible on individuals over long periods in nature, nor can their environment be directly manipulated. In this study, therefore, long-term behaviour was observed in experimental sand-bottomed tanks ('arenas') in the laboratory. The possible effects of food availability and the presence of predators on behaviour were examined by addition of these items to the experimental arenas to determine their effects on the expression of endogenously controlled behaviour in freshly caught fish. Newly hatched *Artemia* nauplii were used as food, since this is an organism on which the juvenile plaice (<30 mm in length) used here readily feed (Riley 1966, Wyatt 1972), while single brown shrimps *Crangon crangon*, the major cause of mortality in juvenile plaice of this size in the Wadden Sea (van der Veer & Bergman 1987), were used as predators.

MATERIALS AND METHODS

Materials. Juvenile plaice and the brown shrimp *Crangon crangon* (hereafter '*Crangon*') were collected from Dunstaffnage Bay, a sheltered area of muddy sand facing northeast, some 5 km north of Oban on the west coast of Scotland (56° 30' N, 5° 20' W). On 20 day-time low tides between 26 April and 20 May 1993, 2 plaice were caught using a hand-pulled 0.5 m net in 0.5 to 1.0 m of water. These plaice ranged in size from 14 to 35 mm in total length, with a mean total length of 24 mm. On alternate sampling occasions, 2 large *Crangon* were also selected from those caught in the net to serve as predators in the experimental arenas. They were from 38 to 54 mm in total length, with a mean of 45 mm.

Newly hatched *Artemia* nauplii (AF grade from Artemia Systems NV, Baasrode, Belgium) were used as prey for the juvenile plaice.

Experimental arenas. Two glass aquarium tanks (60 × 29 × 37 cm) were used for experimental arenas. There were filled to a depth of 2 cm with coarsely sieved (2 mm mesh) and washed wind-blown sand from a local sandy beach and a water depth of 30 cm. The tanks were illuminated from above during the light period with 4 overhead 65 W fluorescent tubes and continuously from one side with single 300 W underwater lamps in a cooling bath with flowing water. Infrared filters with 740 nm minimum transmission wavelength cutting out light visible to the fish (Blaxter 1969) were fitted to the underwater lamps to provide illumination for video recording in the light and dark periods.

The behaviour of the juvenile plaice in each arena was monitored using a black and white video camera also fitted with an infrared filter, positioned to give a full lateral view of the inside of the aquarium tank from its end. These video images were recorded on time-lapse video tape with recorders (Panasonic AG 6024) set at 3.6 frames s⁻¹. The view of each tank was sufficient to allow the plaice and *Crangon* to be observed at all times.

The water temperature in the tanks was controlled by placing them in an air-conditioned room with an air temperature of 8°C. Temperatures in the tanks were between 10.4 and 12.6°C, with a mean of 11.7°C, and were thus raised slightly by the heating effect of the infrared illumination.

Experimental protocol. The *Artemia* nauplii were added in excess to one of the arena tanks (with food treatment, +F). These were replaced every other day by complete siphoning and refilling of the tanks. Single juvenile plaice were added to the arenas within 30 min of collection and their behaviour was videotaped for the next 24 h. On alternate days a single *Crangon* was also added to each tank to serve as a predator (with predator treatment, +P). At the end of each experimental period the fish and *Crangon* were removed, killed with an overdose of anaesthetic (Benzocaine) and preserved in 4% formalin in sea water. Soon after preservation the juvenile plaice were measured and their stomachs removed and dissected. The number of *Artemia* nauplii in the stomachs of those from the with food (+F) treatment was counted as a measure of feeding success.

The arenas were lit in the visible spectrum over a fixed 16 h:8 h light:dark cycle, with lights on between 04:00 and 20:00 h, approximating the natural cycle at the time of the experiment.

Analysis of video recordings. The behaviour of the juvenile plaice was scored during the first 10 min of each hour. Six different elements of behaviour were recognised, similar to those observed in natural conditions (Gibson 1980): (1) Swim, a movement on or close

to the bottom; (2) Rise, a completely pelagic swimming movement; (3) Crawl, when the plaice settled and moved on the glass sides of the tank; (4) Bury; (5) Encounter with the *Crangon* predator; and (6) Bite. The time and duration of these elements were logged with a PC-based keyboard event recorder which registered the video timecode from a video timecode reader (IMP Electronics V90020A).

The *Crangon* was assigned as active if it moved during the 10 min observation period.

RESULTS

Frequency of types of behaviour

The most frequent element of behaviour was short-duration swimming near the bottom (Swim 84.6%). Off-bottom activity, either pelagic swimming (Rise 9.5%) or crawling on the sides of the aquarium tank (Crawl 5.7%), formed the majority of the remaining events. Burying, predator encounters and observed bites were very rare (0.2%).

The juvenile plaice were in motion for 2 to 5% of the total time observed in each hour in the light, with the remaining 95 to 98% spent motionless on the bottom. In the dark, the plaice were typically active for 10 to 35% of the time, especially in the 4 h after the expected time of high water.

Temporal patterns of behaviour in juvenile plaice

The frequencies of the 3 most common elements of behaviour (Swim, Rise, Crawl) per 10 min observation period were subjected to analysis of variance (ANOVA) to look for significant differences among times of day, states of the tide and in the presence and absence of a *Crangon* predator and *Artemia* prey. Frequencies (f) were transformed to $\log_{10}(1+f)$ before analysis. The effects of the presence of a *Crangon* predator and *Artemia* prey were tested by comparing mean frequencies for individual fish within these treatments (see Table 1, Fig. 1). The remaining effects, time, light conditions and the interdependence of treatment effects with time and light, were tested using the hourly frequencies of events in individual trials.

Two ANOVA designs were used. In the first the frequency of behavioural elements was analysed with respect to the time relative to the first high water after capture and whether light or dark. In the second, the frequency of behavioural elements was analysed relative to the time of day.

Benthic swimming movements showed a tidal cycle of occurrence (Fig. 1a; Table 1a; HW1HR effect). In

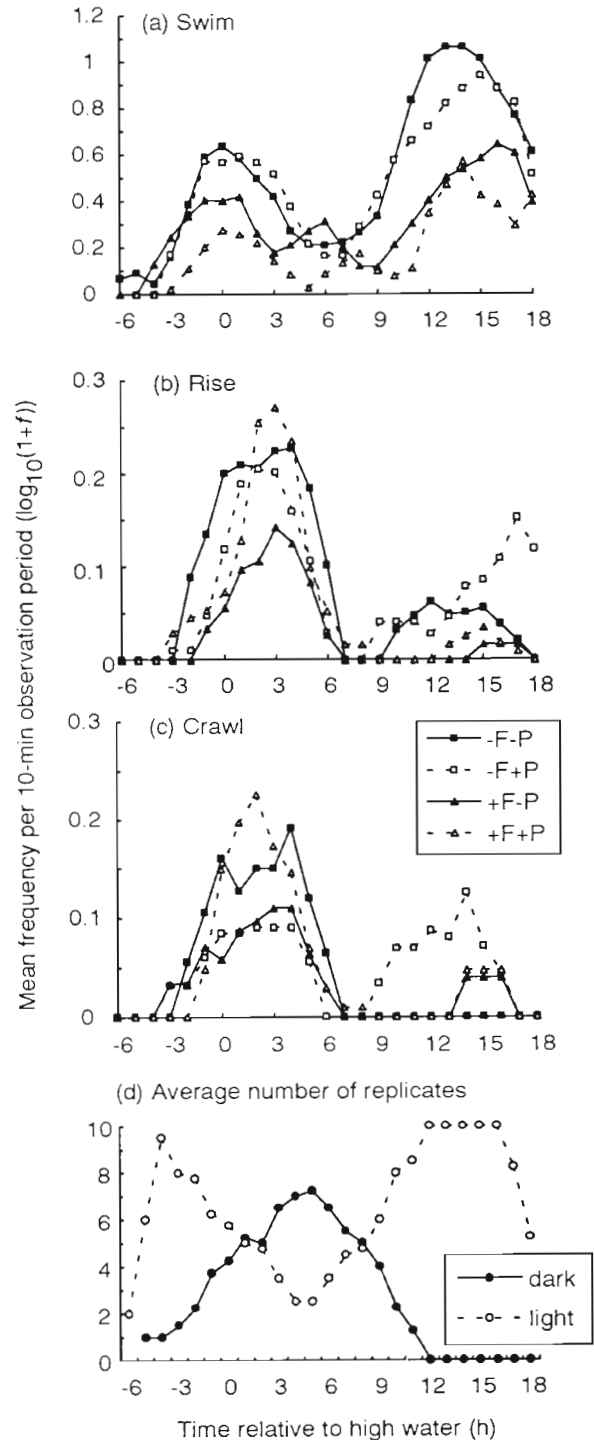


Fig. 1. *Pleuronectes platessa*. Temporal patterns of occurrence of (a) benthic swimming, (b) pelagic swimming, and (c) crawling on the sides of the tank, relative to the expected time of the first high water after capture (0). Each line is a 3 h moving average of the frequency [$\log_{10}(1+f)$ transformed] of events per 10 min observation period per hour, averaged over 10 trials per treatment (-F-P, -F+P, +F-P, +F+P). The lowest plot (d) shows the average number of replicate observations per treatment for each hour occurring in the light (04:00 h to 20:00 h) and in the dark (20:00 to 04:00 h).

Table 1 *Pleuronectes platessa*. Summary of analyses of variance of $\log_{10}(1 + f)$ transformed frequencies of benthic swimming (Swim), pelagic swimming (Rise), and crawling on the sides of the tanks (Crawl). In the top half of the table (a) frequencies were analysed with respect to the hour relative to the time of the first high water (HW1HR: -2 to +11), light conditions (LIGHT: light, dark), and the presence of *Artemia* food (FOOD: with, without) and a *Crangon* predator (PRED: with, without). Main effects of food and a predator were tested over variation between individual fish, while other effects were tested over the residual variation. In the bottom half of the table (b) frequencies were analysed relative to the hour of the day (DHOURL: 0 to 23)

Source	df	Swim p > F	Rise p > F	Crawl p > F
(a) Light conditions and time relative to high water				
PRED	1	0.5560 ns	0.9052 ns	0.9125 ns
FOOD	1	0.0297 *	0.3505 ns	0.6998 ns
PRED × FOOD	1	0.4015 ns	0.4324 ns	0.4729 ns
Fish in trials within treatments	36	0.0001 ***	0.0001 ***	0.0001 ***
HW1HR	12	0.0565 ns	0.0026 **	0.0088 **
PRED × HW1HR	12	0.4326 ns	0.8224 ns	0.8145 ns
FOOD × HW1HR	12	0.7164 ns	0.8261 ns	0.9927 ns
PRED × FOOD × HW1HR	12	0.8839 ns	0.9391 ns	0.8808 ns
LIGHT	1	0.0001 ***	0.0013 **	0.0110 *
PRED × LIGHT	1	0.1717 ns	0.3047 ns	0.0973 ns
FOOD × LIGHT	1	0.0001 ***	0.3978 ns	0.3538 ns
PRED × FOOD × LIGHT	1	0.8280 ns	0.5090 ns	0.5173 ns
HW1HR × LIGHT	12	0.7553 ns	0.1431 ns	0.6430 ns
FOOD × HW1HR × LIGHT	12	0.8940 ns	0.6108 ns	0.8963 ns
PRED × HW1HR × LIGHT	12	0.5592 ns	0.6090 ns	0.7291 ns
(b) Time of day				
PRED	1	0.3684 ns	0.5857 ns	0.6497 ns
FOOD	1	0.0082 **	0.1717 ns	0.6858 ns
PRED × FOOD	1	0.6310 ns	0.6434 ns	0.8875 ns
Fish in trials within treatments	36	0.0001 ***	0.0001 ***	0.0001 ***
DHOURL	23	0.0001 ***	0.0001 ***	0.0001 ***
PRED × DHOURL	23	0.8531 ns	0.7175 ns	0.6850 ns
FOOD × DHOURL	23	0.0078 ***	0.7931 ns	0.3338 ns
PRED × FOOD × DHOURL	23	0.9596 ns	0.6445 ns	0.7731 ns
ns: not significant, p > 0.05; *0.01 < p < 0.05; **0.001 < p < 0.01; ***p < 0.001				

Table 2 *Crangon crangon*. Analyses of variance of activity per 10 min observation period per hour: (a) relative to light conditions (LIGHT: light, dark), the time relative to high water (HW1HR: -6 to +18), and the presence of food (FOOD: with, without); and (b) relative to the hour of the day (DHOURL: 0 to 23). The overall effect of the presence of food was tested over the variation in activity between individual *Crangon* within each treatment. Significance indicated as in Table 1

Source	df	Type III SS	MS	F-value	p > F
(a) Light conditions and time relative to high water					
FOOD	1	0.434	0.434	1.24	0.2798 ns
<i>Crangon</i> in trials within treatments	18	6.297	0.350	2.64	0.0003 ***
HW1HR	25	12.554	0.502	3.79	0.0001 ***
FOOD × HW1HR	25	2.529	0.101	0.76	0.7884 ns
LIGHT	1	5.937	5.937	44.82	0.0001 ***
FOOD × LIGHT	1	0.168	0.168	1.27	0.2602 ns
Error	394	52.197	0.132		
(b) Time of day					
FOOD	1	0.392	0.392	1.08	0.3120 ns
<i>Crangon</i> in trials within treatments	18	6.522	0.362	2.36	0.0015 ***
DHOURL	23	16.575	0.721	4.69	0.0001 ***
FOOD × DHOURL	23	3.713	0.161	1.05	0.4008 ns
Error	400	61.506	0.154		

each treatment a first maximum frequency occurred at or 1 h after the expected time of the first high water after capture. A second larger peak was seen around 14 to 16 h after the first high water. The second peak was larger, being entirely in the light (Fig. 1d) since most benthic swimming was seen in the light with very little in the dark (Table 1a: LIGHT effect; Fig. 2a). The

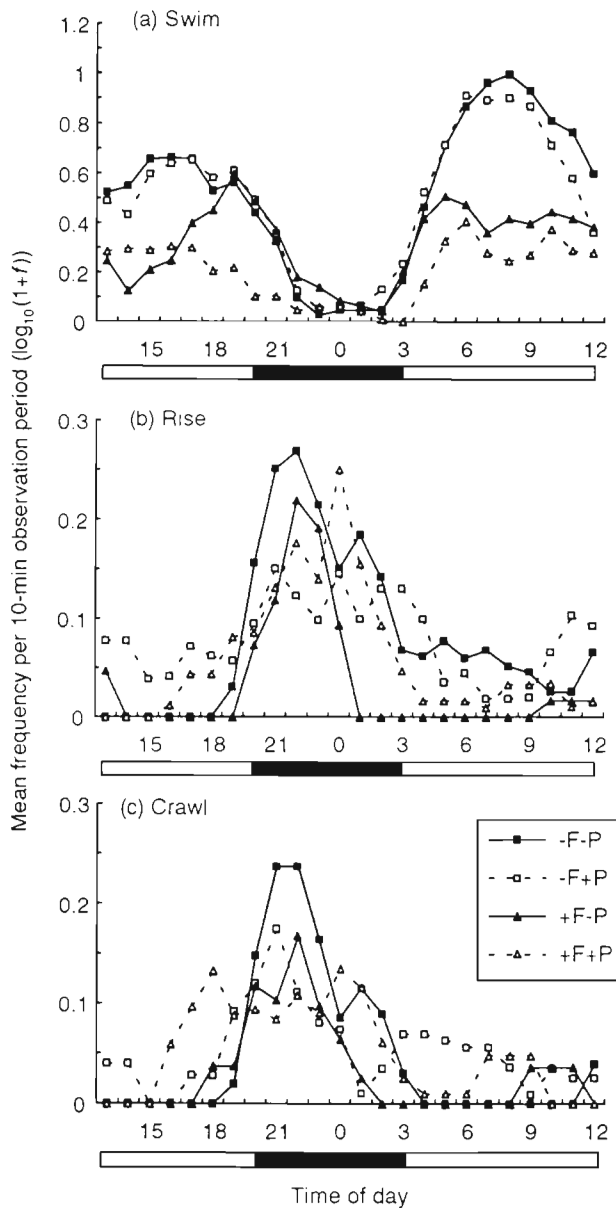


Fig. 2. *Pleuronectes platessa*. Temporal patterns of occurrence of (a) benthic swimming, (b) pelagic swimming, and (c) crawling on the sides of the tank, relative to the time of day. Each line is a 3 h moving average of the frequency [$\log_{10}(1+f)$ transformed] of events per 10 min observation period per hour, averaged over 10 trials per treatment (-F-P, -F+P, +F-P, +F+P). The bar beneath each plot shows the dark and light periods

fish showed more benthic swimming in the absence of food but not at the expected time of low water (+6 h; Table 1a: FOOD \times HW1HR effect). While the presence of food reduced benthic swimming in the light, it had little effect on the much less frequent benthic activity in the dark (FOOD \times LIGHT effect). The effects of light on benthic movements were most strongly evident in the patterns relative to time of day (Fig. 2a; Table 1b: D HOUR). The effects of the presence of food were most evident at the beginning of the light period (Fig. 2a: 05:00 to 12:00 h; Table 1b: FOOD \times D HOUR effect).

Pelagic swimming and crawling on the sides of the tank showed very similar patterns of occurrence among treatments, times of day and states of the tide (compare Fig. 1b with 1c, and Fig. 2b with 2c). Off-bottom activity was also strongly related to the tidal cycle. Crawls and Rises reached peak frequencies 2 to 4 h after the expected time of the first high water, and some 12 h later, 14 to 17 h after the first high water (Fig. 1b, c; Table 1a: Rise and Crawl HW1HR effect). Both these kinds of behaviour were much more evident in the dark (Table 1a: LIGHT effect; Table 1b: D HOUR effect). The presence of food did not affect the amount of off-bottom activity (Table 1: Rise and Crawl, all FOOD effects not significant, $p > 0.05$), nor did the presence of the *Crangon* predator affect pelagic swimming. Juvenile plaice did, however, spend more time crawling on the tank walls in the light in the presence of the *Crangon* (Fig. 1c; Table 1a: PRED \times LIGHT effect).

Temporal patterns of activity in *Crangon*

The individual *Crangon* were most active 2 to 3 h after the expected time of the first high water in both light and dark and both with and without live *Artemia* as food. A second smaller activity peak was also seen in the light 12 h later (Fig. 3a). Activity levels were much greater in the dark (Tables 2a, b: LIGHT, D HOUR effects; Fig. 3a, b) but were not significantly altered by the presence of food.

Feeding success in juvenile plaice

Stomachs of experimental plaice that had fed contained between 126 and 890 *Artemia* nauplii in the +F treatment. Two fish in the -F treatment had 2 to 3 barnacle cyprids in the stomach. The presence of a *Crangon* predator did not affect the number of *Artemia* found in the stomachs of fish in the +F treatment (Kruskal-Wallis non-parametric 1-way ANOVA: $H = 0.344$, $df = 1$, $p = 0.558$).

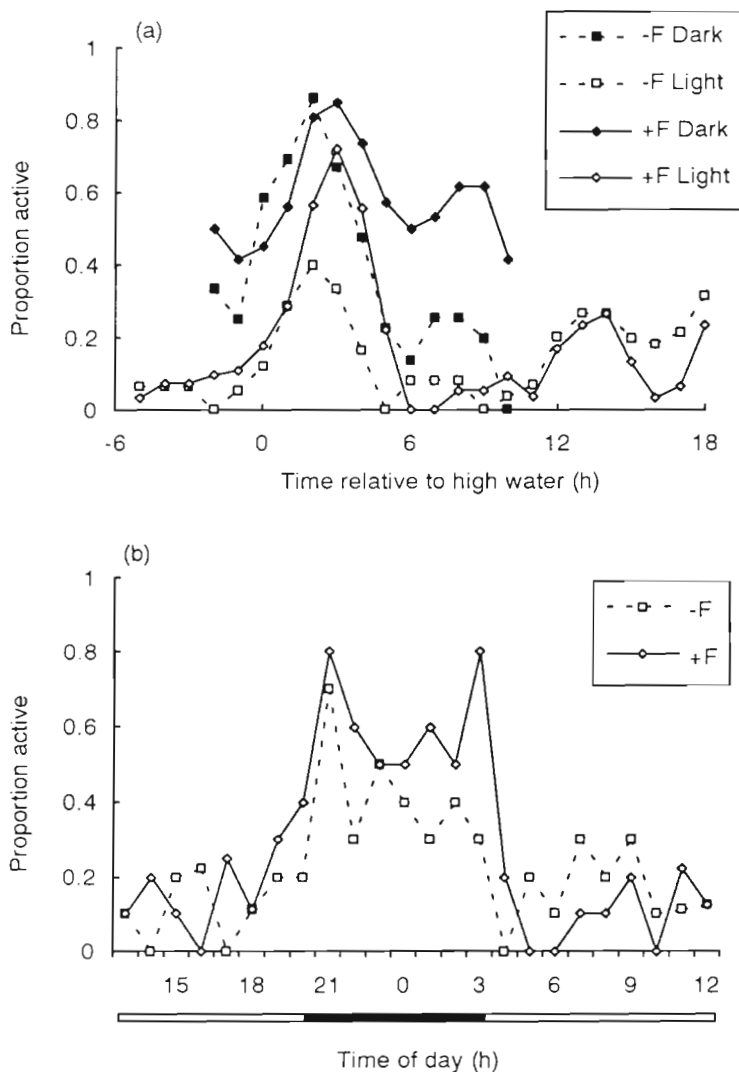


Fig. 3. Activity in the *Crangon crangon* predators (a) relative to the expected time of the first high water in the light and dark, and with and without food, (b) relative to the time of day. Each point is the proportion of the total number of trials in which the *Crangon* showed some movement in the 10 min observation period

Variation in behaviour among individuals

Considerable differences existed between individual fish in benthic and pelagic swimming and crawling on the tank walls. This variation was statistically significant (Table 1). Similar significant variation was also seen among the individual *Crangon* (Table 2). Correlations (35 in total; Table 3) were calculated between these individual measures of behaviour, including the number of *Artemia* in fish stomachs, and the experimental temperature, the sizes of fish and *Crangon* used, and the activity level of the *Crangon* (as the proportion of time spent active). The Bonferroni adjust-

ment to the type I error probability (α) for $k = 35$ tests requires probabilities of correlation coefficients to be less than $(\alpha/k) = 0.0014$ for significance at $\alpha = 0.05$. Significant correlations were found between pelagic swimming and benthic swimming, and between pelagic swimming and movement on the sides of the tank, suggesting differences in overall activity among fish. Total benthic swimming was also significantly positively correlated with plaice size. Neither the number of *Artemia* in plaice stomachs nor shrimp size or activity was correlated with other variables. Feeding rate and *Crangon* activity were, however, positively correlated together.

DISCUSSION

The behaviour of small (15 to 30 mm) 0-group plaice is strongly affected by light conditions and rhythmically synchronised with the tidal cycle. Swimming just above the surface of the sediment (benthic swimming) is largely restricted to the light period and is most frequent 0 to 2 h after the time of predicted high water. Swimming in the water column (pelagic swimming) is much more frequent in darkness and reaches a maximum frequency 2 to 4 h after predicted high water in both light and darkness. Excess *Artemia* nauplii as prey reduces the amount of benthic swimming in the light, while the presence of a *Crangon* predator has apparently no effect on behaviour. Pelagic swimming is not affected by the presence of either food or a predator.

The activity pattern of the *Crangon* predators was similar to that observed by Al-Adhub & Naylor (1975), with greater activity around the time of high water and in the dark. The lack of effect of *Crangon* on the behaviour of these fishes is in contrast with the strong inhibitory effect of juvenile cod *Gadus morhua* on benthic swimming and feeding success of larger juvenile plaice (45 to 90 mm total length; Burrows et al. 1994b). Unlike cod, the shrimps were inactive for much of the time during these experiments, and when they were active the plaice were generally inactive. This resulted in a greatly reduced encounter rate for the plaice with their predators (5 encounters in 160 h observation; cf. 133 encounters with cod in the same period). The lack of direct effect of the presence of a predator may reflect this low encounter rate. The reduced activity of the plaice in darkness may alternatively be a stereotypical

Table 3. Kendall's rank correlations among variables measured for each trial. Symbols and abbreviations include: τ , Kendall's rank correlation coefficient; p, probability of correlation; n, number of trials; TL, plaice *Pleuronectes platessa* total length; SL, plaice standard length; CL, *Crangon crangon* carapace length; CTL, *C. crangon* total length

		Temp. (°C)	Plaice size		<i>Crangon</i> size		No. of	Rise	Swim	Crawl
			TL	SL	CL	CTL	<i>Artemia</i>			
No. of <i>Artemia</i>	τ	-0.0596	0.1603	0.1223	-0.2713	-0.3508	-	-	-	-
	p	0.6741	0.2590	0.3895	0.2623	0.1334				
	n	31	31	31	13	13				
Rise (mean frequency)	τ	0.1031	0.2676	0.3094	0.0406	-0.0222	-0.0448	-	-	-
	p	0.3813	0.0302	0.0126	0.8362	0.9051	0.7554			
	n	40	37	37	18	18	31			
Swim	τ	0.1058	0.4051	0.4422	0.2154	0.0350	-0.1380	0.3791	-	-
	p	0.3536	0.0007	0.0002	0.2590	0.8466	0.3216	0.0010		
	n	40	37	37	18	18	31	40		
Crawl	τ	0.0301	0.1521	0.1945	0.0359	-0.0653	0.0674	0.6433	0.2456	-
	p	0.8069	0.2374	0.1325	0.8599	0.7344	0.6555	0.0001	0.0415	
	n	40	37	37	18	18	31	40	40	
<i>Crangon</i> activity	τ	0.1170	-0.1847	-0.1557	-0.0544	0.0000	0.6621	-0.0515	-0.1425	0.0309
	p	0.4896	0.3168	0.4028	0.7774	1.0000	0.0038	0.7635	0.3939	0.8610
	n	20	17	17	18	18	13	20	20	20

response to the expected increased activity of *Crangon* and other potential predators at night. It is surprising that the plaice showed no response to the *Crangon* given the vulnerability of plaice of this size (38 out of 40 were < 30 mm in length) to this predator in natural conditions (van der Veer & Bergman 1987).

The effects of excess *Artemia* nauplii as food are opposite to those of the bivalve *Donax vittatus* (Burrows et al. 1994b). The presence of *Donax* buried in the sediment increases swimming on the bottom by stimulating searching behaviour. *Artemia* nauplii were very abundant in this study and may have produced satiation, reducing activity in well-fed fish. A similar effect has been observed in sole (Macquart-Moulin et al. 1991) which is thought to be a mechanism to retain fishes in areas of abundant food.

Comparatively few direct observations have been made of the behaviour of juvenile plaice in darkness. Evidence from field sampling of plaice populations (Gibson unpubl. obs.) suggests that intertidal migration continues in the dark hours, although in the Wadden Sea, plaice may venture less far from low water drainage gullies (Berghahn 1986). In a recent study using underwater television to observe movements of fishes near the bottom into the intertidal zone (Burrows et al. 1994a), many juvenile plaice were seen swimming in the light but none were seen in the hours of darkness. From this study it would seem that pelagic swimming produces movements of juvenile plaice in shallow water in darkness while movements in day-

light comprise largely benthic swimming. This would explain the discrepancy between underwater television observations of movements on the bottom, which showed no nocturnal activity, and sampling by trawling (Gibson 1973a, unpubl. obs.) which showed continued movement at night.

A change from swimming on or near the bottom by day to swimming in midwater or at the surface at night has been seen in both larval plaice (Blaxter 1973) and adult plaice in both laboratory (Harder & Hempel 1954, Bregnballe 1961, Verheijen & de Groot 1967, Gibson et al. 1978) and natural conditions (Greer Walker et al. 1978). Similar diurnal changes have also been seen in flounder (Verheijen & de Groot 1967) and sole (Kruuk 1963, de Veen 1967, Champalbert & Castelbon 1989).

Pelagic and benthic swimming may have different functions. Pelagic swimming will reduce the number of encounters with benthic prey and with potential predators searching for food on the bottom (shrimps *Crangon crangon*, van der Veer & Bergman 1987; shore crabs *Carcinus maenas*, A. D. Ansell unpubl. obs.; cod *Gadus morhua*, Edwards & Steele 1968, Brawn 1969), but may increase vulnerability to visual fish and bird predators in the daytime. Benthic swimming brings the fishes into contact with both their prey and their epibenthic predators. Both modes of swimming could be used for migration: benthic movements are oriented in the necessary directions during daytime tidal and diurnal migrations (Gibson 1973a, Burrows et al. 1994a), while pelagic swimming in adults is

strongly directional during the spawning migration (Metcalfe et al. 1993). Plaice larvae do use vertical movements in tidal currents to migrate into inshore areas (Creutzberg et al. 1978). Only benthic swimming could be used for feeding, since plaice feed exclusively on benthic organisms (e.g. Edwards & Steele 1968, Poxton et al. 1983, Ansell & Gibson 1990).

The different rates of encounter of juvenile plaice with their prey and predators during the 2 modes of swimming can be used as the basis for prediction, using optimal foraging theory (Burrows 1994), of the best mode to use in different conditions (Burrows in press). If feeding is visually mediated, benthic swimming should only be used in sufficient light to allow prey capture. In darkness and in areas of high risk of predation, juvenile plaice should use pelagic swimming to avoid contacts with their predators.

Acknowledgements. I am very grateful to Karen Hall for her analysis of the videotapes and to John Joyce, Lois Nickell and Linda Robb for all their help. I also thank Robin Gibson, Alan Ansell and Tim Ellis for useful discussions.

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This article was presented by R. N. Hughes (Senior Editorial Advisor), Bangor, UK

*Manuscript first received: May 6, 1994
Revised version accepted: August 15, 1994*