

# The Causal factors and function of YAWNING in *Microspathodon Chrysurus*

(pices : pimacentridae)

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## INTRODUCTION

The motor pattern 'yawning' has been described for all vertebrate groups. The most intensive study of this behaviour pattern has been made by SAUER & SAUER (1967) in the South African Ostrich. They suggest that yawning assists in the regulation of the physiological state of these birds. It is primarily released and activated by endogenous stimuli, but can also be facilitated and triggered by environmental stimuli when the organism is sufficiently motivated. It is correlated with the periodic appearance of fatigue in the Ostrich and occurs typically in birds whose motor activities have been reduced to a minimum. It was found to induce a relaxation of tension in a group and trigger sleepiness, assuring excited birds of the absence of danger.

Apart from this one intensive study, yawning has been mentioned in many ethological investigations, but its causation and function have usually been merely suggested. Only the motor pattern 'yawning' described for fish will be considered here, as there is some doubt as to whether this behaviour is directly comparable to that seen in birds and mammals.

MORRIS (1954) noticed that males of the River Bullhead (*Cottus gobio*), when first presented with a female, tended to yawn frequently, these yawns being interspersed with the courtship actions. In a later paper on the Tenspined Stickleback *Pygosteus pungitius* (1958), he suggested that yawning could not be termed a 'displacement activity', but was merely a jaw stretching that occurred most often when the fish was 'unoccupied'. He stated that species with strong jaws tend to yawn more intensely and frequently than other species and that the motor pattern 'yawning' in fish was similar to that observed in mammals. TUGENDHAT (1960) in her study of feeding behaviour in the Three-spined Stickleback, *Gasterosteus aculeatus*, found that yawning was associated with 'excess initiation' to feeding and with a slow build-up of feeding motivation. It was found to occur at moments of balance between feeding and interrupted feeding and also when balance was maintained for some time. This she attributed to a slow rate of build-up of feeding motivation while it was increasing from a point below threshold level to one just above it. and postulated that yawning should thus appear at the end rather than at the beginning of an interruption, which was found to be the case.

A similar association between yawning and interruption of an ongoing behaviour has been noticed in free-living *Chromis multilineata* by MYRBERG (pers. comm.) He stated that yawning occurs most frequently under field conditions when a fish is interrupted in feeding, for example, by the approach of a female and before courtship is initiated.

HOAR (person. comm.) states 'the yawning incident which sticks in my memory occurred during some field studies of downstream migrant Sockeye Salmon smolts (*Oncorhynchus nerka*) from Lakelse Lake in northern British Columbia. This is a very large migration involving many thousands of smolts (length 3 to 4 inches). The outlet of the lake was barricaded by a fence and trap; the migration from the lake occurred primarily at dusk or dawn. Large numbers of the smolt trapped during any night were regularly held in pens throughout the next day to be released downstream the next evening. Yawning occurred repeatedly throughout the day. The same fish was observed to yawn frequently and large numbers might be yawning at the same time'.

BARLOW (1964) in his study of the reproductive behaviour of *Badis badis*, found that the frequency of yawning showed a reciprocal relationship with the foraging tempo in these fish,

the slower the fanning tempo, the higher the yawning rate. McCUTCHEON (1962) studied yawning in the Pinfish *Lagodon rhomboides*. from a biophysical aspect and found that it caused swimbladder compression and reduced the body to neutral bouyancy in this species.

All the observation of yawning in fish, apart from the last mentioned, indicate that this behaviour is associated with either a change in the stimulus pattern or the interruption or decrease in intensity of an ongoing response.

#### **MATERIALS AND METHODS**

The fish used in this study were all juveniles of the 'jewel fish' or 'Yellow-tail Demoiselle', *Microspathodon chrysurus*. Individuals ranged from 3 to 5 cm standard length. They were kept isolated in aquaria of approximately 200 L capacity, these being bisected by an opaque PVC partition in which was set an L-shaped tube 4 cm in diameter, attached to a clear glass boule 8 X 3 cm in size on the other side of the partition. The tube and bottle were set in the middle of the partition about 1/3 of the way up from the substrate.

The aquaria were floored with gravel and sand and had a group of corals and rocks in each half. Water temperature was kept at 28° C with heaters regulated by a thermostat and lighting was by 'Day-Glo' strip lamps set on a 12 hour continuous light schedule from 0800 to 2000 hrs. Subsurface illumination was found to range from 5500 to 6000 Lux with the lights on. pH was kept at 8.2 to 8.4 Aeration was by means of sub-sand filters and air-stones and surplus protein in the water was eliminated by means of a 'foamer'. Fish grazed the algae present on the aquarium walls and were also provided with supplementary protein fed in the form of hydrated freeze-dried *Artemia* or chopped mussel flesh once daily at mid-day. Behaviour was recorded with an Esterline Angus 20-channel event recorder and observations were made with the observer sitting as quietly as possible about 1 1/2 m from the aquarium.

#### **DESCRIPTION OF YAWNING AND ITS DIURNAL RHYTHMICITY**

The behaviour pattern yawning was usually preceded by the fish swimming rather slowly with a sculling movement of the pectoral fins and in a head-up position. The forward motion then ceased and the fish raised the median fins maximally, spread the caudal fin and pelvic fins and momentarily stopped the sculling motion of the pectorals. At the same time the mouth was opened, the opercles flared, the hyoid apparatus depressed and the premaxillae projected forward to their maximal extent. During this period of stretch all forward motion stopped and the animal sank slightly in the water. This is probably because the fin motion supporting the body had ceased and the animal is denser than seawater, hence sinks slightly before fin motion is recommenced. The rigid position of the body maintained during a yawn indicates that the lateral musculature is also contracted during its performance, but no external signs of such contraction were evident.

Many variations in the degree of these fin and mouth stretching occur, the culmination of which is the true "yawn", where both median fins and mouth are maximally extended simultaneously. This simultaneous stretch of fin and mouth musculature was the only behaviour recorded as a yawn since the variability in the uncoordinated or weaker fin and mouth stretchings made them difficult to quantify exactly.

Fish were found to have preferred yawning sites, each individual selecting a particular area of the aquarium in which yawns were most frequently performed. The yawning site selected differed between individuals and bore no relation to any particular stationary object in the aquarium. The reasons for the selection of such yawning sites are not known.

In addition to the preference for yawning in a particular place in the aquarium, the animals also showed a difference in the frequency of yawns performed at different times of the day. Five individuals were observed for 10 mn in each half hour starting at 0600 h, when they were still asleep, to 2030 hrs, half an hour after the timed light cycle had ended (the fishes could still be seen as silhouette). Totals were averaged for each hour, starting at the time general (swimming etc.)

activity was first recorded i.e. 0630 + 0700 h etc. The observations were repeated, making a total of 10 observations for 5 individuals. The results obtained are shown in Fig 1. These data show that yawns gradually increase in frequency during the morning, reaching a peak at 1100 h and then decrease rapidly and remain low in frequency for the remainder of the day. All individuals showed the same general cycle with only slight variation.

### **THE INITIATION OF YAWNING BY ENDOGENOUS FACTORS**

The apparatus described in the Materials and Methods section was designed to simulate conditions pertaining during territorial borderline fights. When an antagonist was present on the opposite side of the partition, the experimental fish learned rapidly to negotiate the maze and enter the boule in order to engage in a display fight with this individual. A definite appetite for such aggressive encounters was proved (RASA, 1971).

When the animal's aggressive tendencies were not allowed expression by removal of the antagonist, the frequency of yawning was found to increase markedly during the first few days of isolation. The effect isolation for a 10 day period had on yawning frequency is given in Fig. 2, this being, the average frequency observed for 10 individuals. These data are derived from 3 half hour readings during each of the days in question, readings being taken at 1100, 1400 and 1700 hrs to compensate for diurnal rhythm effects. On day 0 another fish was present on the opposite side of the partition. A few yawns occurred in the glass tube itself on occasions when the antagonist, although visible, did not come to fight. The majority of yawns occurred in the aquarium when the experimental fish could enter the tube, but did not.

At the same time as this change in frequency of yawning was observed, a change in the colour pattern of the animal took place. The normal colour of *M. chrysurus* is dark blue-black with a paler throat, the 'jewels' appearing as dark-ringed light patches against the dark background. During the isolation period, four classes of colour pattern were distinguishable: 'all dark', which was as described above but with or without the paler throat region present; 1/2 light, in which the animal was pale blue up to the level of the pectoral fins; 3/4 light, where the animal had a pale undersurface in addition to the pale front and 'all light', in which the animal was completely pale in colour. These differences in colour pattern are illustrated in fig 3.

Darkening in colour could be produced by any type of external stimulation: feeding; the observer approaching the aquarium; switching the light on and off; increasing the speed of water circulation; introducing an antagonist; frightening the animal etc. It was therefore considered to be an indicator of the (general) excitement level of the animal, this being congruent to the psychological term 'arousal'. To quantify this variable for any particular time interval, the following formula was used and termed the 'colour index' (C.I.):

$$CI = (\text{secs all dark} * 100 + \text{secs } 1/2 \text{ light} * 50 + \text{secs } 3/4 \text{ light} * 25 + \text{secs all light} * 10) / 100$$

To determine the colour index for different days of isolation, 5 individuals were observed for half hour intervals at 1100, 1400 and 1700 hrs on each of the days of isolation, the colour indices for individuals being averaged for each day. The results obtained are shown in Fig. 4, the variations being deviations from the mean for individuals on each of the days in question. These results show that the peak in frequency of yawning observed coincides with the highest level of excitement as indicated by the colour index.

Concurrent with this change in colour pattern, a change in the activity of the animals also took place. As a measure of their kinetic activity level, the number of turns of 90° or more performed during the same observation periods as given above for colour index were determined for each day of isolation. Frequency of turning was selected as the most accurate measure of the kinetic activity in this species. Turns were used as most Pomacentrids perform a "dance" when they are very excited. This is a zig-zag, up and down, rapid swimming action performed at the focal point of the territory, with a large number of rapid angular dashes to and from the focal point. Normal

swimming is rather slow with much fewer turns. Since the territory was physically delineated by the aquarium walls, the restriction on swimming speed was even more rigidly enforced than would be the case in nature. The results obtained for the change in kinetic activity with isolation time are shown in Fig. 5, the results being the average frequency of turns for 3 individuals with maximum and minimum deviations from the mean.

The increase in frequency of yawning observed under isolation conditions therefore coincides with not only a marked increase in colour index i.e. increase in excitement level as evidenced by the darkening in colour, but also a marked decrease in kinetic activity.

To determine whether the changes observed in these variables during isolation could be some of the causal factors of yawning, the following experiment was conducted. Five animals were observed for one hour each on the first day of isolation, readings being taken at 1000 and 1400 hrs and the experimental series then repeated for each individual making a total of 20 observations in all. The same procedure was followed in a second series of experiments, but these were conducted under conditions of high water turbulence, so that the fish were kept swimming actively for the duration of the observation. A strong pump which extracted and returned the aquarium water at a rate of 2000 l/hr was used to maintain this high rate of water flow. The results obtained are shown in Fig. 6. These data show that, when kinetic activity is maintained at a high level concurrent with high excitement level, yawning is rarely performed.

Although turbulence in the water was not equal throughout the aquarium owing to mechanical obstructions such as coral heads, filters etc., the frequency of yawning in these more protected locations was no higher than that in the high turbulence areas. The increase in kinetic activity instigated by the moving water is thought to be the factor inhibiting yawns as, under high excitement with low kinetic activity (slack water on day 1 of isolation) the frequency of yawning increases. Only when the kinetic activity level is artificially raised during this period of isolation by keeping the water moving does the frequency of yawning decrease markedly.

The increase in excitement observed during the first days of isolation has been shown to be the result of frustration of the learned behaviour for aggression (RASA. 1971). Delius (1967) found that, in the Herring Gull, several areas of the forebrain and brainstem, when stimulated electrically via electrodes, elicited yawning- in addition to a series of other behaviours which culminated in sleep. These behaviours were all frequently performed by the animals as 'displacement activities' and he suggested, from this finding, that a homeostatic process must be operant in the brain to cancel the arousal increment generated by conditions such as conflict, thwarting and frustration. To determine whether the behaviour pattern 'yawning' in fish initiated by frustration of fighting could be attributed a 'dearousing' function, the colour pattern of the animal was recorded concurrent with the behaviour. A change in colour within 2 seconds of performance of the behaviour was considered as being associated with it, as colour change in these animals is very rapid. Darkening in colour takes less than a second to become evident and lightening a little longer, but not more than 2 seconds. Yawns occurring in the 'all dark' colour phase were discarded to prevent bias to the data, as the level of excitement could not be accurately determined. The darkening might differ in intensity and such differences would not be clearly evident to the observer.

Five different fish were observed for a total of 10 hours. Of the 34 yawns recorded which were not performed in the 'all dark' phase~ 7 (20,5%) were associated with a darkening in colour after their performance; 26 ( 76,5%) had no colour change associated with their performance and only 1 (2,9%) was associated with a paling in colour pattern. These data indicate that there is no evidence that yawning in fish can be attributed a 'dearousing' function.

Since the darkening in colour associated with frustration during the first few days of isolation was thought to be hormonally as well as neurally initiated, experiments were conducted with the 'stress' hormone ACTH (adrenocorticotropin) to determine whether the change in colour

and behaviour observed during this period could be associated with increased secretion level of this hormone. A solution which would yield a concentration of 0,030 ppm in the aquarium water was introduced by means of a polythene tube inserted into the outlet pipe of the sub-sand filter. This was to prevent water disturbance and bubbles resulting from introduction of the hormone from having an effect on the experimental animal, any such disturbance being masked by the normal bubbles and water flow from the filter. Five animals were isolated for 10 days, observed for 10 minutes, the hormone solution added to the water and the observation continued, for a further half hour. Darkening in colour appeared within 3 to 5 minutes after hormone introduction, this probably being due to the direct effect of the hormone on the skin, as ACTH has the property of causing melanophore pigment dispersion *in vitro*. The results obtained for the influence of this hormone on the frequency of performance of yawning are given in Fig. 7, the data being averaged for each five minute interval of the observation period.

These results show that a gradual increase in the frequency of performance of yawn starts approximately 10 minutes after hormone introduction. Yawning reaches a peak between 15 and 20 minutes and then shows a marked decrease. This decrease can probably be attributed to the fact that ACTH, being a short chain amino acid, is rapidly removed from the water, not only by cohesion with colloidal particles but also by the action of the 'foamer' which is designed to remove surplus protein.

The results of these experiments indicate, therefore, that the behaviour pattern 'yawning' in fish can be initiated not only by conditions of endogenous high excitement instigated by frustration, but also by artificially increased levels of the hormone ACTH when kinetic activity is low in both cases.

#### **THE INITIATION OF YAWING BY EXTERNAL STIMULI**

Apart from being endogenously triggered by conditions of high excitement and low kinetic activity, yawning was also observed to occur when the animal was presensitized by visual stimuli. To test the effect of presentation of such stimuli on the frequency of yawning, two models were used to determine whether the type of visual stimulus presented would affect the frequency of yawning after presentation. One model was a fish model, constructed from a dried specimen of *M. chrysurus* 4 cm in length and painted to appear as natural as possible. This was considered specifically aggression releasing in function and the experimental fish would usually come and display aggressively towards it on its appearance at the front pane of the aquarium. The second model used was the ball model, a sphere of grey 'Nakiplast' 5 mm in diameter which was considered as a non-specific visual stimulus. This elicited approach by the fish on its appearance, but no aggressive display as was seen with the fish model. The fish model was held steady at the center of the front pane, but the ball model was moved up and down over approximately 5 cm distance, as it was found that, after preliminary investigation, a stationary ball evoked no further interest, but a stationary fish model always elicited prolonged response. To keep the two stimulus situations as comparable as possible therefore, the ball model was kept in motion during its presentation.

Ten different individuals were kept isolated for 4 days and the two models presented in two different experimental series, for 0 (control) 5, 10, 20, 30 and 60 seconds. The frequency of yawning was recorded for each five minute interval following model presentation. The results obtained are given in Fig. 8.

These data indicate that there is no marked difference in the frequency of yawning elicited by stimuli influencing specific motivations and those with general arousal properties. The correlation coefficients obtained were +0.76 ( $p = 0.02$ ) for the fish model and +0.95 (0.9,3 ( $p < 0.001$ )) for the ball. Both models increase the frequency of yawning the longer they have been presented to the animal.

It was noticed that, after yawning, the frequency of performance of other behaviours

observed in the experimental situation tendency to increase. The behaviours concerned were 'in boule', the learned appetitive behaviour for aggression, where the animal negotiated the maze and entered the attached bottle in an attempt to instigate a fight; snap, a bite directed towards inanimate objects in the aquarium; pebble carrying, holding a small stone in the mouth and swimming with it; twitch, a convulsive shaking movement of the whole body and chafe, a scratching of the body against objects in the aquarium. To determine what effect presentation of a visual stimulus had on yawning and the frequency of performance of these behaviours following it, the following experiment was conducted.

Five fish were isolated for 10 days, observed for 10 minutes, the ball model presented for 10 seconds and the observation continued for a further 10 minutes, the colour pattern being recorded simultaneously with the behaviour. 12 observations were made on each individual and the data obtained grouped in 20 second intervals for the whole observation period. The colour pattern index was calculated for each individual for each 20 second interval and the results averaged. The data obtained are shown in Fig. 9.

These results demonstrate that presentation of the model results in a tenfold increase in the frequency of yawning in the 20 second interval following, concurrent with an increase in colour index to almost maximum. Practically no other behaviours occur during this 20 second interval, the few snaps and twitches recorded nearly all being observed in instances in which no yawn was elicited. The decline in yawning frequency coincides with that of colour index over the next 40 seconds. After this peak in yawning, the other behaviours show increases in performance level, the degree of increase and the time taken before increase occurred being illustrated schematically in Fig10.

These data therefore confirm the observation that other behaviours increase in frequency of performance after the animal has yawned. Yawning elicited by external stimuli is also associated with an increase in excitement level, as shown by the increase in colour index observed. A similar darkening in colour was noticed in the experiments with the fish and ball models, but was not quantified. As colour index decreases, so does yawning frequency but, from the results obtained previously on the relationship between this behaviour and colour change after its performance, yawning itself cannot be the causal factor for this decrease. A more logical explanation would be that as excitement level decreases, so does the frequency of yawning.

The fact that these experiments were conducted on day 10 of isolation when kinetic activity is extremely low suggests that induced by external stimulation might have the same relationship with excitement and kinetic activity as yawning initiated by endogenous factors. To prove this hypothesis, the fish model was presented to individuals which had been isolated for 8 days, one series of experiments being conducted in calm water and one in turbulent water as described previously. 20 observations were made with 5 individuals in each experimental series. Fish were observed for 30 mn, the model presented for 30 s and the observation continued for a further 30 mn. Data were averaged for each 5 mn interval and the results obtained are given in Fig.11.

These data show that, when the model is presented under conditions of high kinetic activity, a peak in yawning frequency after its appearance no longer occurs. External stimuli therefore cause no increase in the frequency of yawning when the kinetic activity of the animal is maintained at a high level, while under conditions of low kinetic activity, they elicit a marked increase in the number of yawns performed.

## **DISCUSSION**

The results of these experiments have shown that the behaviour pattern 'yawning' in fish is associated with increased excitement level, either endogenously or exogenously produced and low levels of kinetic activity. The reciprocal relationship between this behaviour and kinetic activity

suggests that it may function as a means of increasing this variable, and activity in general has been shown to increase after the performance of a yawn. The behavior pattern yawn itself is merely a state of maximal stretch of the body musculature. An animal which is not in a state of endogenously produced high excitement or aroused by the appearance of a stimulus object could be considered as maintaining a low input-output transfer between the central nervous system and the body musculature. When sensory input is greatly increased as, for example, by the appearance of a novel stimulus object, this is registered as an increase in excitement level in the central nervous system. This would result in a discrepancy between input-output transfer between it and the body musculature, the raised excitement level causing the transmission of a high output signal to the latter, which would manifest itself in strong contraction i.e. a maximal stretch which would be similar to the behaviour pattern 'yawn'. A simplified schema illustrating the mechanisms physiologically underlying such an exogenously produced yawn according to this hypothesis is given in Fig. 12.

Muscle contraction is known to increase blood flow to the muscle fibres, oxygen transfer and heat expenditure, these facilitate tension and thus 'priming' the muscle for further action. In addition, a high spike potential in the nerve fibre would facilitate motor end-plate transmission. Such strong muscular contraction would thus not only facilitate the effector, but also its activator. One would therefore expect that, after strong muscle contraction, such as is evident in a yawn, the animal would be physically more capable of performing other behaviours. This appears to be true as an increase in the frequency of performance of other behaviours after yawning has been shown to occur.

Yawning in fish can therefore be considered as a behaviour by which the animal is able to regulate discrepancies between central nervous system excitation and body musculature tonus. Its performance would result in an increase in muscle tonus and therefore aids in preparing the animal for action. This would be of especial advantage in the case of exogenously instigated yawning as the animals would, after performing this behaviour, be able to respond more rapidly to the stimulus object. As has been demonstrated, the type of stimulus appears unimportant as far as the initiation of the behaviour is concerned. Yawning probably serves as general bodily activator, hence the animal should, after its performance, be facilitated in its response to the incoming stimulus. The type of response made would depend on the specific motivation-activating properties of the stimulus object concerned.

This theory of the causality and function of yawning in fish can be applied to explain the instances previously mentioned of its occurrence in other species. MORRIS (1958) stated that it occurred when *Pygosteus* was unoccupied, i.e. in a state of low kinetic activity, but he does not mention under what conditions this unoccupation occurs. Thus the excitement level of the animal is unknown. TUGENDHAT (1960) stated that it occurred most frequently in *Gasterosteus* when the learned behaviour pattern for feeding is thwarted, the longer the period of feeding interruption, the greater the likelihood that the fish will yawn, a thwarting situation giving rise to increased excitement level without an associated increase in kinetic activity. BARLOW (1964) stated that yawning occurred more frequently in *Badis badis* under low levels of kinetic activity as evidenced by the decrease in fanning tempo. The excitement level of the animal can only be inferred in this case, but is probably high, fanning possibly being the result of an approach - withdrawal conflict (SEVENSTFR, 1961) and any motivational conflict usually results in raised excitement level. Thwarting of migration together with reduced swimming activity, as the fish were held in pens, also results in an increase in yawning as mentioned by HOAR for *Oncorhynchus*. It therefore appears that several cases of thwarting or conflict of motivational variables other than aggression, the motivational variable in this study in conjunction with decreased kinetic activity can result in yawning or an increase in its frequency of performance.

The increase in yawning frequency observed in *Cottus gobio* by MORRIS (1954) and in

*Chromis multilineata* by MYRBERG could be attributed to exogenously induced excitement caused by the appearance of the female in both instances. Interruption of ongoing activities by the appearance of such a stimulating object could initiate a yawn, especially if the general muscle, tonus of the animal is low at the time of its appearance.

The findings of McCUTCHEON (1962), that yawning causes a compensatory swimbladder compression to maintain neutral bouyancy suggests that, ni *Lagodon rhomboides*, yawning has an additional function to raising general motor activity in this species. As yawning causes both isotonic and isometric contraction of the body musculature, it is not unlikely that the muscles controlling swimbladder volume would also be activated. In *M. chrysurus*, however, it cannot be stated that yawning functions to maintain neutral bouyancy since the fish have been observed to sink slightly in the water during its performance.

It is thought unlikely that the function of the behaviour pattern yawning in fish is exactly the same as yawning in birds and mammals from three point of view. Firstly as SAUER & SAUER (1967) have mentioned, one of the functions of yawning in the Ostrich is to relax tension in a group and sleepiness. In *M. Chrysurus* however, its performance appears to have exactly the opposite effect, as the frequency of all other behaviours increases after the performance of a yawn, thus it must have more of an arousing effect than a sleep-inducing one. One would expect that, if yawning were associated with a readiness to sleep in fish, its frequency of performance would increase towards evening, but this is not the case (see Fig. 1), the highest peak in yawning occurring at approximately midday. Its frequency of performance i, the evening is very low compared to that of the morning. An association between yawning and sleepiness is therefore thought to be lacking in fish.

Secondly, it has been shown by DUMPERT (1929), SELBACH & SELBACH (1953) and PEIPER (1963) that in mammals, yawning is associated with deep inhalation and exhalation, there being a homeostatic mechanism between the extrapyramidal motor system and the neural center for breathing. This is activated by insufficient oxygen in the brain arterial system or a surplus of carbon dioxide. The performance of a yawn in mammals is associated with the regulation of the oxygen/carbon dioxide ratio in the brain by means of such deep breathing movements. In fish, yawning, if anything, should result in less oxygen being taken in through the gill filaments. Even though the mouth is opened, the hypid apparatus depressed and the opercles flared (resulting in a larger volume of water prescrit in the oral cavity) all pumping action of water over the gills ceases. In addition, since the animal usually remains motionless while yawning, even passive water movement over the gills caused by the fishes forward swimming movements does not occur. These observations suggest that yawning is unlikely to be associated with breathing in fish and does not act as a mechanism for correcting the oxygen/carbon dioxide ratio in the fish brain.

Thirdly, yawning in fisli does not appear to have the infectious quality noted for the behaviour of the same name in birds and mammals. Apart from HOAR's observation that large numbers of the salmon smolts might be yawning simultaneously, no evidence is available from aquarium or field observations on Pomacentrids to substantiate that it has infectious qualities in this family of fish at least. One individual may yawn up to three times in rapid succession, but this does not appear to be communicated to other individuals in the area. Most of the species studied to date have either been kept isolated in aquaria or are naturally solitary or territorial species. Further observations on schooling and social fish are necessary to support HOAP's observation that many of the salmon smolts were simultaneously, since this might be coincidental as the frequency of yawning was so high. Until further evidence is forthcoming, this behaviour must be considered as non infectious in fish.

In conclusion, it appears that the behaviour pattern yawning in fish is unlikely to be completely analogous to the behaviour of the same name in birds and mammals. In fish it serves asa



mechanism to equate discrepancies between increased excitement level and lowered kinetic activity, raising the latter variable by its performance. It is, as has stated, simply a stretching movement and appears to be unassociated with breathing. In all vertebrates, however, it appears to be triggered by environmental stimuli and can also occur under the influence of endogenous factors, as stated above. It is likely that yawning may basically have the same causation in other vertebrate groups as has been demonstrated here for fish, but has developed secondary functions in the higher vertebrates, especially in social species where it acts as a signal in addition to being physiological regulatory mechanism.