

Development and changes at settlement in the barbel structure of the reef fish, *Upeneus tragula* (Mullidae)

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Synopsis

The development of the sensory barbels of the tropical goatfish, *Upeneus tragula* (Mullidae), was examined from their first appearance early in planktonic life through to the reef-associated juvenile period. The structure of the barbel was examined histologically and found to represent an outgrowth of the gustatory (taste) system, composed of at least 50% sensory tissue at settlement. Abrupt changes in morphology were found to be coincident with the 6–12 h settlement period: barbels rapidly moved forward along the hyoid arch to abut the dentary; the length of the barbels increased by up to 52%; the epidermal layer increased to comprise 75% of the cross-sectional area; and the mean size of the taste bud cells increased by up to 100%. A strong relationship was found between barbel length and mean taste-bud size. This relationship was used to predict the mean taste-bud sizes for 237 newly-settled fish, collected as 12 samples over two recruitment seasons. Mean taste-bud size varied significantly among samples. Experiments examined whether food availability or temperature of the water within the pelagic phase influenced the size of the barbels at settlement. Food availability influenced the relationship between barbel length and fish size. Slower growing fish had larger barbels relative to fish length than those that grew faster. Temperature did not influence the relationship between barbel length and fish size. Variability in sensory development at settlement, and the factors which influence it, may have important ramifications for the potential success of the fish once on the reef.

Introduction

Many reef associated fishes undergo a settlement transition from a pelagic phase to a benthic-oriented juvenile and adult phase. This event involves a major change in the physical characteristics of the environment which the fish inhabits, and in the sensory stimuli perceived by the fish (e.g. McFarland & Munz 1975). Typically this change in habitat is coincident with a rapid change in the morphology of the fish, commonly termed metamorphosis (Youson 1988). The extent of these changes range from subtle changes in body pigmentation (e.g. pomacentrids) to a dramatic mobilization of cellular tissue

and developing body structures (e.g. Elopomorpha and Pleuronectiformes: Forstner et al. 1983, Pfeiler & Luna 1984, Pfeiler 1986, Markle et al. 1992).

The patterns of development that govern the fishes' body characteristics and behaviour at settlement are influenced by environmental and biotic conditions within the pelagos (Hovenkamp & Witte 1991, McCormick & Molony 1992). These factors may also influence the fishes' sensory capabilities and how they perceive their environment (McCormick & Shand 1993). A demonstrable link exists between the development of an appropriate structure which enables the interactive response to the environment, and the ontogeny of behaviour (Balon

1985, Noakes & Godin 1988). Thus, by influencing sensory development, events within the pelagic life-history phase have the potential to influence the behaviour of newly settled fishes, their subsequent patterns of growth, and mortality rates. However, the response of a developing sensory structure to environmental conditions can be complex (Pankhurst 1992). Detailed studies of the interaction between sensory development and the environment are required in order to understand the implications of pelagic life-history on the survival probabilities of newly settling fish.

In this paper I examine the changes that occur in one aspect of the sensory system of a reef fish during settlement. The system examined is the sensory barbels of the goatfish, *Upeneus tragula* (Richardson) (Mullidae), which are outgrowths of the gustatory (chemosensory) system. These are extensively modified branchiostegal rays (Gosline 1984) that are not used in the pelagic life phase, but are important in the detection and manipulation of prey items once the fish has settled to the reef. In this study, the morphology and sensory capabilities of the barbels are described. Their development from the pelagic life-history phase to the juvenile phase is examined and changes that occur at settlement are highlighted. As a measure of the fishes' potential sensory capabilities at settlement, the variability in the state of development of the barbels at settlement is examined from samples of newly-settled fish over two recruitment seasons. Two experiments are undertaken to investigate whether food availability and temperature of the water column during the pelagic life-phase influences development, and whether these factors are able to explain the variability recorded in the field. Finally, the development of the barbel sensory system is compared to other aspects of the teleost sensory system.

Methods

The species

The freckled goatfish, *Upeneus tragula*, is a common component of the ichthyoplankton in the central and northern Great Barrier Reef lagoon. Early

life stages between 8 mm standard length (SL) and settlement size (20–34 mm SL) form large schools with other species of goatfish, and will actively aggregate under drifting debris (McCormick 1992). Settlement involves an obvious change in pigmentation. The silvery pelagic colouration changes to a mottled cream and dark stripes appear along the mid-ventral line and on the caudal and dorsal fins. Concomitantly, the behaviour of the fish changes from schooling in the upper 3 mm of the water column when pelagic, to foraging within centimetres of the substratum once settled.

Collection

Pelagic *Upeneus tragula* were collected from 5 km west of Lizard Island (14°41'S, 145°27'E) on the northern Great Barrier Reef, in approximately 22 m of water during Nov 1989 to Feb 1990 and Nov 1990 to Jan 1991. Fish were attracted to a series of 1 × 1 m plastic aggregation rafts moored for 2 h, and were caught with a 14 × 2 m plankton-mesh purse-seine. Fish were carefully transported to the laboratory at the Lizard Island research station. Overnight, some fish metamorphosed, changed pigmentation and settled to the bottom of their tanks. These fish were regarded as having been competent to settle at the time of capture. There were also fish which had started to attain the characteristic reef-colouration but which had not completely metamorphosed and settled. Individuals in fully- and partially-settled states were preserved for histological examination. Juvenile *U. tragula* were collected using a fence-net from the seagrass beds on the back-reef of Lizard Island, and preserved for comparison to pre-settlement and newly-settled fish.

Barbel development

Morphological development of the barbels was quantified using specimens preserved in either formalin (10% buffered solution in salt water) or formalin-acetic-acid-calcium-chloride (FAACC: McCormick & Molony 1992). Standard length and barbel lengths were recorded. Measurements were

made with calipers on fish larger than 20 mm SL; smaller fish were measured with a calibrated video-microscope. The latter was also used to measure the distance from the tip of the dentary to the end of the hyoid arch to quantify barbel migration throughout development. To quantify the internal development of the barbels a size range of fish (11–45 mm SL), preserved in FAACC, was examined histologically (see below).

Variability in taste-bud size at settlement

Fish were aggregated under rafts and caught as detailed previously. Four samples of *Upeneus tragula* were collected during Nov 1990 to Jan 1991, and 8 samples during Nov 1991 to Dec 1991. All fish captured were carefully brought back live to the laboratory. Those fish which settled overnight were killed by cold shock and their morphological characteristics were measured as above. The mean taste bud size of the barbels from each newly settled fish was predicted from barbel length with a regression relationship. Analysis of variance was used to examine whether taste bud size differed among samples. The nature of the differences found were further examined by a posteriori Tukey's tests.

Effect of food availability and water temperature on barbel development

The influence of food availability and water temperature during the pelagic stage on the development of the barbels up to settlement was examined in two experiments. Experimental methods are described in detail in McCormick & Molony (1992, 1993). Briefly, to examine the influence of food availability, 25 pelagic-phase *Upeneus tragula* were randomly placed in each of three 60 l capacity tanks of four feeding treatments. The four feeding treatments were: fed ad libitum, fed once per day, starved every second day (fed ad libitum on alternate days), and starved 3 d then re-fed ad libitum. Those fish which were to be fed more than once per day always had food in their tank during daylight hours.

In the temperature experiment, pelagic *Upeneus tragula* were randomly assigned to one of two temperature treatments: 25°C or 30°C. Three tanks (20 l) were set-up per treatment, each containing 20 fish. A refrigeration coil in a header tank reduced the ambient water temperature of the flow-through seawater from an average of 28°C to a constant 25°C. Water heaters kept the other tanks at 30°C.

For both experiments, fish were fed *Artemia* sp. (Ocean Star strain) nauplii (36 to 48 h old). Fish that had undergone metamorphosis and settled to the bottom of the tank the night after capture were used as field controls. Tanks were examined for newly settled individuals at 0630 h each day; these were removed, rapidly killed by cold shock and preserved for histological examination.

Histology

To examine the morphology and distribution of taste bud pits, barbels of 3 newly-settled *Upeneus tragula* were preserved for scanning electron microscopy in glutaraldehyde and post-fixed with osmium. Samples were then taken through an alcohol dehydration series, critical-point dried and gold coated with a sputter coater. Samples were then scanned using an Etec Autoscan electron microscope.

Histological sections (6 µm) for light microscopy were made from 4 fish per treatment and stained in Azan. Sections were cut one-third of the total barbel length down from the tip. The area of the main tissue zones was quantified for the experimental fish and those fish collected for ontogenetic examination using a compound microscope linked to a video monitor by a video-analysis computer package. These tissue zones were: the epidermis, taste buds, nerve bundle, connective dermal tissue, and bone. For each fish, mean density of taste buds per millimeter circumference was calculated, and the mean taste-bud cross-sectional area determined by measuring the area of 8 taste buds, which a pilot study had found to yield a precision of about 0.05. Taste bud cells were recorded as being present in a particular section only if they possessed both a neural connection from the dermis and microvilli which

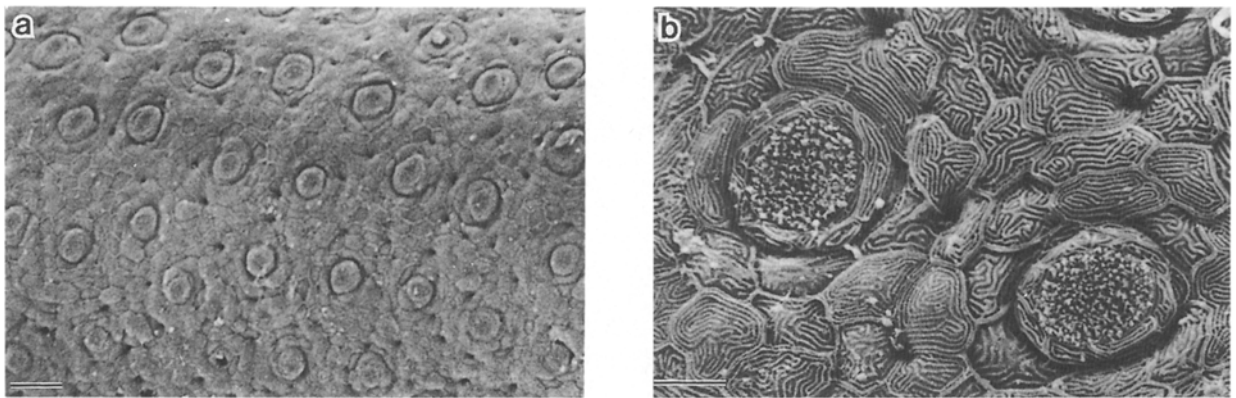


Fig. 1. Scanning electron micrographs of the barbel surface of a newly settled *Upeneus tragula* one third of the length from the distal end: a – Barbel surface showing the sculptured epidermal cells, and regular distribution of taste-bud pits (scale 30 μm). b – Details of the taste-bud pit showing collar cells and microvilli protruding from the pit. Note the pores of the goblet cell between pits (scale 10 μm).

penetrated the outer squamous epidermis through the taste bud pit.

Analysis

A principal component analysis was used to remove the confounding isometric size-component from the morphological data for the two experiments (Somers 1986), allowing the analysis of the remaining shape component. Principal component 2 represented barbel allometric length in both experiments. This measure was compared among the four feeding and two temperature treatments by analysis of variance.

Results

Morphological description

The barbels of goatfish may be described simply as a rod of bone and cartilage supporting neural tissue and its associated external receptors. A scanning EM examination of barbels from three newly-settled *Upeneus tragula* showed that taste-bud pits were regularly arranged over the barbel surface (Fig. 1a), with an average distance between pits of 36 μm . The density of taste-bud pits (analysed as neighbour distances) differed significantly among four regions along the barbel ($F_{3,116} = 2.706$, $p <$

0.049). The distance between pits was smallest as the tip and base of the barbel (34.1, 34.8 μm respectively), and greatest mid-way down the barbel and one-third from the tip (38.2, 38.4 μm respectively). The sensory pits are surrounded by a collar of modified squamous epithelial cells (Fig. 1b). Microvilli protrude from these pits. These are the terminal portions of elongated cells that make up the major part of the taste bud. The size of these pits differed significantly along the barbel ($F_{3,64} = 16.820$, $p < 0.0001$). Mean diameter of these pits (\pm se) was largest one-third the way along the barbel from the tip (15.1 \pm 0.51 μm), smallest at the base of the barbel (10.9 \pm 0.18 μm) and of an intermediate diameter at the tip (13.2 \pm 0.47 μm) and mid-way along the barbel (13.3 \pm 0.41 μm). In addition to these pits, pores were randomly distributed over the barbel surface in similar densities to the taste bud pits (Fig. 1b). Examination of cross sections suggests that these pores do not penetrate deeply into the epidermis, and originate from glandular goblet cells, which have a mucus secretory function.

Cross-sections of the barbels showed that taste buds are located in a stratified squamous epithelium, separated from the dermis by a well defined basal membrane (Fig. 2a, b). These flask-shaped taste buds are similar to those described by Reutter (1982) for the catfish genus *Ictalurus*. The taste bud is linked to the dermis by a papillar protrusion through which nerves connect the nerve plexus of the dermis to the basal cells of the taste bud. The

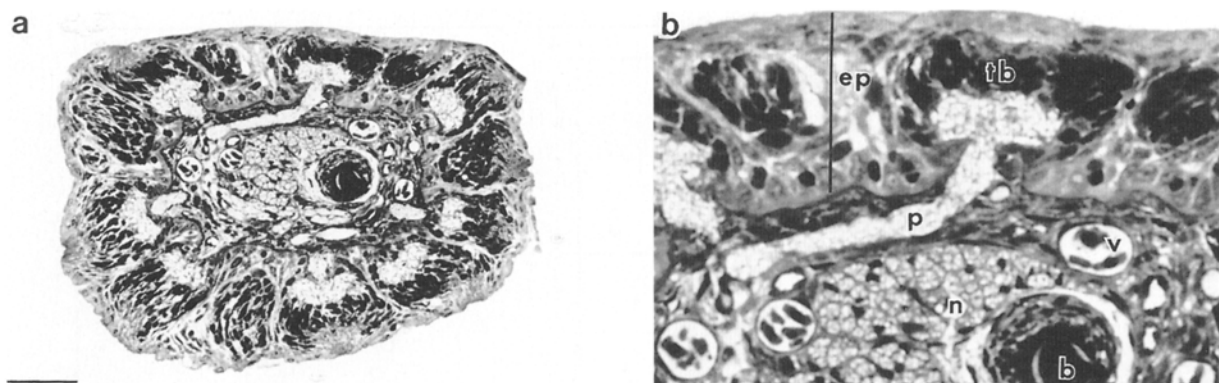


Fig. 2. Cross-section of a barbel of a newly-settled *Upeneus tragula* showing the major structural regions: a – Overview (scale 45 μ m). b – Detail of taste bud and papillar connection to the dermis. (b = bone; ep = epidermis; n = nerve bundle; p = papillary protrusion of dermis; tb = taste bud; v = blood vessel.)

dermis consists of connective tissue, large blood vessels, muscle cells and nervous tissue that emanates from the nerve bundle of the barbel. A large portion of the dermis is made up of bundles of nerve fibres, which represents a large branch of the facial nerve (Holland 1976). This nerve surrounds the ventral half of the supporting rod of bone and associated osteoblast layer (Fig. 2b).

Barbel development

The barbels develop as a modification of the anterior-most branchiostegal ray, articulating on extensions of the anterior end of the hyoid bar (anterior ceratohyal) (Gosline 1984). During larval development this modified ray migrates along the anterior ceratohyal, while at the same time the lower anterior ceratohyal extends forward. Figure 3 illustrates this forward migration as a measurement from the tip of the hyoid complex to the inside of the dentary. This distance is highly variable for a given fish length prior to settlement. Furthermore, the evident drop in hyoid to dentary distance for the newly-settled fish, together with the fact that in 40% of these fish the hyoid abuts the dentary, suggests that the rate of the forward migration of the barbels increases markedly at the time of settlement (Fig. 3).

During the initial stages of barbel development they are attached by a membrane to the ceratohyal. The stages at which this membrane breaks, and con-

sequently the time at which the barbels were potentially capable of functioning, were found to be highly variable both in terms of fish and barbel size. Barbels ranged in size from 0.9 to 2 mm long when first detached, while fish ranged from 10 to 22 mm SL.

During the pelagic phase the barbels exhibited a slightly exponential pattern of growth with fish length (Fig. 4, barbel length = $0.578 e^{(0.069SL)}$, $r^2 = 0.860$, $p < 0.0001$, $n = 180$, zero values excluded). Bar-

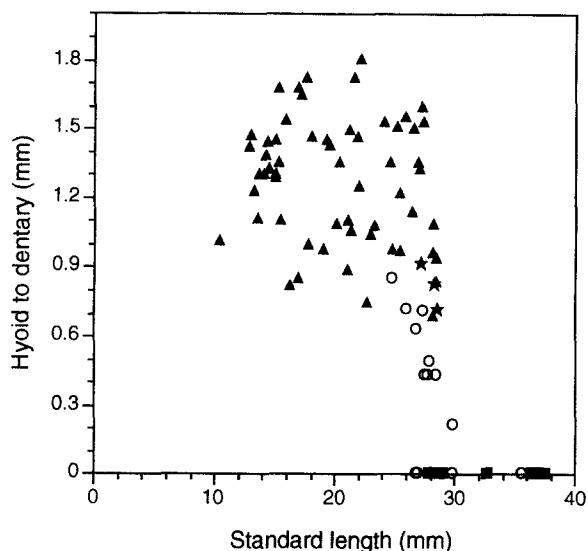


Fig. 3. Migration of *Upeneus tragula* barbels along the anterior ceratohyal as shown by the distance of the hyoid bar from the dentary as a function of fish length. Symbols: juveniles (■), newly-settled (○), partially-pigmented (★) and pelagic phase (▲). Symbols are the same for all other figures.

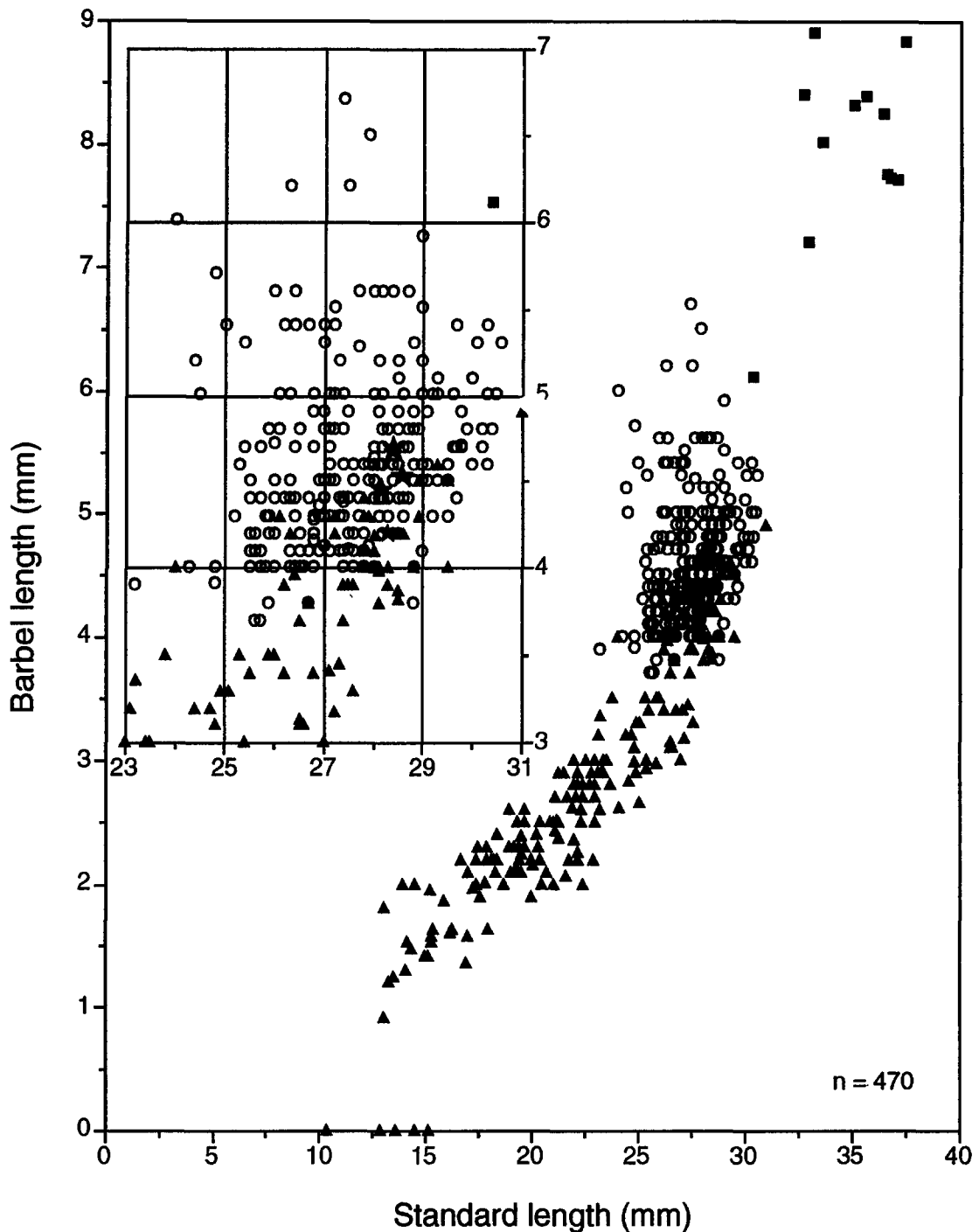


Fig. 4. The development of the barbels of *Upeneus tragula*. Inset shows an expanded section of the graph where the developmental stages of the fish overlap (Symbols as for Fig. 3).

barbels grew rapidly during the metamorphosis associated with settlement; a process which occurred overnight and took between 6 and 12 h in the lab-

oratory. This growth spurt may represent an increase in length of up to 52% in 12 h. Although data are few, there is a suggestion that barbel growth de-

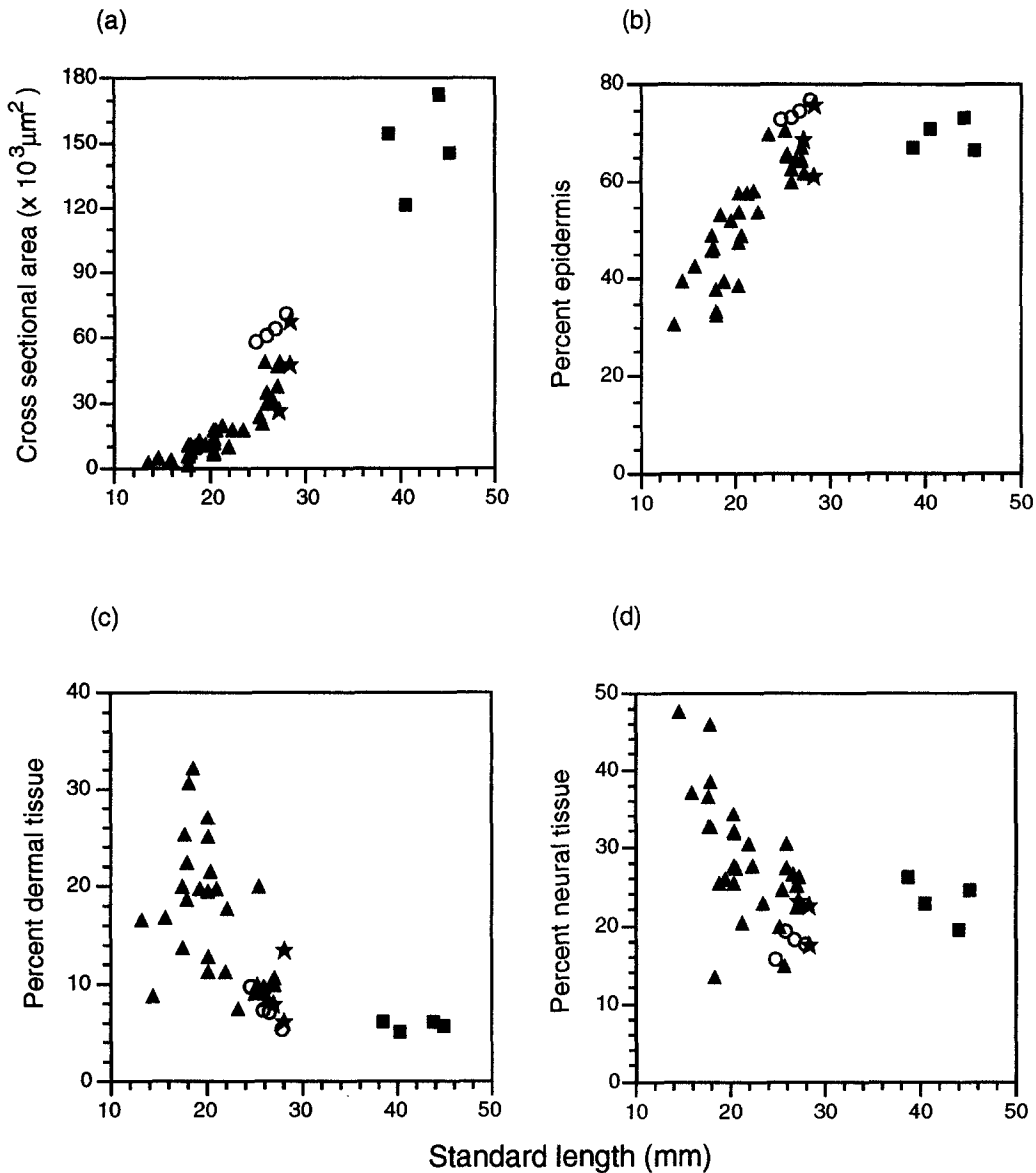


Fig. 5. Histological changes in the barbels with fish length for *Upeneus tragula*: a – Change in cross-sectional area of the barbels (one-third of their length from the tip). b – Change in the percentage of cross-sectional area of the barbel composed of epidermal tissue. c – Change in the percentage of cross-sectional area composed of dermal tissue. d – Change in the percentage of cross-sectional area composed of neural tissue. The four developmental stages are shown (Symbols as for Fig. 3).

creases after settlement (barbel length = $0.163 \text{ SL} + 2.298$, $r^2 = 0.223$, $p < 0.001$, $n = 12$). Barbel lengths from the partially-settled fish support the notion of rapid growth at settlement, being similar in length to that of the newly-settled fish (Fig. 4).

A rapid increase in cross-sectional area of the barbel was found to occur at settlement (one-third

the length from the tip) (Fig. 5a). This was mirrored by an increase in the percentage of the total cross-sectional area made up of epidermis (Fig. 5b). The percentage contribution of the epidermis to the total cross-sectional area exhibited an asymptotic increase which peaked at settlement at approximate-

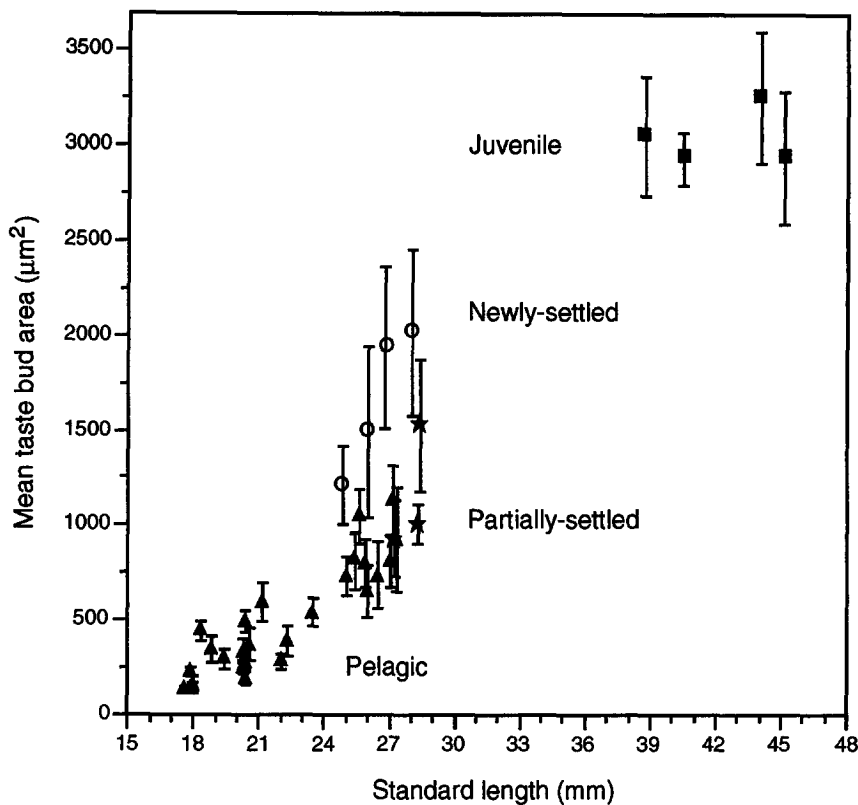


Fig. 6. Change in the area of the taste buds with fish length for the four developmental stages of *Upeneus tragula* examined. Means and 95% confidence limits are given (n = 8). Symbols as for Figure 3.

ly 75% (Fig. 5b). This contribution appears to remain relatively constant in the juvenile period.

At the same time, the dermal layer displayed an asymptotic decrease, with the point of inflection at approximately 18%, corresponding to settlement (Fig. 5c). The percentage contribution of neural tissue displayed a similar trend, maintaining a constant value of 6% after settlement. The amount of

dermal and neural tissue in the barbel prior to settlement was highly variable (Fig. 5c, d). This variability appears to be reduced after settlement, although this may also be a function of the smaller sample size.

The increase in the contribution of the epidermal layer to the cross-sectional area of the barbel is largely due to the contribution of the taste-bud

Table 1. Relationship between barbel length (BL) and four aspects of barbel microstructure for *Upeneus tragula*. All regressions are significant at $p < 0.0001$.

Dependent variable	Equation	r^2	n
Mean taste bud area (μm^2)	$407 \text{ BL} - 608$	0.9357	36
Taste bud density (no. per 0.01 mm)	$2.088 \text{ BL} - 0.226^*$	0.4000	36
Epidermal area (μm^2)	$13.660 \text{ BL} - 24707$	0.9080	41
Neural bundle area (μm^2)	$918 \text{ BL} + 133$	0.5918	40

*juveniles excluded.

Table 2. Comparison of the mean predicted taste-bud sizes for each fish in twelve samples of *Upeneus tragula*, spanning two recruitment seasons (4 in 1990–1991, 8 in 1991–1992). Mean square error associated with regression is accounted for in mean square error of the ANOVA and Tukey's (HSD) tests. Grand means of each sample (μm^2), sampling dates and statistical grouping from Tukey's tests are also given.

Source of variation	DF	Mean square	F value	<i>p</i>								
Sample	11	332782.8	4.956	0.0001								
Residual	225	67142.5										
Sample	3	12	4	2	10	11	5	9	7	6	8	1
Date	8.1.1991	16.12.1991	10.1.1991	5.12.1990	8.12.1991	11.12.1991	9.11.1990	3.12.1991	15.11.1991	13.11.1991	18.11.1991	11.11.1990
Mean	1395	1365	1354	1324	1276	1273	1153	1138	1119	1094	1027	939
Tukey's group	<div style="border-top: 1px solid black; border-bottom: 1px solid black; height: 10px; width: 100%;"></div>											

cells. The number of taste buds present in a 6 micron section increased linearly from none at approximately 18mm SL to a maximum of 8 at settlement. This number was then maintained in the juvenile period. The size of the taste-buds increased with standard length and displayed a similar trend to the change in barbel size. Taste buds increased their size by up to 100% during the 6–12 h period of settlement, reaching an average size of $1663\mu\text{m}^2$ (46–81 μm long axis, 23–58 μm short axis) (Fig. 6).

Both epidermal area and the mean size of the taste-bud cells were highly correlated to barbel length, while the contribution of the neural bundle to cross-sectional area and taste-bud density were only poorly related to barbel length (Table 1). This high correlation between taste-bud area and barbel length enables an examination of the potential sensory capabilities of a large number of fishes at settlement.

Variability in taste-bud size at settlement

There were significant differences between the mean taste-bud sizes, predicted from the relationship between taste-bud area and barbel length (Table 1), for the 12 samples of newly settled fish (Table 2). Mean taste-bud areas among samples ranged from 939 to $1395\mu\text{m}^2$, while overall they ranged from 532 to $1713\mu\text{m}^2$. The distribution of taste-bud

sizes represented a normal distribution (CV = 21.1%) (Fig. 7).

Feeding and temperature experiments

The allometric size of the barbels was found to be affected by the four feeding treatments (Table 3a). Barbels were largest on those fish which had received the least food (starved every second day, and fed once per day) (Fig. 8). This effect was consistent among the three tanks per treatment (Table 3a). Food availability also influenced the internal struc-

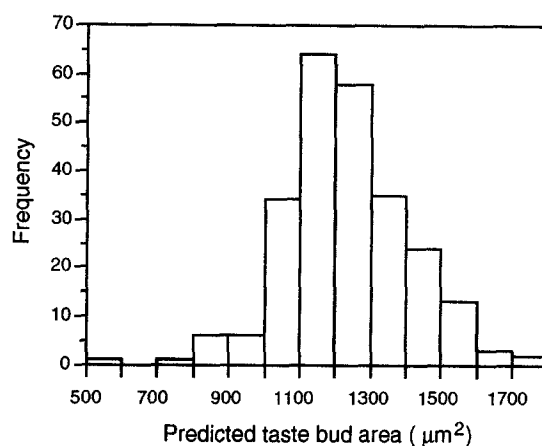


Fig. 7. Size distribution of predicted mean taste-bud areas for *Upeneus tragula* which settled the night after capture ($n = 237$). Taste-bud areas are predicted from the length of the barbels by the equation given in Table 2.

Table 3. The influence of food quantity and temperature in the pelagic phase on the length and microstructure of barbels at settlement: a – Comparison of barbel lengths from fish held within three tanks in four feeding regimes (diet). PCA was used to remove the confounding size component; PC 2, represented barbel allometric length, and accounted for 18% of the variation in the data set. b–d – Comparisons of various microstructural features among four feeding treatments and a field control (n = 4 fish). b – Epidermal area expressed as a percentage of total cross sectional area. c – Mean taste bud sizes, calculated from 8 taste buds areas per fish. d – Taste bud density, expressed as number of taste-buds within a section divided by cross-section circumference (mm). e – Comparison of barbel lengths from fish in 3 tanks at two temperature regimes (25, 30°C). PCA used as for ‘a’, and represented 5% of variation in the data set.

	Variable	Source of variation	DF	Mean square	F value	p
a.	Barbel length (principal component 2)	Diet	3	5.237	13.39	0.002
		Tank (Diet)	8	0.391	0.76	0.635
		Residual	217	0.512		
b.	Percentage epidermal area	Diet	4	173.050	9.59	0.0005
		Residual	15	18.050		
c.	Taste bud size (mm ²)	Diet	4	299.996	15.32	0.0001
		Residual	15	19.584		
d.	Taste bud density (mm ⁻²)	Diet	4	2.125	0.92	0.476
		Residual	15	2.300		
e.	Barbel length (principal component 2)	Temperature	1	0.059	0.33	0.598
		Tank (Temp)	4	0.180	0.66	0.624
		Residual	84	0.274		

ture of the barbels (Table 3b, c). The four feeding treatments did not affect the percentage of the cross-sectional area of the barbel comprised of epidermis, however, overall the feeding treatments did have significantly more epidermis than the field controls (Tukey’s tests). The mean taste-bud size of the fishes significantly differed among treatments, with the ‘starved every second day’ treatment hav-

ing the largest taste-buds, the fully-fed treatment having the smallest, and all the treatments having significantly larger taste-buds than the field-control (Fig. 9, Table 3c). For both the taste bud size and epidermis area, the ranking of the four feeding treatments was similar to that found for barbel length. The density of taste bud cells in a 6 micron section did not significantly differ among the four

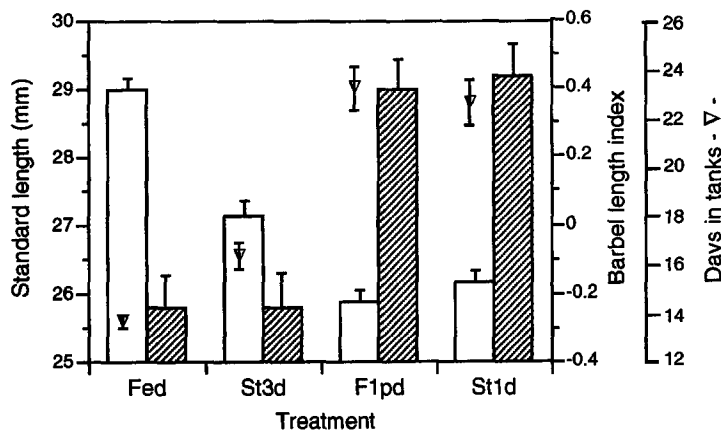


Fig. 8. Results of an experiment to examine the influence of feeding history within the pelagic phase on sensory development at settlement. Four feeding treatments are: fed = Fed ad libitum; ST3d = starved for 3d then re-fed ad libitum; F1pd = fed once per day; St1d = fed at libitum every second day. The fish length (plain bars), allometric barbel length of the fish (principal component standardized, hatched bars) are given. The time that fish were in the four treatments before settling is represented as triangles. Error bars are standard errors.

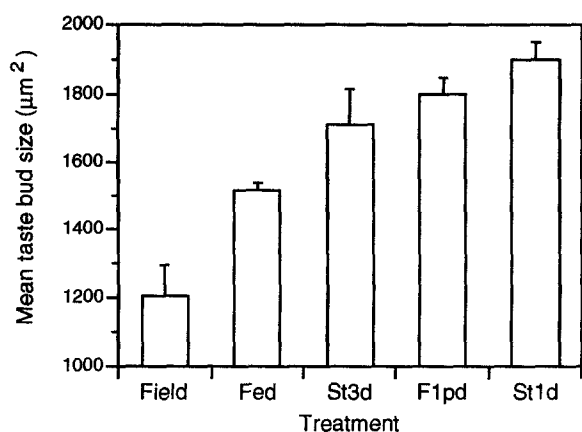


Fig. 9. Mean taste-bud size of barbels from 4 *Upeneus tragula* per treatment (abbreviations as in Fig. 8), for the four feeding regimes and a field control.

treatments or field control (Table 3d), but ranged from an average of 6.5mm^{-1} circumference in the fully-fed fishes, to 8.25mm^{-1} for fishes in the starved-every-second-day treatment.

Interestingly, there was a negative relationship between barbel size and body growth-rate. Fishes in the fully-fed treatment had the highest growth rate, settled at the largest size, but had the smallest barbels (Fig. 8).

There was no effect of temperature on the growth of barbels at the life-history stages used in the experiment (Table 3e), and the dissociation of growth of the body and barbels evident in the feeding ex-

periment did not occur (Fig. 10). Both allometric barbel length (i.e. PCA standardized) and standard length were smaller in the 30°C treatment than when reared at 25°C , although this difference was not statistically significant (Table 3e). Fish in the 25°C treatment did, however, take significantly longer to settle than in the 30°C treatment (Fig. 10).

Discussion

The present study emphasises the complex nature of sensory development and the potential importance of the sensory status of an individual at settlement. Four important points emerge from the results. The barbels of *Upeneus tragula* are rich in chemosensory structures. These sensory barbels show a brief period of rapid growth and differentiation which coincides with the transition from the pelagic to benthic life. The degree of development at settlement varies amongst cohorts of settling fish. This variability in development can be governed by feeding history through the influence of food on somatic growth rates and the timing of settlement. These observations have a number of important implications for our understanding of the development of sensory systems, in particular the relationship between fish size and sensory development.

Reviews of larval-prey/predator interactions stress the importance of the size of fish larvae in de-

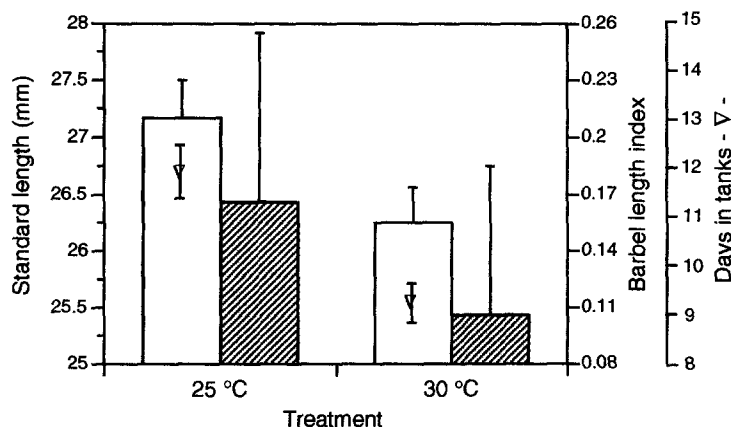


Fig. 10. Results of an experiment to examine the influence of water temperature within the pelagic phase on sensory development at settlement. Standard lengths (plain bars), allometric barbel length (hatched bars), and number of days fish were in tanks before they settled is given for the two temperature treatments.

termining survival, and the multiplicative advantages of a large body size through a positive feedback loop (e.g. Pepin et al. 1987, Yin & Blaxter 1987, Miller et al. 1988, Fuiman 1989, Margulies 1989). In such arguments sensory development is functionally tied to fish size. Generally, researchers have approached these questions pertaining to body size and development from a population perspective. However, when we look in detail at the individuals which make up the population at a particular ecological interval, as in this study, we find considerable variability in development. Furthermore, the sensory state of an individual was found to be under endogenous control and not necessarily tied to somatic growth. Thus, on an individual basis, fish length was not necessarily a good predictor of sensory capability.

Experimental manipulations of feeding history through to settlement found that fish with the fastest somatic growth rates, best muscle development (McCormick & Molony 1992), and largest body size at settlement had the least developed sensory system. Those fish that had the slowest somatic growth rate had the most developed barbels. Given that the ability of a fish to detect and capture prey and avoid predators will be related to both sensory and somatic development, there will be a survival trade-off between the speed at which a fish gets through the pelagic phase and its level of sensory development at settlement. What becomes important then is how ecological constraints, such as disease and predation, act as filters on the variability in the attributes of the population reaching the next developmental state.

Current research suggests that the mechanism behind this developmental response to varying biotic and environmental conditions may be similar for different elements of the teleost sensory system. This study found that food availability within the pelagic stage influenced the development of the barbels, while water temperature over an ecologically meaningful range had little effect. The length of the barbels and size of the taste buds were related to the length of time the fish had been pelagic, rather than the amount of food obtained. Experiments on bones within the labyrinth system have yielded similar results. A number of studies have found that

varying levels of food availability will cause the dissociation between otolith growth and somatic growth rate (e.g. Campana 1983, Reznick et al. 1989, Secor & Dean 1989). Some studies have found that temperature will not influence this relationship (e.g. Marshall & Parker 1982, Neilson & Geen 1982). Recently, Pankhurst (1992) found a similar relationship between somatic growth and visual development. Fish kept under poor feeding conditions had very large eyes relative to their body size compared to field caught fish. The growth and development of the barbels and eyes are likely to follow the model proposed for otoliths in being controlled by an endogenous rhythm that is modified under extreme conditions (e.g. Campana 1983) by the same factors that influence somatic growth (Campana & Neilson 1985, Secor & Dean 1989). The growth and differentiation of sensory tissue has a conservative response to environmental and biotic fluctuations, being an essential part of the developing body maintenance network.

In this conceptual framework metamorphosis of the sensory barbels does not occur as a direct response to the change in environmental cues associated with settlement, but rather is endogenously controlled and simply coincident with the shift between pelagic and benthic life. The magnitude of the sensory changes that occur emphasises the potential importance of settlement as a life-history transition. The changes that occur at metamorphosis and the potential for high mortality have led some researchers to refer to settlement as a 'critical period' (e.g. Blaxter 1988). In *Upeneus tragula*, metamorphosis represented a rapid change in the structure of the hyoid arch and barbels, with a dramatic increase in barbel length and taste bud size. McCormick & Shand (1993) found that a complementary changes in the retina morphology of *Upeneus tragula* occurs during settlement. An unusual double-layer of photoreceptive cone cells and high ratio of processing cells to receptor cells was present in the retina of pelagic *U. tragula*. This configuration resulted in a high visual acuity. During the 6–12 h period over which settlement occurred the cone layers inter-meshed to form a single layer, and information processing efficiency was greatly reduced (McCormick & Shand 1993, Shand 1993).

The present study is one of the few detailed examinations of the changes which occur during the settlement of a reef associated fish. The magnitude and rapidity of the changes (over hours rather than days) that occur in the barbel and visual systems of *U. tragula* have not been documented in other fish species. Unpublished data suggests that although some changes in the sensory systems of most reef fish are likely to occur during the settlement transition, these may be accentuated in the goatfishes (J. Shand personal communication).

The sensory development of a fish at settlement is important since the interaction between the sensory capabilities and behaviour will determine recruitment patterns through site selectivity. However, this paper stresses that the interaction between the ontogeny of the sensory system and the environment are complex. An increasing body of literature on otolith microstructure suggests that there is a three-way interaction between the environment, the sensory structure, and the behavioural response of a fish. Brothers & McFarland (1981) found 5 distinct eco-behavioural stages in the early life history of haemulids. Changes in the behavioural response to environmental cues resulted in changes in growth form of the otoliths in the labyrinth system. Similarly, many studies have found growth discontinuities in otoliths that are correlated with habitat shifts and behavioural change (e.g. Victor 1983, Pitcher 1988, Fowler 1989). Studies of the sensory and somatic development of reef fish both within and between species, together with measures of performance, will be important aids in the interpretation of the processes which influence the numbers reaching the adult stock.

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