

Developmental changes of the light intensity threshold for school formation in the striped jack *Pseudocaranx dentex*

T. Miyazaki^{1,*}, S. Shiozawa², T. Kogane², R. Masuda^{1,**},
K. Maruyama², K. Tsukamoto¹

¹Ocean Research Institute, University of Tokyo, Minamidai, Nakano, Tokyo 164-0014, Japan

²Goto Station, Japan Sea-Farming Association, Arakawa, Tamanoura, Minamimatsura, Nagasaki 853-0501, Japan

ABSTRACT: Light intensity thresholds for school formation were examined in 3 stages (20, 65, and 120 mm) of striped jack *Pseudocaranx dentex* juveniles with behavioural and histological approaches. Behaviour under a light intensity of 300 to 10^{-5} lx was recorded using a video camera, and schooling behaviour, swimming speed, and nearest neighbour distance were analyzed. The retina of fish adapted to each light intensity was histologically examined. The light intensity threshold for schooling behaviour in 20 and 65 mm fish was 5×10^{-2} lx, while that of 120 mm fish was 5×10^{-4} lx. The adaptation ratio, defined as the percentage of cone cell movement, ranged from 30 to 80 %, corresponding with 10^{-3} to 1 lx of light intensity in 120 mm fish, while 20 mm fish showed a much narrower range of adaptation ratio, i.e. from 50 to 70 %. Visual acuity increased exponentially with fish total length from 20 to 120 mm, corresponding with the increase of eye diameter. The higher range of adaptation ratio in 120 mm fish should enable them to recognize other fish even under low light intensity conditions and make their light intensity threshold for schooling lower than that of smaller fish. Establishment of behavioural and histological adaptability to lower light intensity should have relevance to the habitat shift that occurs in this juvenile stage from bright shallow reef pelagic waters to the offshore dark deeper area.

KEY WORDS: *Pseudocaranx dentex* · Carangidae · Schooling behaviour · Light intensity threshold · Visual acuity · Behavioural ontogeny · Habitat shift

INTRODUCTION

The schooling behaviour of fish has various ecological values, such as protection against predators, enhancing prey detection and providing opportunities for social learning (reviewed by Parr 1927, Shaw 1962, 1970, Pitcher & Parrish 1993). In most cases vision is the predominant sensory system used for forming and maintaining schools (Partridge & Pitcher 1980).

Fish visual acuity is reduced under low light intensity conditions (Brunner 1934, Nakamura 1968, Vin-

yard & O'Brien 1976, Confer et al. 1978, Schmidt & O'Brien 1982, Miyazaki & Nakamura 1990, McMahon & Holanov 1995). Under low light intensity, members in the school find it difficult to recognize each other, and thus their ability to maintain the school is probably reduced.

The light intensity threshold for school formation has been reported for several species (Table 1). These thresholds vary widely from 2.1 to 10^{-5} lx depending on the species. This variation in the threshold is probably caused by differences in retinal sensitivity (Tamura et al. 1957, Kobayashi 1972) and/or fish size and stage (Kitamura 1990). Few, if any, researchers have focused on the developmental changes of light intensity threshold in school formation.

Generally, eyes change from photopic to scotopic vision as light intensity decreases, and fish present

Present addresses:

*National Institute of Radiological Sciences, Isozaki, Hitachinaka, Ibaraki 311-1202, Japan.

E-mail: t_miyazaki@nirs.go.jp

**The Oceanic Institute, Waimanalo, Hawaii 96795-1820, USA

Table 1 Light intensity threshold for schooling behaviour in various species. TL: total length; SL: standard length

Species	Fish size	Threshold	Source	Converted to lx
<i>Oncorhynchus</i> spp.	39–34 mm	10^{-4} ft-c	Ali (1959)	10^{-3} lx ^a
<i>Menidia</i> sp.	12–18 mm	0.05 ft-c	Shaw (1961)	0.5 lx ^a
<i>Astyanax mexicanus</i>	75 mm TL	10^{-6} ft-c	John (1964)	10^{-5} lx ^a
<i>Trachurus symmetricus</i>	105–141 mm SL	6×10^{-6} – 6×10^{-7} ft-L	Hunter (1968)	3.5×10^{-5} lx ^b
<i>Pranesus insularum</i>	20–60 mm SL	2.1×10^{-1} ft-c	Major (1977)	2.1 lx ^a
<i>Engraulis mordax</i>	98–105 mm SL	6×10^{-11} W cm ⁻²	Hunter & Nicholl (1985)	2.6×10^{-2} lx ^c
<i>Scomber scombrus</i>	315–341 mm	1.8×10^{-7} μ E m ⁻² s ⁻¹	Glass et al. (1986)	10^{-5} lx ^d
<i>Brevoortia patronus</i>	19–22 mm SL	5×10^{-3} μ E m ⁻² s ⁻¹	Higgs & Fuiman (1996)	2.8×10^{-1} lx ^d

^aConverted as 1 lx = 0.0929 ft-c; ^bconverted by Hunter & Nicholl (1985);
^cconverted by respective authors; ^dconverted as 1 μ E m⁻² s⁻¹ = 5.55 ft-c (Higgs & Fuiman 1996)

their best visual acuity when they have photopic vision. Since school formation requires precise visual acuity, the light intensity at which retinal photomechanical response occurs may affect the threshold of this behaviour. Visual acuity and retinal sensitivity improve as fish grow (reported by Ali 1959, Blaxter & Jones 1967, Li et al. 1985, Pankhurst & Montgomery 1990, Miyazaki 1993, Pankhurst et al. 1993, Flamarique & Hawryshyn 1996, reviewed by Douglas & Djamgoz 1990). The light intensity threshold of schooling is therefore expected to decrease as fish grow.

The object of this study is to investigate the developmental changes of the light intensity threshold for schooling behaviour in the striped jack, which is an important commercial carangid fish in Asia and Oceania, particularly highly prized in Japan (Masuda & Tsukamoto 1998a). Underwater observations have revealed that juveniles larger than 40 mm in length usually form a school of 10 to 100 individuals, occasionally associating with floating objects or reefs in coastal areas, and that adults are caught from offshore waters of about 30 m depth or deeper (Masuda et al. 1993, 1995a). Little is known, however, about their ecology until they reach 40 mm.

We previously observed that striped jack do not school when their vision is impaired (Masuda et al. 1995b). This was in contrast to saithe *Pollachius virens* (Pitcher et al. 1976) or coho salmon *Oncorhynchus kisutch* (Azuma & Iwata 1994), which can join schools using only their lateral line systems. Exclusive dependence on vision in the striped jack may reflect the high visibility of their habitat in sub-tropical waters (Masuda et al. 1993, 1995a).

In the present study, schooling behaviour was compared under various light intensities in 3 different size groups, i.e. the 20, 65, and 120 mm groups. These size groups are ecologically significant for the relation to drift in offshore currents, recruitment to coastal areas, and habitat shift from shallow water to offshore reefs,

respectively (Masuda et al. 1993, 1995a, Masuda & Tsukamoto 1999). Development of visual acuity and the retinomotor response were also examined histologically in these stages. Based on these laboratory experiments and previous behavioural, histological, and field data, the ecology of the juvenile striped jack is discussed with special emphasis on the light intensity in their habitat.

MATERIALS AND METHODS

Fish husbandry. Striped jack juveniles were reared at the Goto Station of the Japan Sea-Farming Association (JASFA) in Nagasaki Prefecture, Japan, in 1993 and 1994. Eggs were stripped from wild caught parents (580 mm total length [TL] on average), fertilized, and maintained in a 0.5 m³ polycarbonate tank. Larvae hatched out 40 h after the fertilization and were transferred to an indoor concrete rearing pond (80 m³) 2 d after hatching. Rotifers *Brachionus plicatilis* and *Artemia salina* nauplii were fed on Days 3 to 40 (3.5 to 20 mm TL) and 20 to 40 (8 to 20 mm TL), respectively, and formula diet (Nissui Co. Ltd) was also provided from age 25 d onwards (10 mm TL). Juveniles over 35 mm TL were transferred to net-cages in the sea and were fed with formula diet. The water temperature of the indoor tank was maintained at 22 to 24°C, and the seawater temperature ranged from 16 to 28°C. Experiments were conducted for 3 sizes of fish of about 20 mm (21.0 ± 3.1 mm, mean ± SD), 65 mm (64.1 ± 4.1 mm), and 120 mm (119.3 ± 5.6 mm) TL.

Experimental protocol. We used 3 different sizes of experimental tanks depending on the size of the fish; 10, 200, or 500 l circular polycarbonate tanks (30, 85, or 117 mm diameter at the bottom) were set in a dark room (1.8 m² area and 1.8 m height) with a water depth of 10, 30, or 30 cm for 20, 65, or 120 mm fish, respec-

tively. Illumination was provided by 10 incandescent bulbs (40 or 100 W). With this lighting, the light spectrum is dominated (70 to 80%) by a wavelength of 550 to 600 nm at 50 cm depth (Koike 1989). Tanks were covered by opal-colored vinyl sheets, the spectral transmission of which was 27.5 to 71.5% for the 400 to 700 nm wavelength and 52.5 to 57.5% for the 550 to 600 nm wavelength (Hayashi et al. 1992). There was a linear relation between the number of sheets and light intensity attenuation. Light intensities of 300, 1, 10^{-1} , 10^{-2} , 10^{-3} , 10^{-4} , or 10^{-5} lx were thus obtained by changing the number of vinyl sheets from 1 to 25. Light intensity from 300 to 10^{-2} lx was measured at 5, 15, or 15 cm depth in the center of each tank by an underwater illuminance meter (ALM-1; wavelength range: 300 to 680 nm, peak wavelength: 620 ± 20 nm, measuring range: 10^{-2} to 10^5 lx, Alec Co.); extrapolated values were used for light intensities of 10^{-3} , 10^{-4} , or 10^{-5} lx. In this study, lx was used as the light intensity unit. The retinas of fish living at 5 to 30 m depth are reported to be most sensitive to the 550 to 600 nm wavelength (Kobayashi 1972). Our illuminance meter covered this range. For video recording, infrared light was provided by an incandescent bulb fitted with an infrared filter (Fuji film IR-78, cut below 730 nm, peak above 870 nm, Fuji Film Co.). This light, invisible to fish, was kept on throughout the duration of our experiments. Infrared radiation enabled us to observe the fish as dark silhouettes against the light background of the tank wall or bottom. Video recording was conducted by a Handy Cam CCD-V700 (SONY Co.) for 300 and 1 lx illumination or by a Night Viewer C3100 equipped with a CCD C3077 (HAMAMATSU Photonics Co.) for light intensity lower than 1 lx. The video camera was set above the centre of the tank, so the experimental video records were made in 2-dimension. The temperature of the experimental tanks was maintained the same as in the rearing tanks, ranging from 19.3 to 23.0°C using a water bath (10 l tank) or by exchanging water at a rate of 80 ml s^{-1} (200 and 500 l tanks).

Ten fish (the minimum number in a school observed in the wild; Masuda & Tsukamoto 1999) in each size group were put in the appropriate size tank and were acclimated to the tank at 300 lx for 1 h. To confirm that the school collapses in complete darkness, light intensity was reduced to 0 lx for 3 min, and then to confirm that the fish can form schools when they have enough light, the light intensity was raised to 300 lx for 2 min. After this initial procedure, each light intensity was tested for 30 min to find the light intensity threshold (light intensity profile is showed in Fig. 1).

Video analysis. Schooling behaviour was analyzed from the video record of the last 10 min at each light intensity. We measured schooling threshold, swimming speed, and nearest neighbour distance (NND).

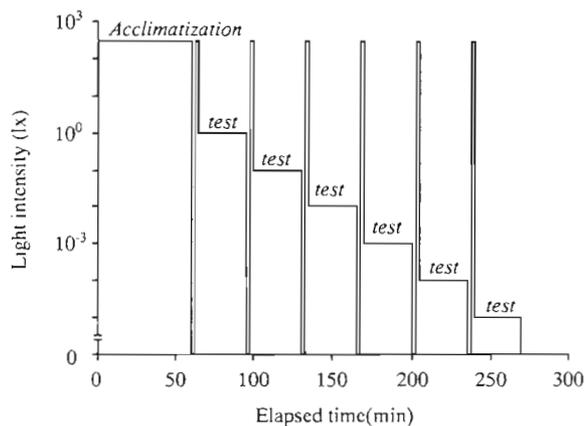


Fig. 1. Light intensity profile of the present experiment

In our study we considered fish to have presented 'schooling' behaviour when 50% of the fish swam in the same direction. At each light intensity a 2 min record was sampled twice, and the percentage of schooling duration was measured and defined as the 'schooling rate'. Average schooling rates in 3 trials were compared using a *t*-test.

Swimming speed was calculated by measuring the time needed to pass a line on the video monitor. The mean total length of the group of each experiment was divided by the time required to pass through the line, and swimming speed was thus obtained. Swimming speed was measured 100 times at each light intensity level by stopping the video record and arbitrarily selecting a fish from 10 fish in the monitor for 100 times, and the mean and standard deviation were calculated. The mean swimming speed for each light intensity was obtained from 3 replicates and compared among different light intensities by ANOVA followed by Bonferroni's test (Howell 1997) using Stat View J-4.51.1.

For each fish, the distance between its snout and the snouts of the nearest neighbours was measured, and the mean of 10 measurements was recorded as the NND (mm) on the frame. NND was measured 10 times for each light level, and the mean and standard deviations of 100 sets of data were calculated. The mean NND of 3 replicate tanks was obtained at each light intensity level and was compared by ANOVA followed by Bonferroni's test.

Histological analysis of vision. Fish were acclimated to each light intensity (300 to 10^{-5} lx) for 1 h (in previous studies salmonid fish *Oncorhynchus* spp. were acclimated for 50 min [Ali 1959], jack mackerel *Trachurus japonicus* for 60 min [Arimoto et al. 1988]). They were then decapitated after anesthesia treatment, and their heads were fixed immediately in Bouin's solution. Eyeballs were enucleated after 24 to 48 h of fixation, and eyeball and lens diameters were measured. Each retina was dissected into 5 mm squares, embedded in paraf-

fin, sectioned transversely at 4 to 7 μm thickness, and stained with haematoxylin and eosin. To estimate the light and dark adaptation level of the retina, the index of 'adaptation ratio' was applied based on the cone migratory position in the retina (Zhang et al. 1993). The distance between the cone ellipsoid and retinal pigment epithelium, and between the outer limiting membrane and retinal pigment epithelium, were measured. The ratio of the former to the latter was defined as the adaptation ratio. The light-adapted retina which was fixed under the natural light condition of daytime (about 10^5 lx) was also sectioned tangentially and stained. The visual acuity (VA) in each size group was calculated from the number of cone cells per 100 μm length of retina and the lens focal distance by the following formula of Neave (1984):

$$\sin \alpha = 1.11/(10d \times F)$$

$$\text{VA} = 1/[\alpha \times (180/\pi) \times 60]$$

where α (radian) is the minimum separable angle, F is the focal distance of the lens estimated from the lens radius (r , mm) using Matthiessen's ratio, and d is the density of cones, with adjustment for shrinkage. Matthiessen's ratio varies from 2.2 to 2.8 depending on fish species and size (Fernald 1990). We used 2.5 in our study ($F = 2.5r$). For the estimation of adaptation ratio and visual acuity, a 5 mm square of retina was dissected from the dorso-temporal region, since cone density was lowest in this area (Miyazaki et al. unpubl.).

RESULTS

Typical behaviour in the experimental tank

Three typical patterns of schooling behaviour were observed. One is that of the well-formed 'school' (Fig. 2a). Individual fish occasionally left the school but immediately rejoined it. The spread and contraction of school size was repeated irregularly. The school was observed under high light intensities (≥ 1 lx). The second pattern is 'aggregation', which occurred when all the fish gathered but their orientation was random (Fig. 2b). Aggregation was most frequently observed under low light levels from 10^{-1} to 10^{-3} lx. We labeled the third pattern 'random movement', and it was typically observed in darkness (Fig. 2c). All fish moved in

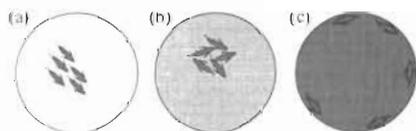


Fig. 2. *Pseudocaranx dentex*. Three typical patterns of schooling behaviour observed at different light intensity levels

random directions, swimming along the tank wall. Their swimming direction was not biased in a clockwise (52%) or counterclockwise (48%) direction (not significantly different in Mann-Whitney's U -test, $p = 0.186$, $n = 30$). Fish occasionally swam across the center of the tank but resumed this circular swimming along the wall after encountering the wall.

Light intensity threshold for schooling behaviour

In 20 mm fish, schooling was observed at 300, 1, and 10^{-1} lx with a relatively low schooling rate of 40.0, 39.1, and 24.3%, respectively (Fig. 3a). At 10^{-2} and 10^{-3} lx 20 mm fish did not form schools and showed random movement. These results indicated that the light intensity threshold for schooling of 20 mm fish exists between 10^{-1} lx and 10^{-2} lx, and thus we conventionally regarded their threshold as 5×10^{-2} lx. In 65 mm fish, the schooling rate was 94.6% at 300 lx, 89.6% at 1 lx, and 83.1% at 10^{-1} lx; these values were more than twice as high as those of 20 mm fish at each light intensity. At 10^{-2} lx, schooling collapsed. The threshold of 65 mm fish was expected to be between 10^{-1} and 10^{-2} lx; 5×10^{-2} lx was considered to be their threshold. Fish of 120 mm size showed compact schooling along

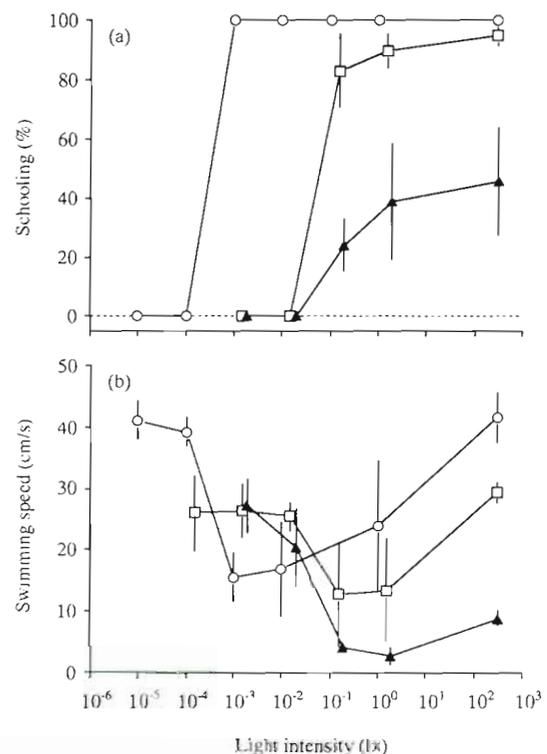


Fig. 3. *Pseudocaranx dentex*. (a) Schooling rate and (b) swimming speed under different light intensities. (○) 120 mm, (◻) 65 mm, and (▲) 20 mm fish; vertical bars indicate standard deviation

Table 2. *Pseudocaranx dentex*. Nearest neighbour distance (NND; mm) at different light intensity levels in each size group. RM: random movement

lx	Average \pm SD (mm)		
	20 mm	65 mm	120 mm
300	28.5 \pm 9.8	83.0 \pm 16.5	117.8 \pm 10.6
1	18.4 \pm 2.7	81.5 \pm 8.6	103.3 \pm 5.1
10 ⁻¹	15.5 \pm 1.4	87.5 \pm 9.5	- ^a
10 ⁻²	RM	RM	124.5 \pm 7.3
10 ⁻³	RM	RM	111.5 \pm 13.0

^aExperiment not conducted

the wall (schooling rate, 100%) when the light intensity was between 300 and 10⁻² lx. At 10⁻³ lx intensity, they tended to form a school at the center of the tank rather than along the wall, but they still maintained the school. At 10⁻⁴ and 10⁻⁵ lx, fish showed random movement, indicating that the threshold of 120 mm fish should be 5 \times 10⁻⁴ lx.

Fish of any size groups showed disordered swimming behaviour at first. After the 30 min acclimatization, schooling behaviour was observed and swimming speed was stabilized at about 15, 40, and 50 cm s⁻¹ in the 20, 65, and 120 mm fish, respectively. At a test light intensity of 300 lx, the average swimming speed was 8.6 cm s⁻¹ (4.3 TL s⁻¹), 29.3 cm s⁻¹ (4.5 TL s⁻¹), and 41.5 cm s⁻¹ (3.5 TL s⁻¹) in the 20, 65, and 120 mm fish, respectively. The swimming speed of all size groups decreased as light intensity decreased, until it reached the threshold; under light intensity below the threshold, swimming speed increased as the light intensity decreased (Fig. 3b).

In the 65 and 120 mm fish, individuals leaving the school were often observed at the light intensities of 1, 10⁻¹, and 10⁻² lx, resulting in a relatively low average and high variation in swimming speed. Swimming speed right above the threshold was 4.0 cm s⁻¹ (2.0 TL s⁻¹), 12.8 cm s⁻¹ (2.6 TL s⁻¹), and 15.6 cm s⁻¹ (1.1 TL s⁻¹) in the 20, 65, and 120 mm fish, respectively. These values were significantly smaller than the swimming speed at 300 lx (*t*-test, *p* < 0.0001). Swimming speed was significantly higher at light intensities below the threshold compared to intensities right above the thresholds (*p* < 0.0007 in 120 mm, *p* < 0.05 in 65 mm, *p* < 0.012 in 20 mm fish, Bonferroni's test). When light intensity was below the threshold, fish occasionally collided with the wall, so the variance of swimming speed was large at these levels.

NND decreased slightly in accordance with the decrease in light intensity in the 20 mm fish (Table 2; Bonferroni's test, *p* < 0.036 between 300 and 10⁻¹ lx). In the 65 mm and 120 mm size groups NND did not show this tendency, although 120 mm fish showed a slightly smaller NND at 1 lx compared to other light intensities

(*p* < 0.025 between 1 and 10⁻² lx in Bonferroni's test).

Visual acuity and adaptation ratio

Both eye diameter and lens diameter increased as fish grew (Fig. 4a,b). Cone cell density decreased until fish reached a TL of 90 mm, and thereafter it remained at a constant value of about 11/0.01 mm length (Fig. 4c). Visual acuity rapidly increased from

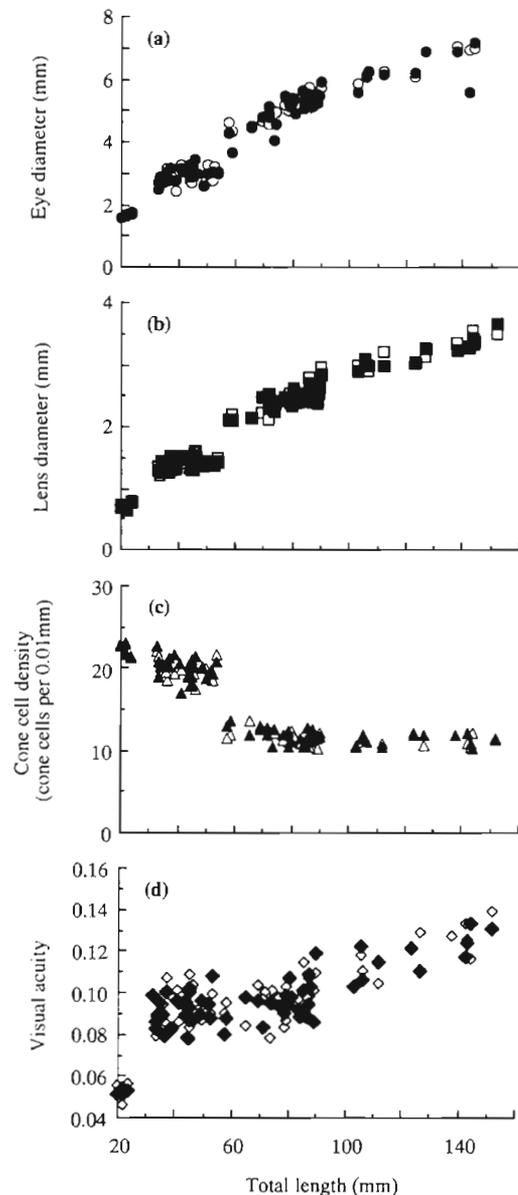


Fig. 4. *Pseudocaranx dentex*. Developmental changes in (a) eye diameter, (b) lens diameter, (c) cone density, and (d) visual acuity. Open symbols: right eye; filled symbols: left eye

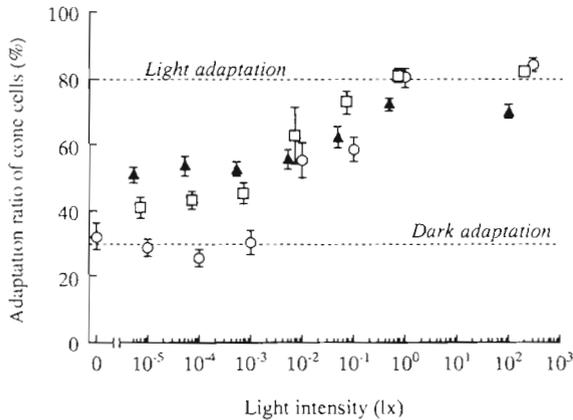


Fig. 5. *Pseudocaranx dentex*. Retinal adaptation of striped jack in (○) 120 mm, (□) 65 mm, and (▲) 20 mm fish

20 to 30 mm, and after that it increased almost linearly with growth (Fig. 4d).

In the 120 mm fish, the adaptation ratio at 300 and 1 lx was 84 and 80%, respectively, which was not significantly different; the ratio decreased to 10^{-3} lx and kept a constant value of about 30% at 10^{-3} to 10^{-5} lx (Fig. 5). It was noteworthy that the value was also 30% even at 0 lx. These results suggested that the adaptation ratio of the retina in the 120 mm striped jack was 80% at light-adaptation and 30% at dark-adaptation, respectively, and that they fully adapted to dark conditions at about 10^{-3} lx. In 20 mm fish, the adaptation ratio was not different between 300 and 1 lx; it decreased from 1 to 10^{-3} lx, and it remained constant

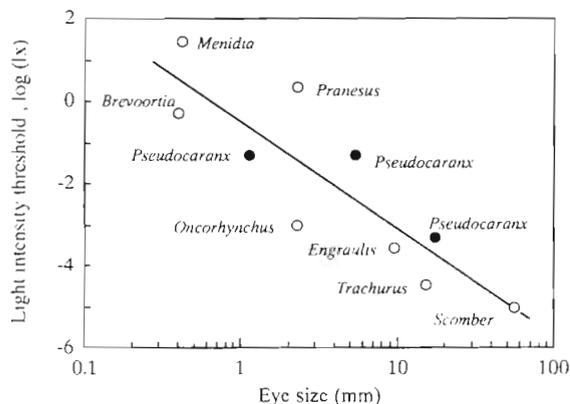


Fig. 6. Relationship between eye size and light intensity threshold of schooling. (●) Present study, (○) previous studies. *Oncorhynchus* spp. (Ali 1959), *Menidia* sp. (Shaw 1961), *Trachurus symmetricus* (Hunter 1966), *Pranesus insularum* (Major 1977), *Engraulis mordax* (Hunter & Nichol 1985), *Scomber scombrus* (Glass et al. 1986), *Brevoortia patronus* (Higgs & Fuiman 1996). Values of eye size in previous studies were redrawn from Higgs & Fuiman (1996). Thresholds were converted to lx (see Table 1) and changed to log scale ($\log(LT) = -0.51 - 2.60 \log(r)$, where LT = light intensity threshold, and r = eye size, correlation coefficient 0.87)

thereafter. Their adaptation ratio, however, was lower at light-adaptation and higher at dark-adaptation compared with that of the 120 mm fish. As for 65 mm fish, the pattern of the adaptation ratio for light intensity was similar to that of 120 mm fish.

DISCUSSION

Developmental changes in vision and schooling behaviour

The light intensity threshold for schooling decreased from 10^{-2} to 10^{-4} lx as fish size increased from 65 to 120 mm (Fig. 3a). If the threshold is affected only by vision, this can be attributed to the development of (1) visual acuity, (2) retinal sensitivity, and (3) eye size.

Visual acuity, which is closely related to schooling behaviour, increased from 0.05 to 0.11 as fish size increased from 20 to 120 mm (Fig. 4d). With these visual changes the maximum distance at which individuals could recognize each other was estimated to increase from 3.4 to 45.4 m in the same period ($D = (\phi \times VA \times 180 \times 60) \pi^{-1}$; where D = distance, ϕ = size of other fish, VA = visual acuity). The chance of losing sight of school members will thus decrease with growth. Retinal sensitivity to light stimuli increases rapidly with the development of rod cells and their increase in density (Guma'a 1982, Kawamura et al. 1984). In striped jack, rod cell formation was confirmed at 12 mm TL (Masuda & Tsukamoto 1996). Due to the appearance of rod cells, the striped jack's retinal sensitivity should increase significantly, enabling them to see each other while schooling even at low light intensity conditions.

Higgs & Fuiman (1996) summarized the relation between eye size (the square of eye radius) and light intensity threshold for schooling in several species and found that there is a strong correlation between these parameters (Fig. 6). Present data for striped jack fit this correlation well. These inter- and intraspecies comparisons support the assumption that eye size is the important determinant factor for the light intensity thresholds of school formation.

In coho salmon juveniles (130 mm TL), NND increased as light intensity decreased, suggesting that low visual acuity under the dark adaptation negatively impacts vision and schooling (Azuma & Iwata 1994). In our experiment such a tendency was observed only in the 20 mm fish but not in 65 or 120 mm fish. This discrepancy may be attributed to species- and/or stage-specific characteristics.

The schooling rate was higher in the larger fish (Fig. 3a). The lower schooling rate in 20 mm fish group may be due to (1) immature schooling behaviour, (2) difference in light intensity preference, and/or (3) differ-

ence in schooling motivation under the experimental condition. Striped jack are known to school at about 16 mm TL, and their NND decreases gradually until they reach the size of 30 mm (Masuda & Tsukamoto 1998b). Although buccal lateral lines were complete at 18 mm, trunk lateral lines were only formed from 20 to 30 mm (Masuda & Tsukamoto 1996). Therefore at 20 mm, schooling behaviour might not be fully matured. Retinal sensitivity to light stimuli might be different depending on size, which may well result in the light intensity preference. Striped jack juveniles at 12, 20, or 28 mm TL preferred 10^4 lx compared to 10^3 or 10^5 lx (Masuda & Tsukamoto 1996). Although we have no data on the light intensity preference of striped jack larger than 28 mm, 65 and 120 mm fish may well have lower light intensity preferences, since retinal sensitivity of fish generally increases along with retina development (Blaxter & Jones 1967, Kawamura et al. 1984, Champalbert et al. 1991). Given this, 20 mm fish could have shown a higher schooling rate at light intensities above 300 lx.

We used a water bath for 20 mm fish and circulation systems for 65 and 120 mm fish. The presence of water circulation in the larger group may have induced higher rates of schooling. However, it is not sensible to attribute the collapse of schooling to the presence or absence of circulation, since 20 mm fish resumed their schooling behaviour when light intensity was recovered to 300 lx. Further experiments will be required to understand the possible involvement of sensory organs other than the eyes.

Behaviour of wild fish under low light intensity conditions

Kobayashi (1972) reported that fish living at 5 to 30 m depth have maximum luminous efficiency of the retina at 550 to 600 nm, which is equal to the maximum wavelength transmitting in coastal water (Jerlov 1967). Although we have no information about the spectral luminous efficiency in the striped jack, we presume that this species has the same characteristics as other coastal species. Fig. 7 shows the relationship between depth and the attenuation coefficient ($k = 0.088 \text{ m}^{-1}$) measured in the sea off the Goto Station, JASFA (33° N , 129° E). As we consider light intensity as the major component of light attenuation, the underwater light intensity at the depth of 5 m is about 13% of that at the surface. Since the light intensity at the sea surface under a full moon is about 5×10^{-1} lx (US Navy Illuminance Chart [1952] referred to by Glass et al. [1986]), it is estimated to be about 6.5×10^{-2} lx at 5 m depth and about 5.1×10^{-4} lx at 60 m depth (Jerlov 1967: $I_m = I_0 \times \exp(-km)$; where I_m and I_0 = the illuminance at meter depth, m , and the sea surface, respectively). Present

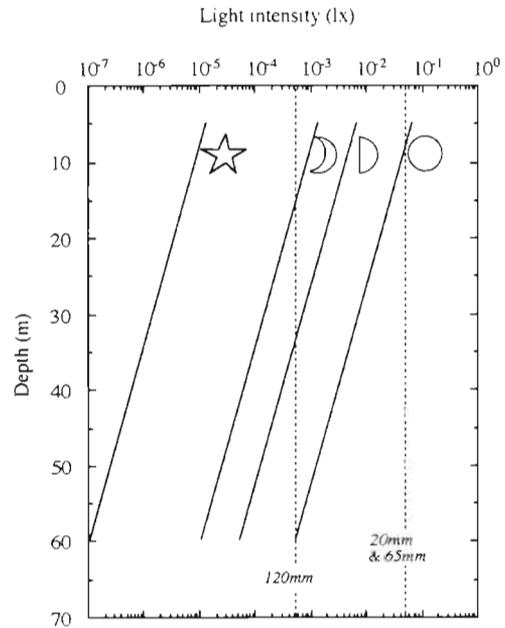


Fig. 7 Distribution of the light intensity in the sea estimated from the attenuation coefficient. Light intensity in each moon phase was redrawn from Glass et al. (1985)

work shows that 120 mm striped jack can form schools at 60 m depth in the full moon as the light level is higher than their threshold. Similarly, the limit of depth at which they can school is estimated to be 34 m during a half moon night (5×10^{-2} lx at the surface), and 16 m during a crescent moon night (1×10^{-2} lx at the surface). Striped jacks cannot maintain a school under new moon (star light) conditions because light intensity is only 10^{-4} lx even at the sea surface. Both 20 and 65 mm fish can school at 8 m or shallower under a full moon, and they cannot school under a half moon.

In the present experiment, fish swimming speed decreased when light intensity decreased. It should be difficult to continue parallel orientation under low light intensity conditions, since the striped jack maintain school by vision. Striped jack showed rapid and random swimming when light intensity was below the threshold. This might reflect their frantic condition caused by the lack of visual information about their school members. In the wild condition such a situation would be prevented in some way, since field observation revealed that the same group of striped jack remains in the same place over several nights (Masuda et al. 1993). Sogard & Olla (1996) reported that walleye pollock juveniles migrate close to the surface, become less active, and disperse their school at night. Such vertical migration has never been observed in the striped jack.

In natural waters at night, striped jack have been observed to associate with floating objects (Masuda et al. 1993), algae, and mooring ropes (Kuwada et al. unpubl.). These behaviours, defined as association

behaviours, have been reported in many species of fish (reviewed by Kingsford 1993). In laboratory conditions striped jack first associate with floating objects at 12 mm TL, show very strong association behaviour at 20 mm, and this tendency gradually decreases later on (Masuda & Tsukamoto 1999, Shiozawa et al. unpubl. data). When the light intensity is not enough to maintain schooling behaviour, they might utilize this association behaviour to keep aggregation. Strong association in 20 mm fish might supplement their relatively high light intensity thresholds, thus preventing the dispersion of school members at night.

The life history of striped jack is summarized as follows with respect to light intensity thresholds. Striped jack of 20 mm size typically drift with the current, probably associating with floating objects (Masuda & Tsukamoto 1999). At this stage their habitat is shallow water, and although their visual acuity is not as yet well developed, they can prevent dispersion at night by associating with floating objects. They migrate to coastal areas at 40 mm TL (Masuda et al. 1993, 1995a), and at 65 mm TL they are typically found at shallow shore reefs and their swimming depth is about 1 to 2 m (Masuda et al. 1993). Because their habitat is still shallow at this stage, they do not require a very low light intensity threshold to maintain a school. Their habitat gradually changes to deeper areas as they grow (Masuda et al. 1993); this may well be supported by the decrease in light intensity threshold shown in the present work.

We made our observations under controlled laboratory conditions using hatchery-origin juveniles. There is a possibility that experimental tank scales and hatchery conditions might have biased some of the behavioural characteristics of this species. For example, Petersen & Gadomski (1994) reported that chinook salmon *Oncorhynchus tshawytscha* can swim faster in a larger tank than in a smaller tank, resulting in a lower predation rate by their predators (northern squawfish *Ptychocheilus oregonensis*). McCartt et al. (1997) demonstrated that wild bluegills *Lepomis macrochirus* switch from schooling to hiding as light intensity increases, while hatchery fish extensively hide in shade at all light levels. To understand the mechanism of how schooled wild striped jack prevent dispersion at very low light intensity as in a new moon condition, further field experiments such as tracking by acoustic tags will be required.

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