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Modelling on Contrast Threshold and Minimum Resolvable Angle of Fish Vision

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어류의 시각 예민도-명암대비 역치와 최소 분해각-에 관한 모델링

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요 약

수중에서 어류들이 색이시 생물적인 목표물이나 어로작업시 어구 등의 시각자극과 최대탐지거리 등을 예측하기 위해서 어류의 주된 시각 예민도 요소인 명암대비 역치와 최소 분해각을 수치모델링 하였다. 어류시각의 명반응과 순반응에 따라 명암대비 역치와 최소분해각은 배경휘도와 체장에 따른 자연대수의 함수로 표현하였다. 이 때 관련된 수식의 계수들은 기존의 실험 결과나 어종간의 시각 예민도 등에서 추정할 수 있었으며 또한 생리생태나 개체차 등도 조정할 수 있다. 본 모델은 먹이생물이나 어구 등의 시각자극에 의한 시인정도와 시정 등의 추산에 이용될 수 있으며, 아울러 전반적인 수중 광학적인 조건하에서 시각자극의 세기에 따른 시각 예민도와 그 반응에 의한 어류행동 모델에 응용될 수 있을 것이다.

Introduction

The visual sensitivity has the most important role in fish response to an object, when background light is greater than the brightness threshold for the specific fish species in feeding (Langsdale, 1993, Utne, 1997), in schooling (Pitcher and Parrish, 1993) or in fishing operation (Glass and Wardle, 1989, Wardle, 1993) while the lateral line sensitivity to water flow or sound pressure may become a more effective factor when light conditions are below the light threshold (Chapman, 1969, Hawkins, 1993).

The visual capabilities of fish with respect to behavioural responses are reviewed by Douglas and Hawryshyn (1990). Visual sensitivity has many aspects and can be measured as brightness sensitivity, brightness contrast sensitivity, spatial resolution (minimum resolvable angle), movement detection, shape discrimination, colour vision. When considering underwater light conditions and the visual stimulus of the fishing gear among them (Wardle, 1993), the main sensitivity of fish vision could be regarded as the three sensitivities of brightness, contrast and spatial resolution. For these three visual sensitivities, published data do not include the most relevant species and do not compare data under the same light conditions or other experimental conditions. Existing studies do show quite large differences in sensitivity values although many of their differences may be because unlike vision tests of human these data were analysed using response behaviour.

Visual sensitivity measurements of fish vary according to species, size, and experimental condition as well as being due to the observation method and the visual stimulus used. Therefore, it is necessary to generalize in order to access the visual sensitivity of commercially valuable fish in particular underwater light conditions, in order to predict the sensitivity of the fish to visual stimulus of fishing gear. Modelling the visual sensitivity of fish in this study was carried out using values for the threshold of brightness contrast and the minimum resolvable acuity, based on the adaptation of existing data. This model of visual sensitivity in fish is used in the prediction of visibility in fish eye and the visual perception of visual stimulus intensity of the fishing gear or biological object in relation to a fish behaviour model.

Methods and Modelling

1. Assumptions

① The three main limitations for fish responding to the visual stimulus of an object are brightness threshold, brightness contrast threshold and minimum resolvable angle.

② The visual spectral sensitivity of fish is treated as monochromatic within the light wave lengths between blue and green.

③ In addition, the visual sensitivity of fish may vary with species, body length and background light level.

④ The brightness contrast threshold and minimum resolvable angle estimated in this study are regarded as mean values.

2. Modelling the brightness contrast threshold of fish eye

The light sensitivity of the fish was reported with a range of variances, dependent on the species and measurement method. The minimum luminance for detection of an object by goldfish (*Carassius auratus*) was found to be -7.5 ($log\ cd/m^2$) (Northmore, 1977). However, the Atlantic mackerel (*Scomber scombrus*) maintains schooling at -7 ($log\ lux$) (Glass *et al.*, 1986) while its brightness threshold to a certain type of twine was at most -3.6 ($log\ lux$) (Cui *et al.*, 1991). The illumination sensitivity must be reconsidered taking brightness contrast into account, for a clearer definition of what is seen, or not seen, by the fish eye.

The contrast threshold value of the Atlantic cod, *Gadus morhua* (Anthony, 1981) and bluegill sunfish, *Lepomis macrochirus* (Hawryshyn *et al.*, 1988) was adapted at each light intensity with an approximate conversion of the radiance unit (W/srm^2) to a luminance unit (cd/m^2) by Anthony (1981). The contrast threshold C_t at each background luminance can be expressed by the empirical exponential equation with total fish length B_L (m) using the data of Anthony (1981) as follows:

$$C_t = C_a \exp(-H_L B_L) \qquad (1)$$

where the slope $C_a = 6.1$ and power $H_L = 2.0$ for cod (Number of data $N = 29$, correlation coefficient $r=0.75$, $p<0.0001$). The slope C_a was closely related to the background luminance L_b (*log cd/m*^{2}) as in the following exponential equation:

$$C_a = C_o \exp(-H_b L_b) \qquad (2)$$

where C_o is intercept and H_b is power.

The power H_b can be estimated with two steps as a photopic to a scotopic adaptation for the Atlantic cod and is about 0.43 for scotopic and 0.6 for photopic (number of data $N=7{\sim}8$, $r=0.97{\sim}0.99$, $p<0.0001$) and for sunfish between 0.57 for green scotopic to 1.7 for red photopic ($N=15{\sim}20$, $r=0.92{\sim}0.99$, $p<0.0001$). The light level that causes photopic to scotopic adaptation to occur was reported to be between -2 and -3 (*log lux*) for the Atlantic cod (Protasov, 1968), between 1 and -2 (*log lux*) for plaice (*Pleuronectes platessa*) and between 1 and -1 (*log lux*) for herring, *Clupea harengus* (Blaxter, 1970). Considering this light adaptation of rod to cone response, the above calculated power H_b in equation (2) can be represented with transient light level for scotopic L_s and for photopic L_p and the coefficient H_b for scotopic H_s and for photopic H_p as follows:

$$H_b = H_s - (H_s - H_p)(L_b - L_s)/(L_p - L_s) \quad (L_s < L_b < L_p) \qquad (3)$$

If $L_b < L_s$, $H_b = H_a$ and If $L_b > L_p$, $H_b = H_p$.

Consequently, by substitution and adjustment of the above equations (2) and (3) the resulting contrast threshold C_t with light intensity, light adaptation and fish size is approximated as follows:

$$C_t = C_o \exp(-H_b L_b - H_L B_L) \qquad (4)$$

Unfortunately, contrast thresholds of the other valuable commercial fishes in fisheries have not yet been investigated. The coefficients in equation (4) can only be approximated from a general knowledge of the capability of a fish eye found from other aspects of visual sensitivity (Martin, 1983, Schellart and Prins, 1993).

3. Modelling the minimum resolvable angle of fish eye

The spatial resolution of a fish eye is the minimum resolvable angle of an object at the fish eye with the unit of minutes of arc (*arc min*). The spatial acuity is generally determined by factors such as the focal length of the lens, the size of the eye and the density of the visual cells in a fish eye retina (Tamura, 1957, Tamura and Wisby, 1963, Fernald, 1990). Accordingly it follows that there are more variances in minimum resolvable angle depending on fish species and body length as well as the kinds of objects being viewed and how much light intensity there is.

The relationship between minimum resolvable angle and body length in herring (*C. harengus*) was estimated by the measurement of the focal length and the density of the retinal cell (Blaxter and Jones, 1967). The result of calculated resolvable angle A_L (*arc min*) in herring can be expressed as empirical regression equation with body length B_L (*m*) in the range 0.1~0.3 *m* from adapted data by Blaxter and Jones (1967) as follows:

$$A_L = j_L \exp(-k_L B_L) \qquad (5)$$

The coefficients j_L and k_L of herring are 48.93 and 2.11 ($N=12$, $r=0.83$, $p<0.001$).

The minimum resolvable angles of fish were also changed by the background light intensity from measurements using yellowfin tuna

(*Thunnus albacares*), skipjack tuna (*Katsuwonus pelamis*), and little tunny (*Euthynnus affinis*) by Nakamura (1969), and other 3 species (goldfish, *Microcanthus strigatus and Phoxinus laevis*) from Douglas and Hawryshyn (1990). The relationship between minimum resolvable angle A_b (*arc min*) and background luminance L_b (*log cd/m²* as converted after Meyer - Arendt, 1968) was recalculated with the data of the above 6 species as the following exponential equation:

$$A_b = j_b \exp(-k_b L_b) \qquad (6)$$

where j_b and k_b are coefficients. The range of coefficients k_b for yellowfin tuna, skipjack and little tunny using adapted data by Nakamura (1969) is $j_b = 5.4 \sim 8.3$, $k_b = 0.37 \sim 0.41$ ($N = 17 \sim 21$, $r = 0.89 \sim 0.93$, $p < 0.001$) and for the other 3 species $j_b = 16.5$, $k_b = 0.38$ ($N = 25$, $r = 0.91$, $p < 0.001$).

To generalize the effects of fish size and light, let us combine the above two equations into general minimum resolvable angle A_m with the coefficient k_L of fish length, k_b of light intensity and A_o of resultant intercept with j_L and jb as follows:

$$A_m = A_o \exp(-k_b L_b - k_L B_L) \qquad (7)$$

The coefficients A_o, k_b and k_L should be adjusted and approximated in order to use the equation for the minimum resolvable angle for the fish. The abstracted data on minimum resolvable angle for fish are available in the table by Douglas and Hawryshyn (1990). Another approach was used by Schellart and Prins (1993) who suggested the possible use of the visual index to estimate the spatial acuity. If the lighting condition and fish size of a particular species is known, the coefficient A_0 for minimum resolvable angle can be estimated using the values of the visual index under constant k_b and k_L.

Results

The coefficients of equations (4) and (7) for the visual capability of marine fish are roughly adjusted from previous coefficient for relevant species and referring to published results on visual sensitivity (Douglas and Hawryshyn ,1990) in Table 1.

Table 1. The approximate coefficients of brightness contrast threshold in equation (4) and minimum resolvable angle in equation (7) for 9 species of round - fish and a flatfish

Species	Contrast threshold*		Resolvable angle*	
	C_o	H_b	A_o	k_b
Haddock, whiting	4	0.60	9	0.46
Mackerel, tuna, skipjack	3	0.65	6	0.50
Flatfish, place	10	0.45	15	0.40
Cod, saithe	5	0.60	9	0.45
Herring	4	0.60	9	0.45
Salmon	6	0.60	10	0.45

* $H_L \fallingdotseq k_L \fallingdotseq 1.5$
haddock (*Melanogrammus aeglefinus*),
whiting (*Merlangius merlangus*),
saithe (*Pollachius virens*), salmon (*Oncorhychus mykiss*)

The relationship between the intercept C_o in equation (4) or A_o in equation (7) as approximated values in Table 1 and visual index V_i from Schellart and Prins (1993) were shown in Fig.1. From close relationship between V_i and minimum resolvable angle demonstrated by Schellart and Prins (1993) it can be represented as following exponential equation:

$$C_o = 22.98 \exp(-0.389\, V_i) \quad (n=6, r=0.94, p<0.01)$$
$$A_o = 17.32 \exp(-0.544\, V_i) \quad (n=6, r=0.93, p<0.01) \qquad (8)$$

Consequently, intercept C_o or A_o and power

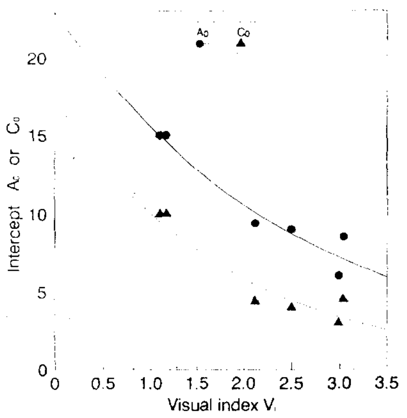

Fig. 1. The relationship between the intercept C_0 in equation (4) or A_0 in equation (7) as approximated values in Table 1 and visual index V_i from Schellart and Prins (1993). (V_i for herring was assumed as 2.5 due to lack of data).

H_b or k_b for other species of fish can be estimated by allometry of visual index V_i.

An example of the calculated contrast threshold for cod with three different body lengths and coefficients C_0, H_b and H_L in Table 1 is plotted against background luminance in Fig. 2 fitting well with the measured values by Anthony (1981). The estimated minimum resolvable angle of herring with coefficients A_0, k_b and k_L shown in Table 1 was also plotted with different body lengths and light levels in Fig. 3. The estimated minimum resolvable angles for herring against background light levels, were shown to fit closely to the original data given by Blaxter and Jones (1967). Above results of visual sensitivity model for cod and herring are derived from empirical data and therefore test between measurement and model is unnecessary. For other species, further statistical test of this model is impossible at the present because of lack of data on visual sensitivity under different conditions.

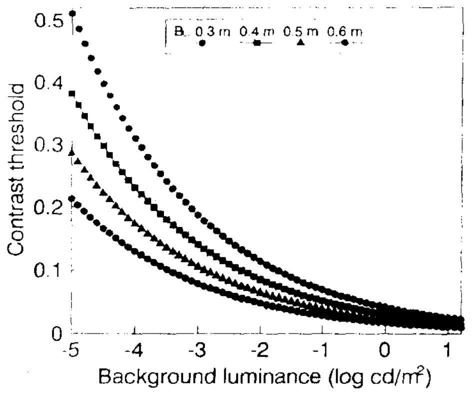

Fig. 2. An example of the calculated contrast threshold for the Atlantic cod for four body lengths (B_L), against background light intensity. (Refer to measured values by Anthony, 1981).

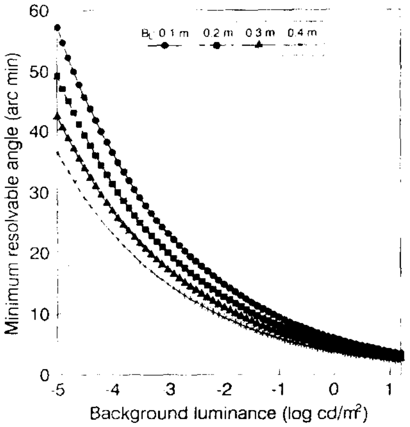

Fig. 3. The estimated minimum resolvable angle of herring for four body lengths (B_L) against background light level. (Refer to measured values by Blaxter and Jones, 1967).

Discussion

The brightness contrast threshold and minimum resolvable angle of a fish eye can be estimated by using this model with body length, background light level and water temperature as well as physiological conditions of fish. The minimum brightness contrast threshold have been measured as 0.003 for red colour wavelength to 0.007 for green light for bluegill sunfish by Hawryshyn *et al.*(1988) and 0.006 for squid (*Todarodes pacificus*) by Siriraksophon *et al.*(1995).

The calculated values of minimum resolvable angle of fish, from the focal lengths and the density of retinal cells showed a minimum 2 *arc min* for tuna (*Thunnus atlanticus and Tetrapturus albidus*) (Tamura and Wisby, 1963). A behaviourally measured minimum value of 3 *arc min* was reported for herring (Blaxter and Jones, 1967). The variations in the contrast threshold or angular acuities of fish could be predicted using the developed model of visual sensitivity with adjustment of the coefficients in relevant equations considering the differences of species.

The visual stimulus of the trawl gear to the fish eye as established in the model was considered as a dynamic visual stimulus when in a moving net. For example moving objects can be more easily detected by fish or human eyes than stationary objects. It was demonstrated that the contrast sensitivity function was the function of contrast threshold to spatial frequency of an object. The contrast threshold of goldfish was decreased from about 0.4 at an object frequency 0.3 – 0.4 *cycles/deg* to about 0.04 at 3 *cycles/deg* (Northmore and Dvorak, 1979). The threshold of flickering frequency of haddock, whiting and mackerel were increased with light intensity (Gosden, 1994). However, flickering effects of the moving net as mesh pattern in the field has not been verified for response behaviour of fish.

Furthermore, objects showing both positive and negative contrasts, so – called spatial contrast to background, can also be seen more clearly than objects with homogeneous contrast. The actual images of the trawl gear during operation were revealed to be a complex of positive and negative contrasts (Kim and Wardle, 1998a). The contrast threshold of fish measured in static conditions therefore must be reconsidered in modelling the fish's recognition of visual stimulus from the trawl gear. Effect of water temperature on visual sensitivity as, the contrast threshold of goldfish was also observed from 0.05 at a water temperature of 20 ℃ to 0.1 at 35 ℃ according to the physiological conditions (Hester, 1968). In this model, the intercept C_0 of the equation (4) should be modified according to species and surrounding conditions for this reason.

The next point to consider with the minimum resolvable angle of fish is the contrast value of the object when experiments are carried out. Most of the angular sensitivity values are given as minimum resolvable angles abstracted in the table by Douglas and Hawryshyn (1990) and were obtained when the object contrast was equal to or near 1. However, it was predicted to be less discernible at lower contrast. Furthermore, the image size alters with the viewing angle of the object and the dominantly visible zone of the object is sometimes different from the actual size of the object, depending on zenith and light intensity, as described Kim and Wardle (1998a). As observed in the contrast of nets and floats, the reflected area or size was changed with the zenith angle giving a range of positive and negative contrast, especially with spherical or cylindrical surfaces.

Fish can be considered to discriminate the shape of objects such as a net or a predator and prey, as well as size and distance if there is enough light and significant contrast (Douglas and Hawryshyn, 1990). The colour sensitivity and critical flicker frequency of fish vision are regarded as less important in fishing operation than either contrast or spatial acuity when considering the underwater light conditions and fishing conditions.

The visibility S_v (m) as minimum resolvable angle A_m can be expressed with visible size of the object D_v (m) was expressed by Kim and Wardle (1998a) as follows:

$$S_v = D_v/\tan(A_m) \tag{9}$$

The visibility by the brightness contrast threshold of fish C_t and inherent contrast C_i of an object was represented with integration of differential $d(S_v)$ from 0 to S_v involving underwater light transmission from Kim and Wardle (1998b) as follows:

$$\ln(C_t/C_i) = \int k_c\{-c+k\cos(Z_a)\}d(S_v) \tag{10}$$

where c is a beam attenuation coefficient, k is a vertical attenuation coefficient, Z_a is a viewing zenith angle and k_c is a coefficient. The maximum S_v which is satisfied equations (9) and (10) can be considered as visibility of fish at viewing geometry and light conditions. There are some results on visibility and reaction distance of fish (Nakamura, 1989, Langsdale, 1993, Gregory, 1993) and fishing operation (Zhang and Arimoto, 1993). However, visibility for specific object should be considered by sensitivity of fish eye and surrounding light conditions as a whole.

Consequently, the visual sensitivity of fish to the visual stimulus such as prey, predator or fishing gear must consider as a whole the fish, the object and the light. If the visual stimuli of the object are greater than the brightness contrast threshold in equation (4) and minimum resolvable angle in equation (7), fish can detect the parts of the object under the viewing geometry and light conditions. By this model and by including some assumptions, both the visual ability of the fish as visibility and the intensity of the visual stimulus in a viewing geometry can be predicted for any fish species, with biological or physical objects and background light conditions as given in fishing operation Kim and Wardle (1998b) as well as feeding and schooling function.

Conclusion

The visual sensitivity of fish as mainly brightness contrast threshold and minimum resolvable angle was formulated in order to predict the visibility and intensity of visual stimulus such as biological object in feeding or physical object in fishing operation. The brightness contrast threshold and minimum resolvable angle of fish were linearly varied with background luminance and body length as expressed in relevant exponential equations involving scotopic and photopic adaptation of fish eye. The parameters of the above equations were deduced for some commercially important fishes by measurement results or by comparing the sensitivities between species. These models could allow for the prediction of a maximum detection distance of fish by visual stimulus such as prey or predator in feeding as well as in fishing gear and are related to predictions of the intensities of this stimulus in a fish behaviour model under optical conditions of sea as a whole.

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