Modification of Teleost Visual Feeding Range Model for Cuttlefish:

A Visual-Systems Comparison

by

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With human activity causing increases in turbidity in coastal marine waters, it is of economic and ecological importance to understand how this increase will affect organisms living in these areas. At most risk may be predators, such as many teleosts and cephalopods, reliant on vision to detect and capture prey. While many studies have examined how turbidity changes the visual range of feeding fish, none have been found for cephalopods, major invertebrate predators. This study compared aspects of teleost and cephalopod visual systems using a model developed for feeding teleosts in turbid environments. When the properties of the visual system between cephalopods and teleosts were compared for their response to environmental attributes, some aspects were similar while others were divergent. With the variability between the visual systems, I found that a model for vertebrates could not be easily applied to invertebrates. However, I was able to identify areas of continued and future study. With research in these areas, it will become possible to model the impact of turbidity on the visual range of feeding cephalopods.

Bachelor of Arts in International Studies in Biology
Thesis of Rebekah E. Ebel
Presented on August 26, 2011

Approved:

Thesis Advisor

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I understand that my thesis will become part of the collection of Oregon State University. My signature below authorizes release of my thesis to any reader upon request. I also affirm that the work represented in this thesis is my own work.

Rebekah E. Ebel, Author

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Introduction

Mainly due to human activity induced increase in nutrients, eutrophication is dramatically increasing in marine environments globally (Bennet et al 2001, Glibert et al 2006). This eutrophication often results in an increased frequency of algal blooms that in turn increase turbidity of oceanic water. Decreasing water clarity affects the abilities of many marine organisms to perform a variety of behaviors at the individual, such as predation, and community levels (Bak & Meesters 1999, Gregory & Levings 1998, Järvenpää & Lindström 2004, Utne-Palme 2002). While extensive research has been done on the effects of turbidity on the behavior of teleost fish, comparatively little has been done on those of cephalopods. Cephalopods, like teleosts, use vision to detect and capture prey and are thus subjected to the same vision-related predation difficulties caused by turbidity. A decline in successful feeding might be expected to cause declines in cephalopod populations globally. This paper compares the visual systems of cephalopods and teleosts as a means of 1) determining the potential use of a model designed for teleosts as a model of turbidity's effect on visual feeding by cephalopods and 2) discerning directions for future research in this area.

The comparison of the visual systems of cephalopods and teleosts has been a major point of interest for many researchers over the decades. The "convergent" evolution of the cephalopod camera eyes with those of vertebrates has sparked interest in examining the physiological and image processing similarities between these two types of eyes. I will compare the ecological niche and visual systems of teleosts and cephalopods with special attention given to cuttlefish. Then this information will be used to evaluate a model produced by Aksnes and Utne (1997), produced to predict the minimum distance at which a teleost is able to detect its prey under different environmental conditions. The model also accounts for variation in prey size, fish size, and neural processing of visual information. My hypothesis is that the similarities in eye structure and function between cephalopods and teleosts will allow for this mathematical model designed to predict visual range for feeding by teleosts to be applied to or modified for cephalopods.

Ecological Comparability of Cephalopods and Teleosts

Both fish and cephalopods live throughout the ocean's depths, a region spanning from shallow near-shore tide-pools to the lightless abyss. Different species are adapted to fit different environments within this range, and similar adaptations are found between species sharing a similar environment. Thus, species of teleosts and octopus can be found occupying similar environments within the ocean (Packard 1972). For example, cuttlefish often occupy the same habitat type as flatfish, the common octopus with groupers, and various squid with various species of shoaling fish. Gobies occupy a range of habitats in shallow coastal waters. Likewise, most known octopus species are found in shallower waters along the continental shelf. Various species of *Sepia* (cuttlefish) can be found along the entire vertical range of the continental shelf (Figure 1). The environmental conditions encountered in waters in this depth range vary greatly, so cuttlefish and shallow dwelling teleosts are adapted to living in dynamic environments (Packard 1972).

Through varying depths of water, several abiotic factors change, and these factors will change the environment faced by organisms and subsequently their ability to interact with their environment. With increasing depth, these changes include decreased penetration of light and increased pressure. For these abiotic factors, vertebrates and invertebrate eyes might be expected to have similar adaptations. In the eyes of both animals, the lens is spherical, allowing it to withstand pressure and to capture light travelling through water. Cephalopods maintain the ability to detect and interpret polarized light as easily as teleosts. Polarized light detection is important for prey detection for cephalopods and especially for vertical orientation in water in both cephalopods and teleosts. Teleosts have more visual pigments than cephalopods, which only have one. The one exception is *Watasenia scintillans*, the firefly squid, which has three photopigments (Land & Nilsson 2002). Other forms of light detection include polarization sensitivity and ultraviolet detection.

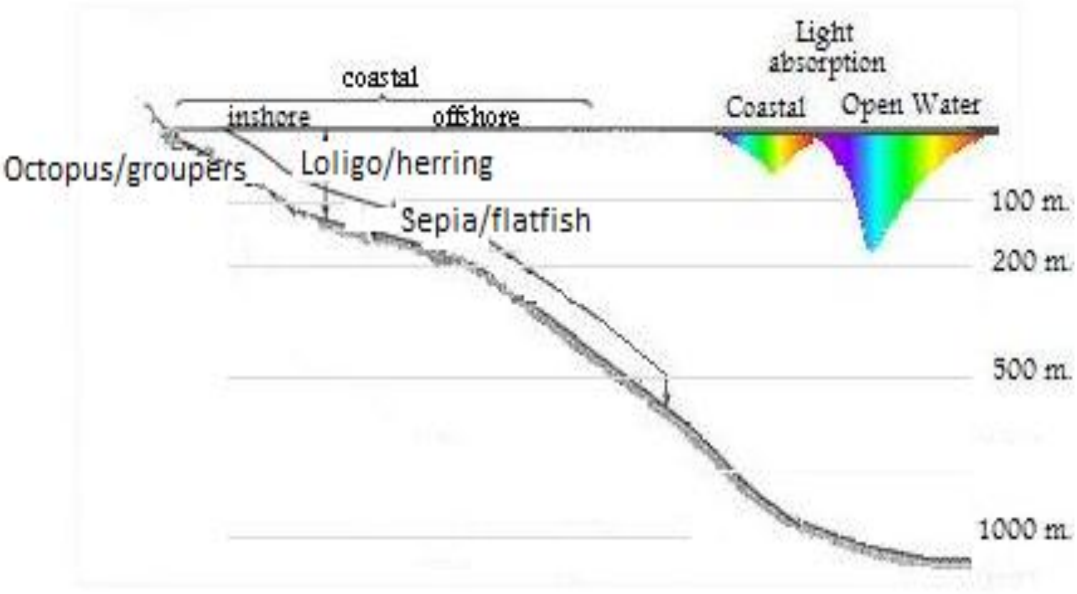

Figure 1.1 Distribution of several cephalopod genera through the ocean and light penetration depth of specific wavelengths [adapted from Packard (1972) and Hollocher (2002)].

Fish and cephalopods exhibit similar trends in their life histories. Settlement behaviors are similar in that cephalopod larvae and most teleost larvae are planktonic before settling. However, settling behaviors within and between fish and cephalopods vary greatly. Several species of fish, octopus, and cuttlefish settle in a range of shallow coastal depths. Other species of squids, pelagic octopods, and marlin are fully pelagic their entire lives. There are also examples of fish and cephalopods found in the aphotic, low oxygen deep sea and include the angler fish and the vampire squid.

The Teleost and Cephalopod Eye

Fish have eyes very much like those of most other vertebrates. Fish have spherical lenses made of soluble proteins that refract light with a short focal length of about 2.5 lens radii (Land & Nilsson 2002). A spherical lens that is not made of completely homogenous protein causes the effect of spherical aberration, or image distortion (Land & Nilsson 2002). They also experience chromatic aberration, meaning that a lens cannot focus on all wavelengths simultaneously (Land & Nilsson 2002). Marshall (1966) found that the proteins in the lens give fish eyes the highest refractive index of all vertebrates (as cited in Moyle and Cech 2004). Cech and Moyle (2004) also state that because the lens is spherical while the eye is elliptical, the way light is received by the retina gives fish nearsightedness towards the front and farsightedness to the sides, aiding in prey capture. Light is received by rods and cones, each with its own refractive index and containing the photochemically active pigment rhodopsin (Wolken 1995). In shallow water fishes, rods and cones are both found to exist in high densities (Moyle and Cech 2004).

When light enters the eye of a cephalopod, it passes through a lens that is very similar to that of a teleost. However, one major difference is in the way that the two lenses develop. In fish the lens is its own entity, but in cephalopods it is thought that the lens develops as a cellular by-product since it is formed as two hemispheres rather than one continuous structure (Packard 1972). There is very little difference in the way that light passes through the vertebrate and cephalopod lenses. The Mathiessen’s ratio is a way of measuring the strength of the lens, or its focusing power, and is calculated as the distance from the lens to the retina divided by the radius of the lens. In teleosts and cephalopods, this ratio generally hovers around 2.5, but there is a wider range of possible ratios in fish, generally from 2.3 to 3.6 (Garner et al 2001, Shand et al 1999). Sivak et al (1994) found that the ratios for four species of squid ranged between 2.56 and 2.79 and that the cuttlefish had one of 2.65, demonstrating a similar range for cephalopods and teleosts.

After passing through the lens, the image is projected on the retina. In teleosts the image is inverted while is cephalopods the image is direct and upright. In teleosts, the photoreceptors face backwards into the eye and the nerves are located between the retina and the lens. In cephalopods however, the photoreceptors directly face the incoming light, while nerve cells are located behind the photoreceptors (Land & Nilsson 2002). This is significant because it means that the photoreceptors in vertebrates do not directly face incoming light and the light has the obstruction of the nerve mass to pass through. In cephalopods, it is the opposite- there is a unidirectional path from lens to receptors to nerves to optic lobe (Land 1984). A significant difference in the ability to process visual information due to this path has not been recognized. Cephalopods have one photoreceptor pigment that absorbs light of 475-500 λ (Hamasaki 1968, Hanlon and Messenger 1996).

Retinal ganglion density increases with age and size of the eye in teleosts, and the same has been found with cuttlefish (Hao et al 2010). An increase in retinal ganglion density is well known to correlate to an increased visual acuity. While many interspecific comparative studies of this correlation have been done in terrestrial animals and marine vertebrates, very little has been done on the retinal topography of cephalopods (New & Bull 2011, Pettigrew & Manger 2008, Shand 1997, Talbot & Marshall 2011).

The Visual Feeding Model

A mathematical model for estimating visual feeding, or the range at which prey can be detected, by teleosts was derived by Aksnes and Giske (1993), and was later revised to account for changes in saturation at varying light intensities by Aksnes and Utne (1997). This model takes many factors into consideration to estimate the visual range including factors such as light intensity, prey size, and superficial neural processing at the eye. There have been several studies that test this model using experimental data analysis described after the following description of the revised and original models.

The model is only useful if the number of photons entering the eye surpasses the sensitivity threshold, the smallest detectable change in photons on the retina from background to background and prey. This means that there needs to be enough light available for differentiating the prey from the environment. If there is no light, nothing can be seen, but as light availability increases, sight becomes clearer to the point where the eye can detect the difference between prey and its background; this is called the sensitivity threshold.

One way of calculating this threshold is by multiplying the contrast of the prey's image on the retina, the background irradiance on the retina, and the size of the prey's image on the retina. There are many factors that affect the ability of an eye to detect differences between prey and environment including and summarized by the factors listed above. The clarity of the water greatly influences ability to see as it is more difficult to detect the outlines of prey in turbid or suspension filled water. The size of the prey is also an important factor in that it is generally harder to see small objects than large object when all other factors are held constant. Similarly, it is easier to detect prey that is at a nearer distance than a farther one. The changes in distance cause the prey to seem larger or smaller when the images are reflected onto the retina. The mathematical derivation of many of these factors is described in detail in Aksnes and Giske (1993).

In addition to this information, the model also includes the effect of neural processing on prey detection ability. To do this, the equation for threshold is multiplied by the coefficient that converts radiant energy to neural activity to get the amount of neural activity when prey is detectable. Ultimately, this step considers the amount of neural processing that occurs for a given animal when it first is able to recognize prey. Finally, the model accounts for the distance between the prey and the fish lens and the movement of light through this distance.

To summarize, the equation incorporates the minimal amount of radiant flux needed for detection of prey, the transformation of light energy to neural activity, the distance from the prey to the lens and how light travels in that distance. A final equation, after rearrangement for clarity, is as follows.

$$r^2 \exp(cr) = |C_0| A_p E' \frac{E_b}{K_e + E_b}$$

Range can be calculated if all of the following are known: the light energy to neural activity transformation coefficient, sensitivity threshold, maximal light transmission to retina that can be processed, contrast of the prey, size of the prey, background irradiance, and the attenuation coefficient.

In testing their model, Aksnes and Utne were able to positively show that the revised model more accurately represented real data than the original model (Figure 2). They tested their model for detection distance at varying levels of brightness against two species of prey copepods.

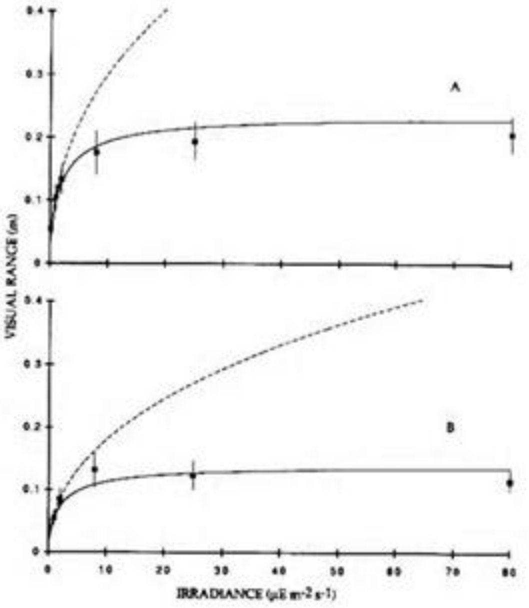

Figure 1.2 Experimental data compared to the model’s projected visual range showing the improvement of the revised model A compared to the old model B (from Aksnes & Utne 1997).

This model can be used as a predictor for the distance at which a fish sees its prey, and while it was formed for feeding on copepods by goldfish, it has been experimentally shown that the success of predation of a variety of prey sizes from plankton to small fish can be increased with a higher range of visibility (Benfield & Minello 1996, Gregory & Levings 1998). The biological and ecological factors needed to fulfill the requirements of using this model are what are used for the comparative analysis between cuttlefish and teleosts.

Methods

This paper is primarily a literature review designed to compare the visual systems of cephalopods and teleosts from an ecological stand point. As such, an extensive review of journal articles, books, and other sources was performed over a long period of time. The information was categorized as ecology, biology, and neurology for either cephalopod or teleost. Topics not falling under these categories were less common so categorization was unnecessary.

The Aksnes & Utne model for predicting the visual range of underwater predators was chosen, because it estimates a fish's ability to see under conditions (example: turbidity) that in recent years are changing and could jeopardize a predator's ability to survive. This model is also used because the biological factors used are comparable to those found in cephalopods.

As demonstrated previously, substantial research of many types has been done on a variety of teleosts over the last century, but less has been done on cephalopods. The cuttlefish was found to be the cephalopod with the most research available for use in this study, which is why it is used as a model organism for comparison. For this comparison, taxonomically comparable categories are used. Cephalopoda is a class, and Teleostei is an infraclass. Since cuttlefish are used as a model organism, it is important to note that cuttlefish comprise an order within the class, while the information about fish systems comes from a variety of classes. When possible, information on other coleoid cephalopods is provided to better support comparability.

In order to quantify the similarities and differences between cuttlefish and teleosts, a method was devised specifically for this study that rates the comparative categories on a scale. These values are used to show how similar a characteristic is between the two classes relative to other characteristics. If enough information is not available, the data is clearly marked and factored into the score to limit misrepresentation of similarity.

Topics are chosen based on 1) the relevance to the model and 2) the prevalence of research in the literature- that is, the recurring points of focus in the literature. Research to which special and substantial attention has been given for comparisons of teleosts and cephalopods is given high priority in determining the topics used here. This list of topics is by no means completely comprehensive, but is a representation of the main topics discovered while reviewing the literature. In this method, topic specificity for comparison is determined based on availability of information. Topics are general if the majority of information available on that topic is general, likewise for specificity. Example topics include the “presence of extra-ocular photoreceptors” and “perceived wavelengths.” Scoring accounts for both similarities and differences within a topic simultaneously to give a relative “overall” similarity.

The topics for comparison are provided in tabular form along with specific information to be used for analysis. The scores are presented in a similar table with explanations given that defend the score. These tables are found in the “Findings” and “Analysis” sections of this paper, respectively. To help organize the topics of comparison, there are four categories of topics: “Image Formation,” “Light Sensing,” and “Visual Acuity.” Each category is represented by its own tables.

The scale for scoring is from 0% - 100% where 0% signifies no similarities or no basis for comparison (no information available), and 100% suggests that the two groups compare as virtually identical for the topic. If substantial information is not available, the score is followed by a superscript “I” for incomplete. The list of scores for all the comparison topics is used to indicate directions for new research. The way that the score is calculated is described here.

1) An initial score (S^0) of 100% similar is given for the topic subject to comparison.
2) The magnitude of the difference (d) between cephalopod and teleost for that topic is determined.
   a. If the topic is numerical (such as average eye diameter), the magnitude is found by subtracting the smaller value from the larger value and then dividing by the larger value. Multiply by 100. This gives a percent.
   b. If the topic is categorical (such as types of photopigments), the different traits are counted and then divided by the number of similar traits plus different traits. Multiply by 100. This gives a percent.
3) The magnitude of information still needed (i) is determined for the topic.
   a. If a lot of information is still needed, a value of 15 is used.
   b. If some information is needed, a value of 10 is used.
   c. If very little information is still needed, a value of 5 is used.
4) The magnitudes of difference and of information still needed are rounded, then subtracted from S^0 to give the final score (S): $S = S^0 - d - i$

The other goal of this paper is to discuss the potential for using the Aksnes & Utne model using cuttlefish as the subject of interest. To estimate the potential of using the model for cuttlefish based on information found in this review, the average of the scores was taken.

To help assess the international scope of this project, a pie chart of the international distribution of authors cited was made using the program Microsoft Excel. This information was taken from the affiliation information found on every paper. Authors were counted multiple times if they were on multiple papers. Also from the list, a percentage was calculated by hand of papers that had international collaboration between authors on the same paper (also using the affiliation information). This information is presented in the "Discussion" section.

Findings

Table 3.1 Information is listed on the comparable topics under the category of Image Formation.

		Teleosts	Cuttlefish
Image Formation	Extraocular photoreceptors	Opsins are present in the pineal gland in the brain (Bertolucci & Foa 2004)	Opsin transcripts in skin are the same as in retina, epistellar body is suggested in cuttlefish and confirmed in octopus and squid (Cobb & Williamson 1998a & 1998b, Mathger et al 2010, Tong et al 2009)
	Ocular photoreceptor pigment	Rod opsins are variable. The gene lacks an intron, lost in evolutionary process. Teleosts found in intermediate depth coastal waters generally have 2 pigments in the cones (Bellingham et al 1998, Bowmaker & Hunt 2006), Levine & MacNichol 1979, Lythgoe & Partridge 1991)	Rhodopsin is the only pigment and its genetic sequence contains an intron not found in vertebrates or many other invertebrates (Bellingham et al 1998, Cronin 1986)
	Ocular photoreceptor structure	Rods and cones are present, lamellar, and occur in bundles of cells (Land 1984, Braekevelt 1982)	There is only one photoreceptor type, microvilli-covered (Land 1984, Hao et al 2010)
	Lens shape	The lens is spherical and has an axial thickness of 2% less than the equatorial diameter of the lens (Jagger & Sands 1996)	The lens is spherical and has an axial thickness of 5% less than the equatorial diameter of the lens, making it less spherical than that of a teleost (Jagger & Sands 1999)
	Lens movement	The lens is adjusted by 6 muscles, and it develops as one unit (Land & Nillson 2002)	The lens is adjusted by 6 functional muscle groups, and it develops as 2 hemispheres separated by a layer of living cells (Land & Nillson 2002)

	Lens functionality	Teleosts have a graded refractive index with a focal length of approximately 2.5 times the radius. The lens is solely responsible for image formation (Groeger et al 2005, Shand 1997, Shand et al 1999, Sivak & Luer 1991, Sivak et al 1994)	There is a graded refractive index with a focal length of 2.5 times the radius, enabling high quality imaging. The lens is solely responsible for image formation (Hanlon & Messenger 1996, Sivak & Luer 1991)

Table 3.2 Information is listed on the comparable topics under the category of Visual Systems.

		Teleosts	Cuttlefish
Light Sensing	Polarized light detection	It is used for orientation in the water and is possibly used for enhancing image formation in color-rich shallower coastal waters (Hawryshyn 2010, Kamermans & Hawryshyn 2011)	It has an important role in prey detection, although there is some experimental evidence suggesting that some cuttlefish may process polarized light differently (Shashar et al 2000, Darmaillacq & Shashar 2008)
	Polarized light sensitivity (target detection experiment)	Fish did not respond at all when presented with the same stimulus as the cephalopods (Pignatelli et al 2011)	Two species of squid and one of cuttlefish responded when presented with the target, showing ability to respond to polarized light (Pignatelli et al 2011)
	Wavelength filtering	Yellow light (570-590 nm) is filtered out by the eye. This may increase visual acuity (Guthrie & Muntz 1993)	Wavelengths below 370nm, above 590nm, and the UV range are filtered out. Photoreceptor length can be changed to effect this (Shashar et al 1998, Packard 1972)
	Wavelength discernment	The full spectral range of red to ultraviolet is visible due to presence of rods and cones, with maximal absorption at approximately 490 nm (Foster 2004)	The visible range is 475-500nm, with a maximal absorption around 490 nm. They are color-blind. (Mathger et al 2006)

Table 3.3 Information is listed on the comparable topics under the category of Visual Acuity.

		Teleosts	Cuttlefish
Visual Acuity	Response to light intensity changes	Reactive distance decreases with increased light intensity, to a threshold (Mazur & Beauchamp 2003, Richmond et al 2004, Vogel & Beauchamp 1999)	A positive correlation of visual acuity and light intensity exists (Groeger et al 2005)
	Pupil response to light intensity change	There is a very slow to non-existent response (Guthrie & Muntz 1993, Muntz 1999)	The immediate pupil change is the "fastest in animal kingdom." This may make the eye superior to that of fish (Douglas et al 2005, Packard 1972)
	Pupil shape/mobility	The pupil is round and, in most cases, unable to be contracted (Muntz 1999, Schaeffel et al 1999)	In cuttlefish, it is W-shaped and easily contractible, allowing for light to be focused onto specific parts of the retina (Muntz 1999, Schaeffel et al 1999)
	Visual acuity peaks	The best found among teleosts is 0.49 (Bluefin tuna) (Kawamura et al 1981)	In *Sepia esculenta*, acuity has been measured at 0.36 (Watanuki et al 2000)
	Visual processing Pathway	Visual information is processed in the retina. See Figure 3.1 (Land & Nillson 2002)	Visual information processed outside the eye, but the eye is close to optic lobe. See Figure 3.1 (Land & Nillson 2002)

Table 3.4 Information is listed for comparing topics in the Ecology category.

		Teleosts	Cuttlefish
Ecology	Early life	There is variability, with examples from pelagic to epibenthic/near shore larvae (Shand 1997)	Octopus are not benthic until they reach 173 mg. Cuttlefish are also pelagic as larvae then become benthic (Villanueva 1995, Perez-Losada et al 2002)
	Vertical distribution	This is highly variable (Packard 1972)	This is highly variable (Packard 1972)
	Body size	This is comparable to those of cephalopods (Packard 1972)	This is comparable to teleosts (Packard 1972)
	Predation strategy	There are difference in locomotor tactic depending on predator species not on prey species, with 1 tactic per species (Webb 1984)	This is a complicated, 3-step, process. In the third step, there are 2 prey type dependent options (Messenger 1968)
	Primary prey types	Diet includes copepods, crustaceans, and fish. Some fish have diet change from invertebrates to other fish as they age (Marks 1993, Plattell & Potter 2001)	Diet includes fish, crab, shrimp, annelids and other cephalopods. There is a shift from invertebrates to fish as they increase in age (Adamo 2006, Blanc 1998)
	Response to prey shoaling behavior during hunting	Predation will be deterred (Neill & Cullen 1974)	Predation will be deterred (Neill & Cullen 1974)
	Life history/reproductive	Strategies are variable between orders (Rochet 2000)	Strategies are relatively similar between cuttlefish, octopus and some squid (Rocha et al 2001)

	strategies		

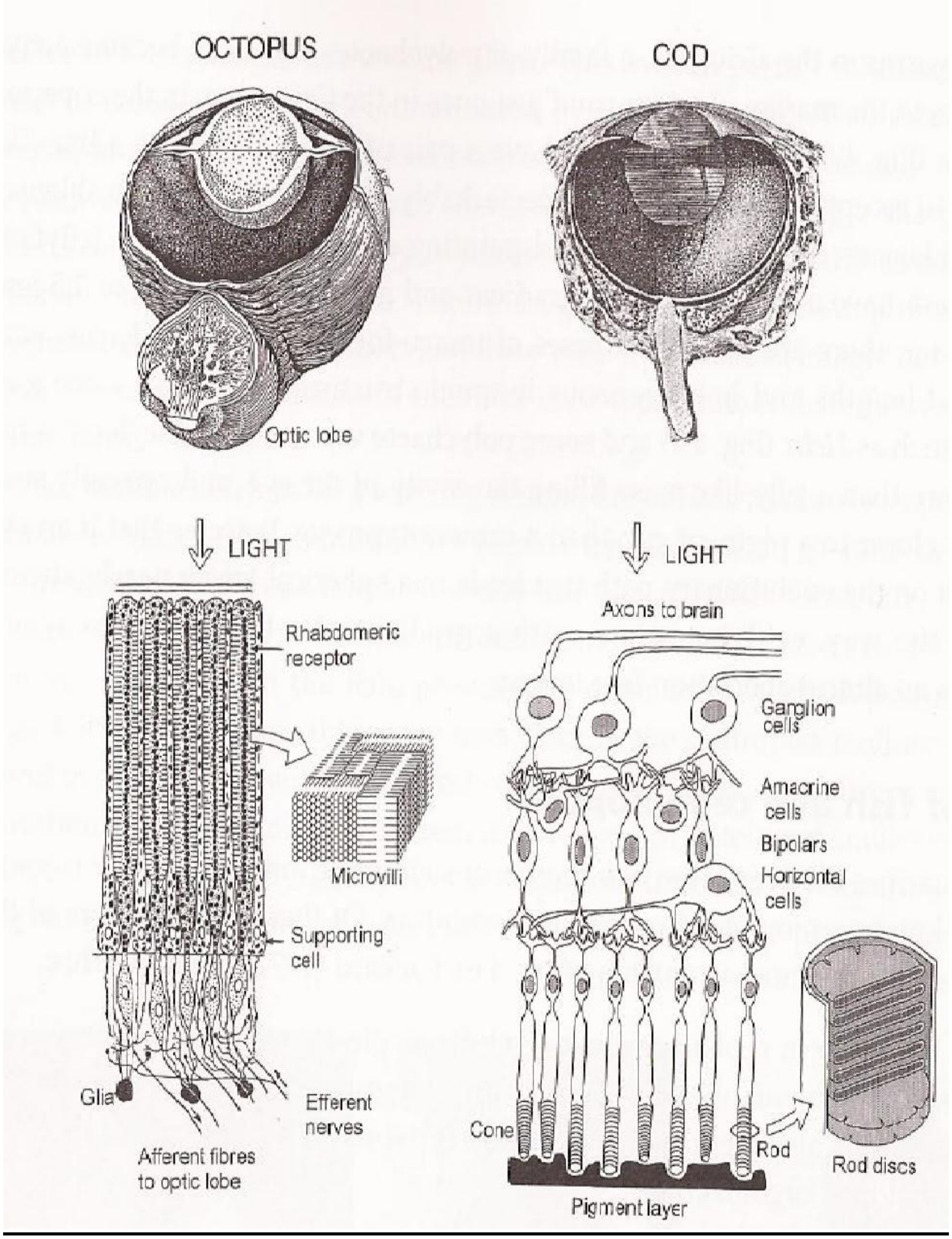

Figure 3.1 Diagram of the convergence of pathways of cephalopod and teleost visual systems (from Land & Nillson 2002).

Analysis

Table 4.1 Scores and explanations for topics compared in the Image Formation category.

		Comparability		
	Topic	Score	Calculation (100-*d*-*i*)	Reasoning
Image Formation	Extraocular photo-receptors	28%[I]	100-(100*2/3)-5	Both teleosts and cuttlefish have opsins located in the skin that are identical to those located in their respective retinas. More research necessary
	Ocular photo-receptor pigment	28%[I]	100-(100*2/3)-5	The intron mentioned is not known to have an impact on visual performance, so it is considered by an *i*-value of 5.
	Ocular photo-receptor structure	40%[I]	100-(100*3/6)-10	The aspects that are considered similar are that both groups have a photoreceptor, the photoreceptors are approximately the same size, and have the same function. An *i*-value of 10 is given due to the lack of knowledge on how the difference in photoreceptors may play into a difference in visual capacity.
	Lens shape	97%	100-3-0	It was experimentally determined that they varied in shape by 3%. The experimental outcome is assumed complete information.
	Lens movement	65%[I]	100-(100*2/8)-10	An *i*-value of 10 is given for lack of information on the effect on visual acuity represented by the cell layer found in the cephalopod lens. Difference points are for development and muscle versus muscle functional group.

	Lens functionality	83%	100-(100*(1/2)/3)-0	A difference of 1/2 is given for variability between orders within Teleostei. For the teleosts found in the same region as cuttlefish, most are similar in this trait. Extensive literature is available on this topic for both groups.

Table 4.2 Scores and explanations for topics compared in the Light Sensing category.

		Comparability		
	Topic	Score	Calculation (100-*d*-*i*)	Reasoning
Light Sensing	Polarized light detection	62%[I]	100-(100*1/3)-5	An incomplete value of 5 is given to suggest more studies be done on the role of polarization detection for both groups
	Polarized light sensitivity (target detection experiment)	0%[I]	100-(100*1/1)	This value is incomplete, because of the rarity of experiments like this. The value is zero, because there was an obvious response from cephalopods and no response from teleosts.
	Wavelength filtering	67%	100-(100*1/3)-0	A difference value of 1 is given for the filtering of yellow light, since it is in the visual range.
	Wavelength discernment	13%	100-(100*7/8)-0	One point of difference is given for each color in the visible range. A point of similarity is given for the maxima.

Table 4.3 Scores and explanations for topics compared in the Visual Acuity category.

		Comparability		
	Topic	Score	Calculation (100-*d*-*i*)	Reasoning
Visual Acuity	Response to light intensity changes	95%[I]	100-0-5	An incomplete value of 5 is given due to the type of information available for cuttlefish. Experimental procedures resembling those of teleosts should be pursued.
	Pupil response to light intensity change	0%	100-(100*1/1)-0	This value is not incomplete due to the abundance of information found clarifying this point.
	Pupil shape/mobility	40%	100-(100*3/5)-0	The similarities are that they have pupils and that they are of roughly the same size.
	Visual acuity peaks	68%[I]	100-(100*(0.49-0.36/0.49))-5	An incomplete value of 5 is given, because for this to be representative, a more representative range of acuities should be used.
	Visual processing pathway	45%[I]	100-(100*2/4)-5	There are 2 differences: the location of processing, and the orientation of the photoreceptors compared to the retinal ganglion. The similarities are the pathway up to the retina and the sending of information to the brain. An *i* is given to encourage research on the effect of the difference in organization.

Table 4.4 Scores and explanations for topics compared in the Ecology category.

		Comparability		
	Topic	Score	Calculation (100-d-i)	Reasoning
Ecology	Early life	100%	-	The groups are similar in the larval stage in distribution, diet, and size.
	Vertical distribution	100%	-	There are species of cephalopods everywhere that marine teleosts can be found.
	Body size	100%	-	The body sizes of cephalopods are comparable to the body sizes of teleosts. The same applies to eye sizes with the exception of *Architeuthis*, which has dinner plate sized eyes and is pelagic and lives in dimly lit water.
	Predation strategy	25%	100-(100*3/4)-0	The similarity is that both groups contain specific tactics.
	Primary prey types	88%	100-(100*1/8)-0	There is an abundance of literature on this topic. Cephalopods tend to share the same prey as teleosts when of comparable size, with the exception of cannibalization by cephalopods.
	Response to prey shoaling behavior during hunting	100%	-	Neither group has an advantage over the other due to the social behaviors of prey fish.

Discussion

The original hypothesis for this paper was that the extent of similarities between the cephalopod and teleost visual systems would be similar enough that the model for visual feeding in fish could be applied to cuttlefish. However, the average of the scores given for the topics compared between the two groups was a 59%. This number suggests that while there are more similarities than differences, that the two groups may not be similar enough to share the same model.

This average is, however, by no means conclusive evidence for or against the claim that modelling for teleosts can function for cephalopods as well. The average shows a very strong need for further research. In reviewing the literature for this study, countless studies were found on the effects of turbidity on the prey detection range of fish. Oppositely, there were none found that detailed cuttlefish behaviors in turbid environments. It is suggested that studies like these be done for cephalopods.

There are several assumptions and areas for potential skewing of the percentages through the method used for scoring the topics. First of all, there was a wide range of specificity of topic. It can be expected that the categories “lens size” and “visual processing pathway” are going to vary hugely in both accuracy of scoring and in weight of importance. Lens size is a very specific topic with exact information available for analysis. Visual processing pathway, however, is a topic that could be a category on its own.

Another assumption that this average makes is that all possible topics for comparison are covered. The scope of this project is small; it takes a sample from literature found in a relatively brief period of literature review and isolates the most prominent and most common topics discussed in the literature reviewed.

A third assumption made that influenced the scores was the decision to subtract points for incomplete information. It is possible that if the unknown information was available, that the topic would be more similar between teleosts and cuttlefish. While this may have made the actual average percent similar lower than it should be, it prevents overestimation of similarity. Subtracting from the estimated score also made it possible to further emphasize which topics should be further studied.

The second purpose of this study was to point out directions for new research in the area of comparing teleosts and cephalopods. There are information sources available that define structures and pathways in cephalopod and teleost visual systems. There are even many studies that compare these between the two groups. Even with all of these studies, few explain whether or not a difference in structure can cause a difference in functionality between the two groups. The two differences that stick out the most under this circumstance are the existence of the living cell layer through the middle of the cephalopod lens and the fact that the image is formed right side up on the cephalopod retina due to the arrangement of photoreceptors in relation to the position of the ganglia (see Figure 3.1). Even though both of these differences were mentioned in multiple sources, their possible impact on image processing was never mentioned. Another area of interest is polarization sensitivity. While there is a trend towards researching this more in both fish and cephalopods (Hawryshyn 2010, Kamermans & Hawryshyn 2011, Shashar et al 2000, Pignatelli et al 2011), there are still few studies in this area.

An aspect of research that is very important is international collaboration. To help show this importance, an analysis of the international scope of this project was conducted. This was accomplished by finding out how many different countries were represented, and by how many authors, as well as how many of the articles were written from an international perspective. Of the articles cited in this paper that had more than one author, twenty-six articles were written where all authors were from the same country. Twelve of the articles were written with two countries represented, but no articles were written with more than two countries represented. This is important, because one third of the articles cited in this paper that had more than one author were made possible through international collaboration.

The other analysis of international scope was the breakdown of which countries were represented and how heavily. A pie chart was created to help establish this point (see Figure 5.1). As seen in the chart, even though the U.S. is the most represented country, it is only represented by a quarter of all the authors cited. The next two countries with the highest representation are the U.K. and Australia. There are representatives from five continents, excluding Antarctica and South America. The three most heavily weighted countries have an abundance of research institutions ranging from government agencies to educational facilities. The 13 other countries represented are roughly equally weighted and are economically fairly reliant on fisheries.

In conclusion, it may be possible to use for cephalopods models similar to or the same as those designed for fish. However, in order to do this, more research is necessary on the significance of distinct differences between cephalopods and fish. Does a small difference cause a measurable advantage for one of the groups? To be able to have a complete, comprehensive view of the differences in visual perception, international collaboration is encouraged.

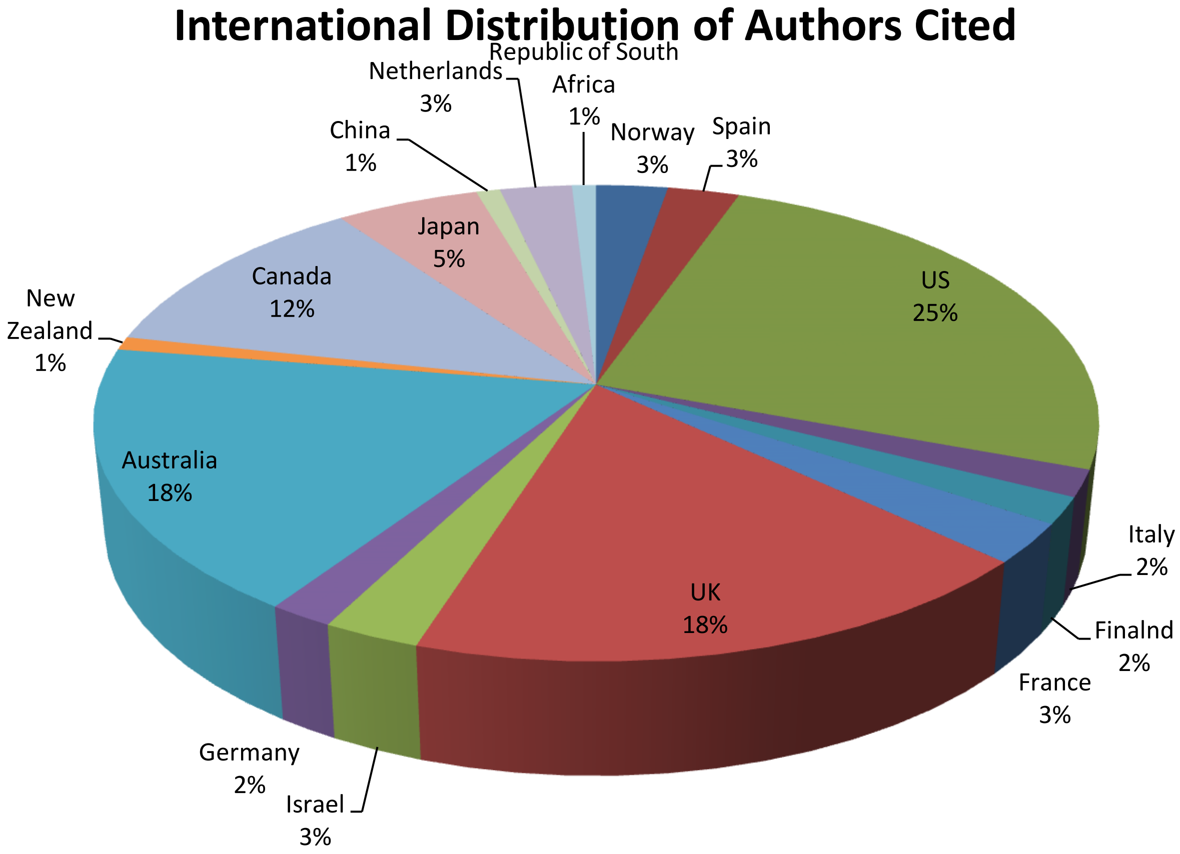

Figure 5.1 National affiliations of authors cited in this paper as a percent of the total number of authors.

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