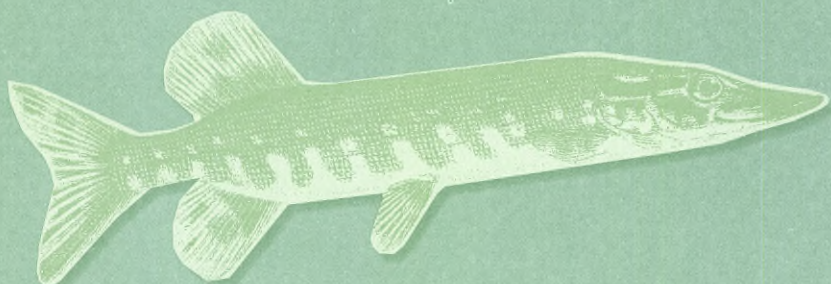




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A review of the literature on acoustic herding and attraction of fish

MAGNUS WAHLBERG



Visual ecology of fish – a review with special reference to percids

ALFRED SANDSTRÖM



Reproduction biology of the viviparous blenny (Zoarces viviparus L.)

MARKUS VETEMAA



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Innehåll

A review of the literature on acoustic herding and attraction of fish	sid 5-43
Visual ecology of fish – a review with special reference to percids	sid 45-80
Reproduction biology of the viviparous blenny (<i>Zoarces viviparus</i> L.)	sid 81-96

A review of the literature on acoustic herding and attraction of fish

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Summary	7
Introduction	8
Hearing in fish	9
The lateral line	12
Acoustics in fishing technique	13
Acoustic herding	15
Passive steering by acoustical cues	18
Considerations on the generation of Aeolian tones	20
Acoustic attraction	22
General problems on acoustic herding and attraction	23
Considerations on efficient sound production	23
Acknowledgements	25
References	26
Appendix A	32
Appendix B	36
Appendix C	38
Appendix D	42

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ISSN 1104-5906

Summary

A literature study of fishing methods using acoustic herding, passive acoustic steering and acoustic attraction is presented. All three techniques are used world-wide in traditional fishing, but their applications to modern fisheries are very few. Optimization in terms of selectivity and increase in catches seems promising for acoustic attraction, and many successful trials have been carried out on various fish species of different hearing abilities. The results from acoustic herding are more negative and a more thorough knowledge of fish behaviour is needed before such techniques can be improved. When examining passive acoustic steering, little evidence has been found that fish actually use acoustic cues to detect fishing gear. Theoretical calculations show that claims that fish can detect the

Aeolean tones generated by the water flowing through the net can probably be discounted, but measurements of the acoustic field around the fishing gear have to be made to finally confirm this. However, it has been shown that the fishing gear leading structures currently used are far from optimal. Studies of the sensory basis of gear detection by fish are needed to improve such structures. Psychoacoustic studies have shown that fish are essentially sensitive to very low frequency sounds. Therefore, improving acoustic fishing techniques demands an efficient, low-frequency sound source. It is shown that the fishing boat itself can be modified to become a relatively efficient transducer at the desired frequencies.

Introduction

An important consideration for successful fishing is knowledge of how fish behave in relation to sensory inputs, such as chemical, visual and acoustic cues. Fishermen have gathered a considerable amount of experience in this field. Intensive scientific investigations have added to this knowledge, so that today we have a good understanding of fish sensory biology.

Fishermen all over the world use their experience of fish behaviour in the development of new fishing methods. Traditional fishing gear often shows signs of such considerations in its construction. Visual (e.g. colour of net) and chemical (e.g. bait) cues are often the highest priority. Most fishermen are well aware of the importance of acoustic and hydro-mechanical cues, but the function of these cues is less well-understood, and therefore they are seldom considered in fishing gear design.

Scientifically, the function of fish hearing has only come to be thoroughly understood during the last decade, and this new knowledge has not yet been implemented in fishing. Some acoustic considerations are nowadays made in pelagic trawling operations, although very few coastal fishing techniques rely on acoustic cues.

The aim of this literature review has been to gather together both the research done on traditional fishing techniques making use of acoustic cues and experiments carried out on modern fishing gear design to develop these techniques.

We begin by looking at the physiological basis of fish hearing. Fish have two organs used for detection of hydrodynamic and acoustic fields: the inner ear and the lateral line system. Both systems rely on hair cells as the primary sensory unit.

Hearing in fish

In the inner ear of teleost fish, the hair cells are located on a sensory maculae facing one of the three *otoliths*, calcareous structures of much higher density than the fish tissue. As the fish is rocked by a passing sound wave, the otoliths are rocked momentarily later and a shearing force is detected by the hair cells (Popper, 1983). This system detects sound waves from below 0.1 Hz up to the resonance frequency of the system, around 200 Hz (Enger *et al.*, 1993). The system works as an accelerometer at low frequencies, a velocimeter at higher frequencies, and a displacement detector at even higher frequencies (Lewis, 1984). It is not clear at what frequencies the accelerometer-velocimeter and the velocimeter-displacement detector transitions occur, but some studies hint at around 20 Hz and 120 Hz, respectively (Kalmijn, 1988). Thus, depending on the frequency in question, different modes of the acoustic field will cause a stimuli. At infrasound frequencies (below 20 Hz) sensitivity is very similar in all fish species measured so far, about 10^{-4} m/s² (Figure 1).

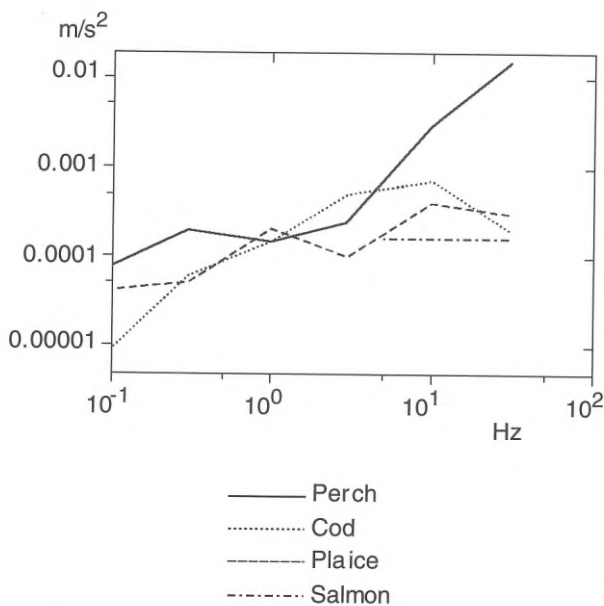


Figure 1. Acceleration audiograms for various fish species. Compilation from Westerg, 1993; including references to original results).

The matter is further complicated when we consider swimbladdered fish. The varying pressure field of an acoustic wave causes the swimbladder to oscillate. The displacement field created by the motion of the swimbladder wall is propagated through the fish and is detected by the otolith organ. At practical sound intensities, frequencies well above 10 Hz (probably around 50 Hz) are needed in order to create swimbladder wall displacements large enough to be detected by the otolithic organ (Sand and Hawkins, 1973). Depending on how closely connected the swimbladder and the inner ear are physically, the sensitivity and frequency range for sound pressure detection varies between different classes of fish (Sand and Enger, 1973a; Sand and Enger, 1973b).

Some investigators have reported the ability of fish to detect intense ultrasound. The mechanism behind such an ability remains unclear (Astrup and Møhl, 1993; Mann *et al.*, 1997).

Elasmobranch fish (including rays and sharks) show wide anatomical differences in their inner ears. A single otolith-hair cell system and a hair-cell covered non-otolithic channel serve as primary receptors of acoustic stimuli (Corwin, 1989). Few audiograms of sharks and rays have been made, but the ones available suggest a pattern similar to the one described for teleost fish without swimbladders (e.g. Corwin, 1981).

Based on this knowledge of acoustic perception, fishes in this report have been classified according to the following following categories (Figure 2):

Non-specialists with no swimbladder. Maximum sensitivity in terms of sound pressure level (SPL) at around 100 Hz is about 80–100 dB re 1 μ Pa. Above 100 Hz sensitivity falls off very rapidly, and non-specialists are essentially deaf above 200 Hz. This group includes the order *Pleuronectiformes*, and some families of *Perciformes* (such as *Scombridae*). In this study,

all fish of the class *Chondrichthyes* (including sharks and rays) are considered as non-specialists. Crabs (*Decapoda*) and squid (*Mollusca*) also fall into this group, as the few studies performed on these animals indicate their hearing ability most resembles non-specialist fish (see Offutt, 1970 for decapods and Packard *et al.*, 1990 for squid).

Generalists include fishes with swimbladders (but no special connection between the swimbladder and the inner ear; see the specialists category below). The sensitivity is increased some 20 dB (down to less than 80 dB re 1 μ Pa in cod), and the maximum audible frequency to about 500 Hz. Depending on the amount of gas contained in the swimbladder and the distance between the swimbladder and

inner ear, the sensitivity and maximum audible frequency may vary considerably. This group includes the vast majority of teleost fishes, such as the orders *Anguilliformes*, *Salmoniformes*, *Gadiformes*, *Scorpaeniformes*, and most families of the order *Perciformes* (excluding among others the family *Scombridae*).

Specialists have special connections between their swimbladder and the inner ear, extending upper hearing limit by several kilohertz. In some groups (all fish of the series *Otophysi*) increased hearing sensitivity is reached at a threshold below 60 dB re 1 μ Pa, which is close to what is considered to be the theoretical maximum sensitivity for any vertebrate acoustic detection system (Fay, 1992). This acoustic intensity corresponds to about 0 dB re 20 μ Pa in air, which is the hearing threshold of humans at 1 kHz. The specialists include the orders *Clupeiformes*, *Cypriniformes*, and *Siluriformes*.

The directional hearing abilities of fish have only been consistently studied in a few species. Cod (*Gadus morhua*) are able to distinguish the direction of a sound source accurately to within 20 degrees both horizontally (Schuijf, 1975) and vertically (Hawkins and Sand, 1977). Fish can neither make use of phase cues (due to the high sound velocity in water) nor intensity difference cues (due to the lack of shielding between the inner ears) to discern the direction of the sound source, as is common in land vertebrates. Instead, fish can use the inherent directionality in the acoustic displacement field. There is an intricate polarized pattern of hair cells on the sensory maculae of the fish ear which helps to give directionality cues (Fay, 1981; Hawkins and Horner, 1981; Platt and Popper, 1981; Popper, 1983). However, there is still an unexplained 180 degree ambiguity. This ambiguity may be resolved in swimbladdered fish by comparing the phase of the displacement and pressure component of the sound field (Figure 3; Schuijf,

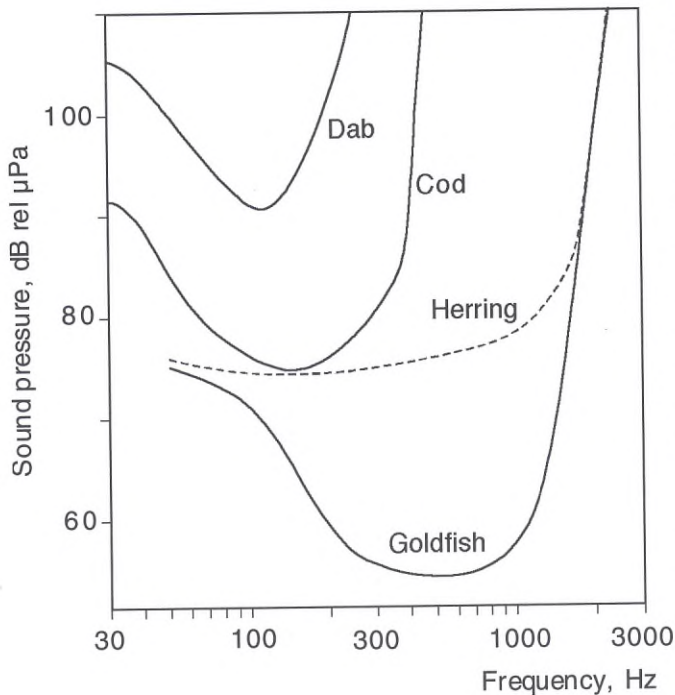


Figure 2. Sound pressure audiogram for various fish species: dab (non-specialist), cod (generalist), herring and goldfish (specialists). Sound pressure scale modified to dB re 1 μ Pa. Adapted from Sand and Enger, 1973b; includes references to original results, except the freely sketched dab audiogram after Chapman and Sand, 1974).

1981)). Such a mechanism would also explain the fact that cod are able to discern the distance to a close sound source, without making use of intensity cues (Schuijff and Hawkins, 1983). In this case, cod may exploit the fact that the phase difference between the pressure and displacement field varies rapidly within the acoustic near field. In this way, swimbladdered fish may have complete three-dimensional sound localization in the area around them. It should be remembered, however, that experimental evidence for these theories is small (however, see Popper *et al.* (1973), and the presumed capacity of non-swimbladdered fish for unambiguous directional hearing remains to be explained.

Other important aspects of fish hearing, such as pitch and level discrimination, have only been studied in a few species. It seems that the hearing generalists and specialists perform as well as land vertebrates, with a pitch discrimination of pure tones of about 3–5% and sound level discrimination of the order of 1.5 dB (see review in Popper and Fay, 1993). There is evidence of some pitch discrimination peripherally in the otolith organ, as the otolith has been shown to change its pattern of vibration depending on frequency (Sand and Michelsen, 1978). This shows that the crude model of otolithic function outlined above is probably over-simplified, and more peripheral auditory processing may be involved in fish hearing than has been previously assumed.

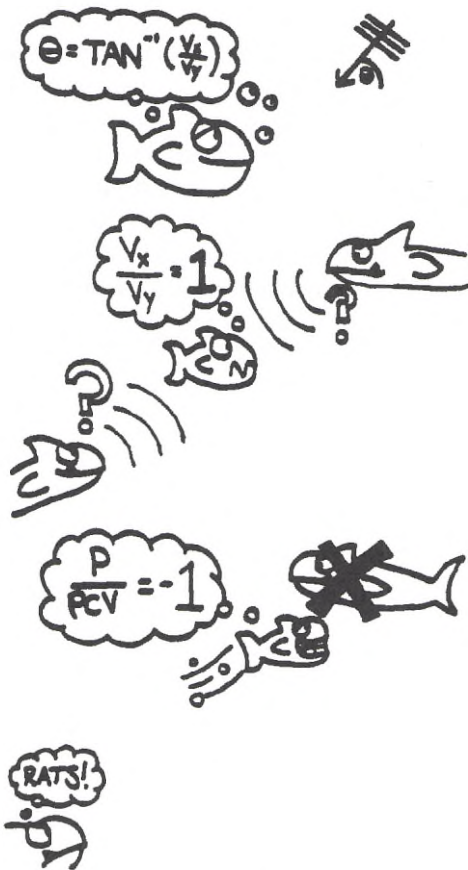


Figure 3. Illustration of the proposed mechanism for unambiguous sound localization in swimbladdered fish. Copy from Rogers and Cox, 1988.

The lateral line

The second sensory organ that fish possess to detect hydrodynamic fields is the lateral line system of which there is great diversity of form, ranging from free neuromasts on the body surface to canals with neuromasts connecting to the body surface through pores (Coombs *et al.*, 1988). The hair cells in the lateral line system are covered with a *cupula*. The cupula has almost the same density as the fish tissue (which in turn is very close to the density of water; Sand, 1984). When a fish is rocked by an acoustic field, the cupula moves in phase with the fish body. Therefore, no shear force is produced between the cupula and the neuromast (the exception being when within about one fish length from the sound source; Denton and Gray, 1982). However, the flow of water around the body of the fish causes the hair cells to be bent by the cupula. Thus, the lateral line system is not principally an acoustic detector, but a detector of hydromechanical stimuli.

Hydromechanical events usually die off very rapidly with the distance from the source, and it is therefore believed that the lateral line system only serves as a detector within very close range of the fish (in the order of tens of centimetres; Sand, 1984).

The question of the adequate stimuli is even more difficult to answer than in the case of the inner ear organ. It seems that the free neuromasts and the trunk lateral line respond to various time derivatives of the particle displacement in the hydromechanical field (Denton and Gray, 1989; Kalmijn, 1988). Very little is known about the variation in detection sensitivity of different species. The maximum frequency for hydromechanical detection seems to be about 150 Hz (Sand, 1984). It is not clear what the minimum detectable frequency is (but certainly below 10 Hz; Kalmijn, 1989; Sand, 1981; Sand, 1984). The lowest threshold which has been experimentally established is in the order of 10^{-6} m/s (Sand, 1984).

In this study, little attention has been paid to lateral line stimuli. It should be remembered, however, that hydromechanical stimuli play an important role in fish perception at very close range, e.g. during schooling or predation (Bleckmann *et al.*, 1991; Enger *et al.*, 1989; Montgomery, 1989; Partridge and Pitcher, 1980; Weiswert and Campenhausen, 1981). Lateral line stimuli may therefore be relevant in the design of some types of fishing gear.

Acoustics in fishing techniques

There are three basic methods for improving catches using sound to influence the fish:

acoustic herding: fish are actively steered (scared) away from a sound source towards the fishing gear;

passive acoustic steering: fish are steered towards the fishing gear with structures detected by the acoustico-lateralis system; and

acoustic attraction: fish are attracted to the fishing gear by a sound source.

Study of the literature showed that many attempts have been made to investigate fish behaviour and catch efficiency using these three techniques. Unfortunately, the authors usually concentrated on fish behaviour and catches, and apparently forgot to measure and/or report important acoustic information. Therefore, it has proved very difficult to systemise the reported results. I have used the following criteria and definitions in this report:

Successful study: fish are reported to react consistently to sound.

Trial: an independent investigation of one or more fish species belonging to a certain hearing category. All fish investigated in the same report belonging to one hearing category have been grouped together as if they had been one trial, whereas species belonging to different hearing categories but dealt with in the same report have been treated as separate trials.

Sound pressure level (SPL) at the position of the fish: Very few studies reported both the source level of stimuli and range for fish reacting to sound. Therefore, it was rarely possible to calculate the sound pressure level (SPL) at the position of the fish; in the SPL column of the tables, such calculations have been made in the few cases possible.

Frequency range: for unsuccessful trials the various reported frequency ranges of sound stimuli have been added together to cover the entire frequency range investigated all-together. For successful trials, the reported frequency ranges have been subtracted one from the other, in order to establish the relevant stimuli that produced the successful response.

Acoustic herding (Appendix A)

A total of 60 attempts to steer fish away from a sound source were reported in the literature, of which 40 were successful (Appendix A). Only 15 of these attempts involved active acoustic steering of fish into the fishing gear and none of these investigations gave an satisfactory assessment of any increased catches in the fishery.

All successful stimulations involved frequencies below 100 Hz. Sound pressure levels used in successful trials ranged from 140 to 167 dB re 1 μ Pa. Few investigators reported the sound pressure level used, and there is no relationship between source level and hearing ability (Table 1).

Fish became habituated to the acoustic stimuli after some time in several of

the successful trials (Table 1). The degree of habituation both depended on the frequency content of the stimuli used (Knudsen *et al.*, 1992; Knudsen *et al.*, 1994) and on how often the fish were exposed to the sound (Dunning *et al.*, 1992).

Possibly, the avoidance reaction observed in response to low frequency sound serves an antipredatory function. A swimming predator will generate low frequency sound that may be detectable by the fish (Bleckmann *et al.*, 1991; Kalmijn, 1988; Moulton, 1960). In a few cases, fish have also been stressed by very intense ultrasounds (Table 2), indicating that they may detect echolocation signals from dolphins (Astrup and Møhl, 1993; Nestler *et al.*, 1992). Natural predatory sounds, such as the sounds of dolphins, have also been used successfully to drive fish into a net (Hashimoto and Maniwa, 1971).

Table 1. Reported trials on scaring fish with sound. Values in parenthesis indicate number of trials included in estimates. Explanation of frequency range: see text. Responses to ultrasound are not included, but reported separately in Table 2.

Herding	Hearing ability	Total nr of trials	Nr of trials with signs of habituation	Nr of trials with no signs of habituation	SPL at fish (dB re 1 μ Pa) mean +/- s.d. of dB)	Frequency range
Failure	non-specialist	1	0	0	—	—
	generalist	14	3	0	200+/-6 (2)	60Hz–70kHz(4)
	specialist	3	1	0	—	<100–20kHz(3)
	unspecified	2	0	0	—	0.5–3kHz(1)
Success	non-specialist	4	0	0	142(1)	peak:300Hz(1)
	generalist	10	2	2	167+/-0(2)	10–100 (5)
	specialist	17	4	2	145+/-7 (2)	1–60 Hz (6)
	unspecified	9	0	0	—	—

Table 2. Reports on ultrasound detection by fish

Species	Hearing ability	Hearing ability f_{peak} (kHz)	SPL at fish (dB re 1 μ Pa)	Reference
cod Gadus morhua	generalist	38	195	Astrup and Møhl, 1993
alewife Alosa pseudoharengus	specialist	110–125	163	Dunning <i>et al.</i> , 1992
blueback herring Alosa aestivalis	specialist	110–140	150–160	Nestler <i>et al.</i> , 1992
American shad Alosa sapidissima	specialist	35	140	Mann <i>et al.</i> , 1997

Table 3. Reports of acoustic herding methods used in coastal fisheries in different parts of the world.

Area	Fishing technique	Reference
Baltic Sea	trout and whitefish netting	Nordqvist, 1922
Norway	herring purse seining	F Ugarte (pers. comm.)
Mediterranean	raft and seine netting	Sahrhage and Lundbeck, 1992; von Brandt, 1964
Malaysia	purse seining	Parry, 1954
Philippines	drive-in fishing	von Brandt, 1964
Russia	drive-in fishing	von Brandt, 1964
Micronesia	gill netting	Anonymous, 1948

The fact that acoustic herding has been implemented independently in many parts of the world (Table 3) might suggest that such techniques can substantially increase catches. However, most of the techniques are traditional, and very little use of acoustic herding has been made in modern fishing operations.

An interesting observation of unintentional acoustic herding was made by Engås *et al.*, 1991. The movements of acoustically tagged cod were observed as a fishing vessel approached. Two of the cod maintained an almost constant distance of 60–70 m directly ahead of the approaching vessel. The fish zig-zagged on their course in front of the vessel, turning suddenly at about 50 m to the side of

the trackline. It seems that these fish used their directional hearing capability to sense the ‘wings’ of the typical butterfly pattern noise field around the vessel (Figure 4).

Optimising acoustic herding would require a directional sound source and a predictable escape response in the target species. We, therefore, face two major problems: first, fish are usually scared by low frequency sounds, it being difficult to produce such sounds with high efficiency and directionality. Secondly, it is difficult to direct the fish towards the fishing gear. The most common avoidance reaction is a change in swimming direction away from the source and down to greater depths. Additionally, schooling fish

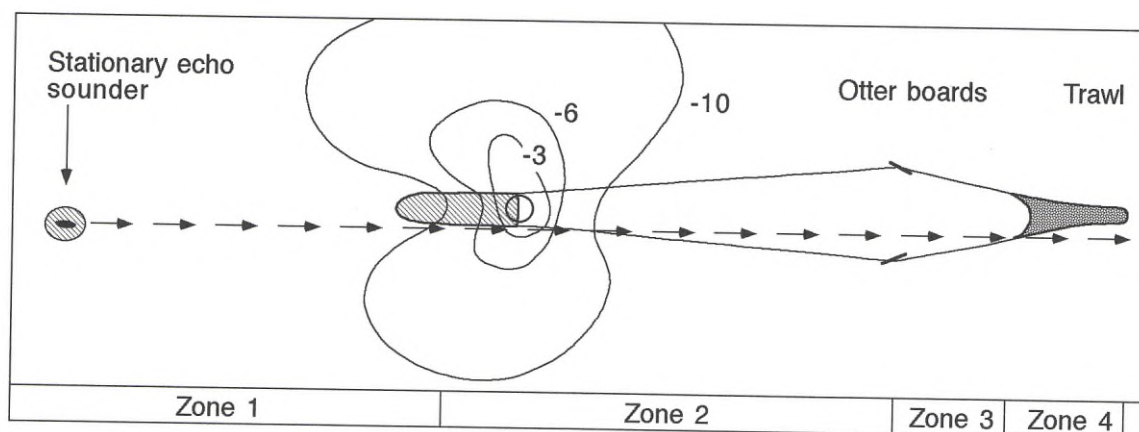


Figure 4. The noise pattern generated by a typical fishing boat, measured in terms of dB relative to the source level of the engine. From: Ona and Godö, 1990.

usually disperse when scared by sound. In coastal zones however geographical features (bottom topography, inlets etc.) may help to steer the fish in the desired direction to help solve this problem.

The fact that high frequency sounds may elicit avoidance responses in some species of fish (Table 2) should not be forgotten, as ultrasounds are much easier to generate in an efficient and directionally-controlled manner.

There have been very few systematic investigations on acoustic herding and further studies are needed to understand its full potential. With a more thorough knowledge of fish behaviour in relation to sound the catches of existing fisheries using acoustic herding may be optimized which might reduce some of the present conflicts of interest that occur with, for example, tourism. Today, high speed boats are often used as sound generators, wasting energy at suboptimal high frequencies and causing public irritation.

Passive steering by acoustical cues (Appendix B)

In the literature there are some suggestions of fish being steered towards the gear apparently by hydromechanical or acoustical cues (Appendix B; Table 4). Usually the researchers hypothesize that fish may detect acoustic signals generated when water passes through the fishing gear's guiding structure (Figure 5), but I know of no studies which have investigated these types of sounds.

The sensory basis of net leader detection is not well-understood. Both visual (Leggett and Jones, 1971), tactile (Inoue and Arimoto, 1988) and acoustic (Table 4) cues have been suggested. Some leaders contain

gaps in their structures large enough for fish to pass straight through (Bourdon, 1954; Inoue and Arimoto, 1988; Westenberg, 1953), and behavioural studies indicate that the majority of fish are guided towards the trap instead of swimming through the leader (Inoue and Arimoto, 1988), suggesting that cues other than visual may be involved in guiding the fish.

Additionally, Westerberg (1982a & 1992b) reported awareness reactions to the leader amongst migrating salmon and eels at a distance that was probably outside visual range (Figure 6). The fish never entered the trap, but rounded it suggesting that the efficiency of such leader designs may be far from optimal.

Table 4. Reports of guiding structures of fishing gear where acoustical or hydromechanical cues have been suggested.

<i>Fishery</i>	<i>Area</i>	<i>species</i>	<i>Structure</i>	<i>Reference</i>
trap net	Baltic Sea	salmon (Salmonidae)	leader net	Westerberg, 1982b
trap net	Japan, Alaska, Mediterranean	–	leader net	von Brandt, 1964
drift gill net	North America	shad (Clupeidae)	gill net	Leggett and Jones, 1971
palisade trap	Singapore	–	poles	Bourdon, 1954
trap net	Indonesia	salmon (Salmonidae)	poles	Westenberg, 1953

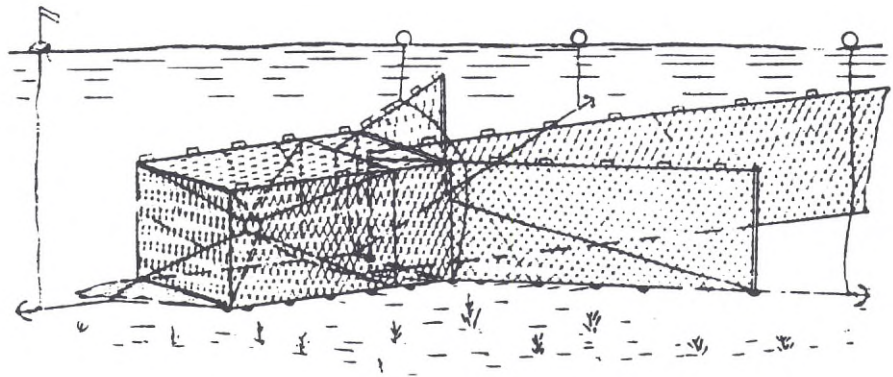


Figure 5a.

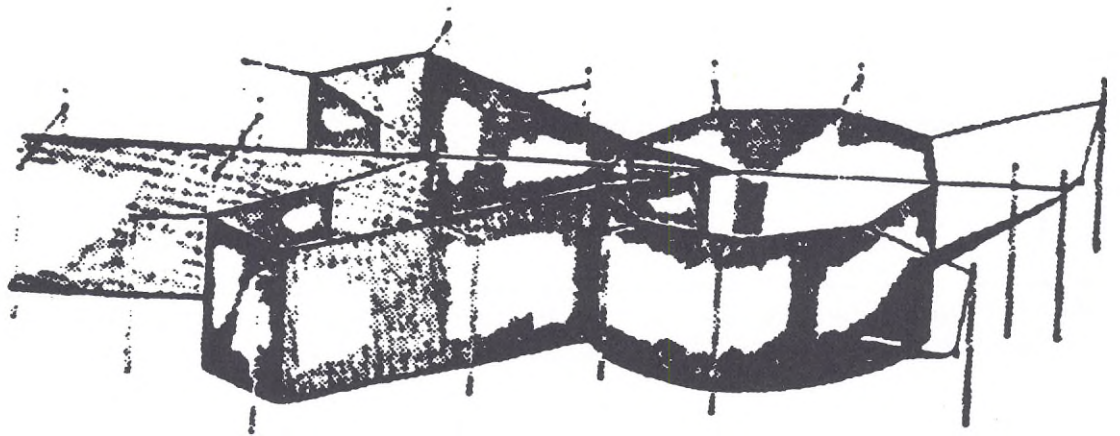


Figure 5b.

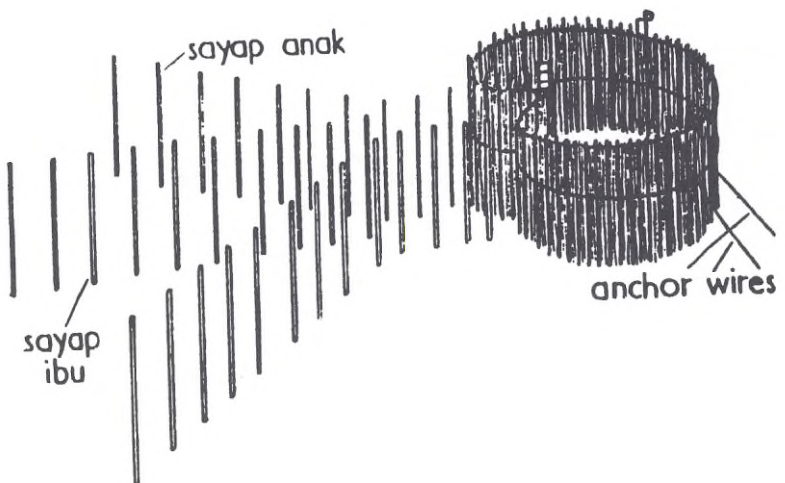


Figure 5c.

Figure 5. Some examples of guiding structures in different types of fishing gear: **a)** Leader net in fyke net from Russia (copy from Berka, 1990), and in **b)** Danish 'bundgarn' (copy from Klust, 1959; in von Brandt, 1964); **c)** kelong from Malaysia with poled leaders (copy from Parry, 1954).

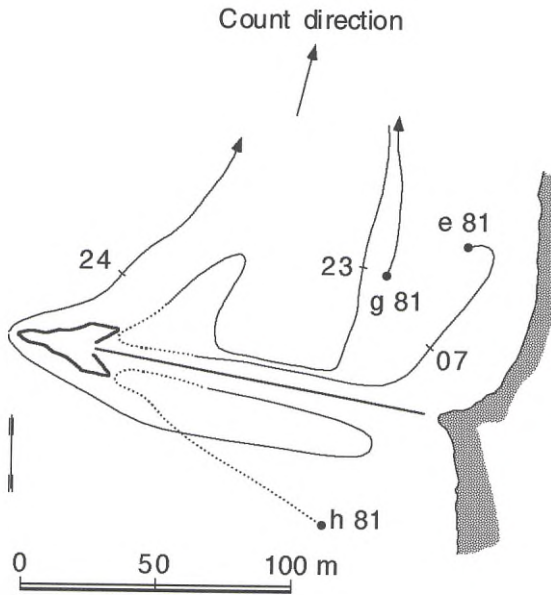


Figure 6. Ultrasonic telemetry of eel released in the vicinity of a fish trap. The study was carried out in Lake Hjälmaren at night (visibility only a few centimetres). The eel turned away from the fishing gear at a distance of about 5 metres. From: Westerberg, 1982a.

Considerations on the generation of Aeolian tones

If fish can react to fishing gear beyond visual range (Figure 6), one wonders just what cues might be involved? It has been suggested that fish detect the *Aeolian tones* generated from the water running through the fishing gear (Westerberg, 1953).

Aeolian tone generation is predictable both in its frequency content and intensity and is dependent only on water velocity and the diameter of the structure (Blevins, 1990). If we consider a net thread diameter of $D=1\text{ mm}$ and a water current of $U=10\text{ cm/s}$, we obtain a Reynolds number of $Re=UD/\eta=83$, where $\eta=1.2\cdot 10^{-6}\text{ m}^2/\text{s}$ is the kinematic viscosity of water. At such a low Reynolds number, vortices are induced in the wake of the thread (Figure 7). The Strouhal number at $Re=83$ is $S=0.2$, giving a vortex-inducing frequency of $f=S\cdot U/D=20\text{ Hz}$. The sound created by the vortices will have a major energy content at this frequency (Blevins, 1990).

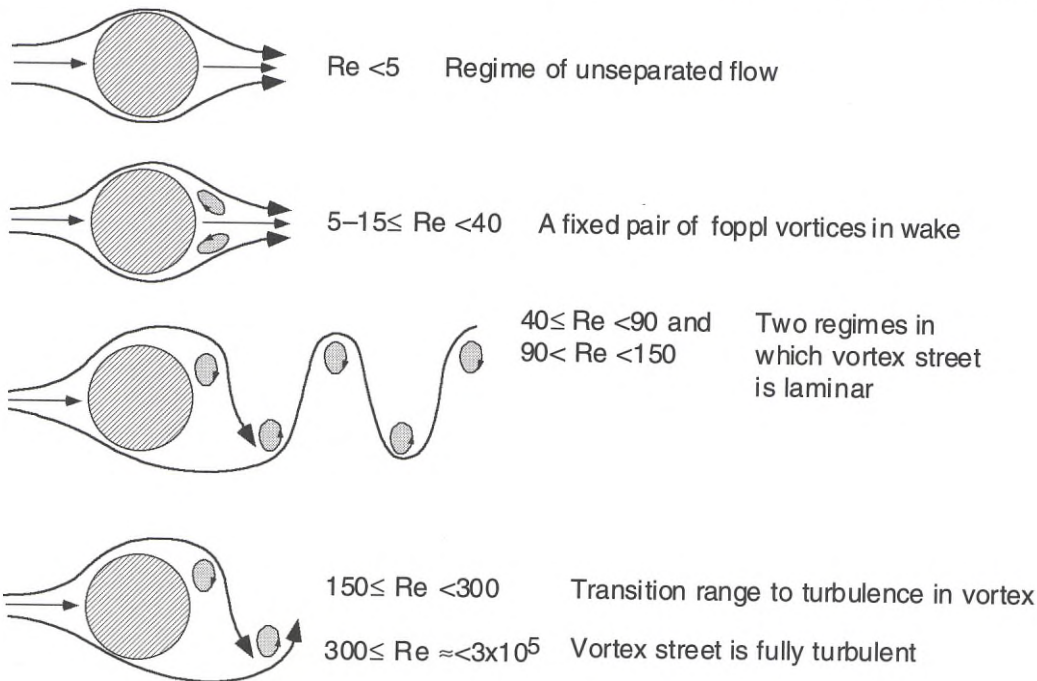


Figure 7. Vortex induction around a circular cylinder in a laminar flow. Explanations in the text. From: Blevins, 1990).

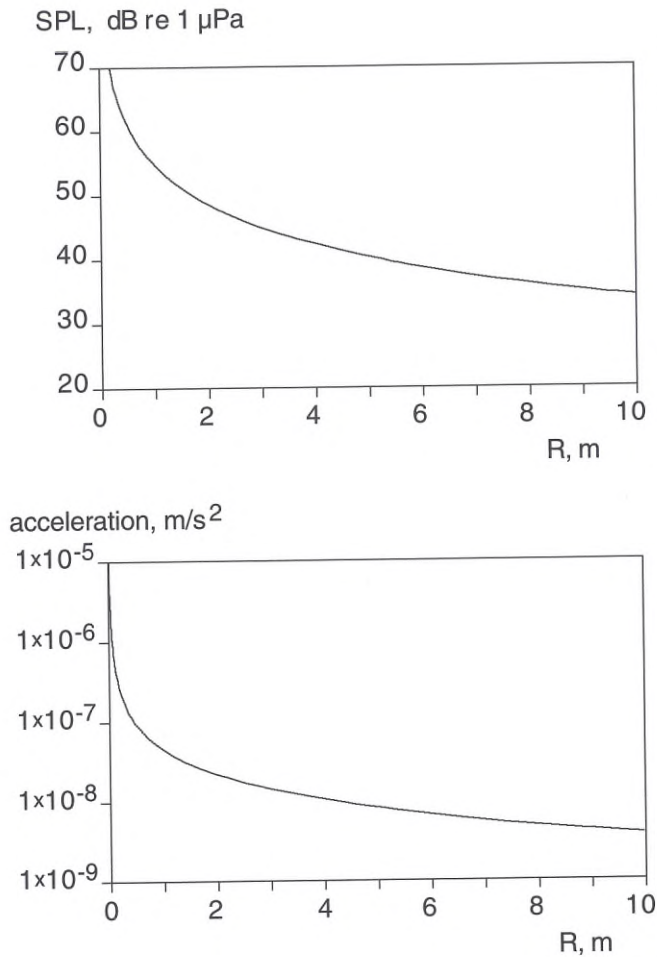


Figure 8. Sound pressure level in the flow direction from a cylinder in a laminar flow. Calculated on Mathcad 4.0 with the help of formulaes in Blevins (1990). The SPL curve represents the pressure in the direction of flow velocity, i.e. the maximum. Observe that the range of interest is well within the near-field, so that the deduced acceleration field is erroneously calculated from the acoustic free-field impedance.

It has already been noted that fish are very sensitive to sound at such low frequencies (Figure 1). However, a calculation of the sound pressure levels generated from such vortices give intensities well below the hearing threshold of fish (Figure 8). In Figure 8, it is assumed that the thread is 100 m long. The additional effect of several threads (as in a fishing net) will in the most constructive interference case add to the sound pressure level as $SPL(n) = SPL(1) + 20 \log n$, where n is the number of 100 m long threads (deduced from (Blevins, 1990)). In a typical leader net with a mesh size of 10 cm, there will be 100 horizontal threads if the net is 10 meter deep. There will also be 1000 vertical threads of 10 meters length, which in this case may be regarded as 100 threads of 100 meters. Altogether, there are $n=200$ threads which in a situation of maximum interference will increase the sound pressure level by $20 \log 200 = 46$ dB compared with the curve given in Figure 8. The sound pressure level at 5 meters distance would then in the most extreme case be about 88 dB re 1 μPa, many orders of magnitude less than the free-field pressure threshold level for fish at infrasonic frequencies.

Close to the surface, the floats will pull the net up and down with the waves, which may create a relative water flow through the net considerably stronger than the regular current. Assuming a relative water velocity of 1 m/s, the sound pressure level will increase by some 60 dB, and all of a sudden we are well within the hearing range of fish at a distance of tens of meters; note that the relevant frequency in this case would be 200 Hz.

It should be remembered that the relevant stimuli for fish hearing at low frequencies is acceleration (or possibly velocity). The acoustic near-field around the sound source may give a complicated pattern in the acceleration field not predictable by the theory. Acceleration may reach values several orders of magnitude

higher than can be predicted from Figure 8. Measurements of the acceleration field around the fishing gear in flowing water are needed before the hypothesis of fish detecting the gear with acoustic cues can be fully evaluated.

Additionally, the net will work as a turbulence grid in the water current, and turbulence generation is associated with sound production. At such low water velocities as 0.1 m/s, it is regarded as impossible for these sounds to be audible by fish. Of course, the turbulence itself may be detected at very short range by the lateral line system, but this would not explain the symmetry of reaction to the fishing gear both upstream and downstream as shown in Figure 6.

Other sounds are created by floats moving up and down in the waves. Airborne sounds from floats are very characteristic in the vicinity of fish traps, but to my knowledge their intensity under water has not yet been measured.

It is unclear what effect acoustics may have on gear detection by fish. I have not found any explicit test to confirm suggestions made in the literature of fish using acoustic cues, and observations as presented in Figure 6 have yet to be explained.

Acoustic attraction (Appendix C)

A total of 41 trials for attracting fish by sound were compiled (Appendix C; Table 5). Only 8 of these were unsuccessful. (This high success rate is probably due to a reluctance to publish those studies which did not produce positive results.) There is no correlation between the sound intensities used and the hearing abilities of the fish concerned in successful trials. Several studies showed that sharks were attracted by low frequency sounds, presumably due to the similarity of sounds produced by struggling fish.

Table 5. *Trials on acoustical attraction of fish. Explanations to table: see Table 1.*

<i>Attracting</i>	<i>Hearing ability</i>	<i>No of reported trials</i>	<i>SPL at fish (dB re 1 μPa +/- s.d. of dB)</i>	<i>Frequency range</i>
Failure	nonspecialist	3	—	50 Hz – 70 kHz (2)
	generalist	3	—	25 Hz – 200 Hz(1)
	specialist	—	—	—
	unspecified	2	—	100 Hz– 7 kHz (1)
Success	nonspecialist	16	120+/-3(3)	<100 Hz(6);2 kHz(1)
	generalist	12	124(1)	<100 Hz(5);2–5 kHz(2)
	specialist	4	—	—
	unspecified	1	—	—

Both hearing generalists and specialists usually responded positively to feeding sounds recorded from conspecifics (Figure 9).

Some old as well as present fisheries in different parts of the world have reported increased catches through acoustical attracting of fish towards the fishing gear (Table 6). Most of the sounds used resemble bait-eating sounds.

Table 6. Areas where acoustical attraction is, and has been, used in fisheries.

Area	Fishery	Reference
Baltic Sea	perch netting	Wolff, 1967
Indonesia	herring netting	Westenberg, 1953
Japan	squid angling	Maniwa, 1976
West Africa	harpooning	Busnel, 1959

It is difficult to draw any consistent conclusions from the available data on acoustic attraction. It seems that several attempts have been made to increase cat-

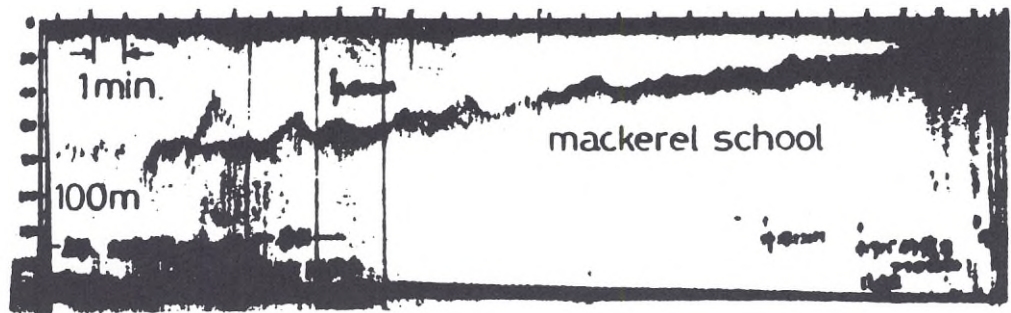
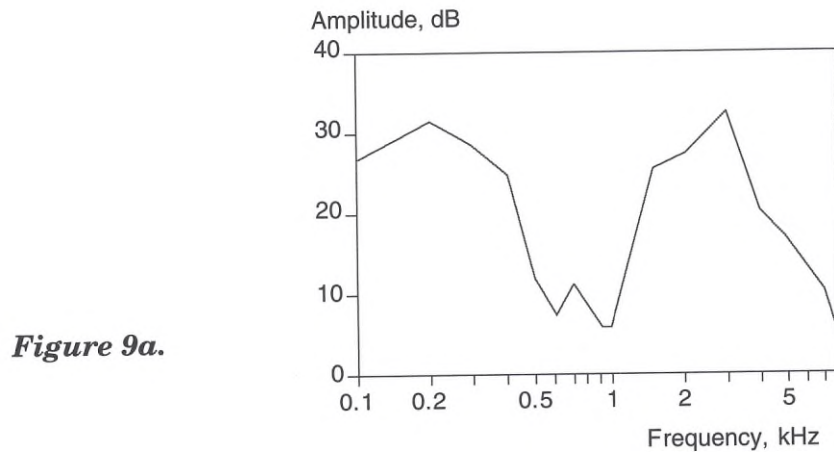


Figure 9b.

Figure 9. Attracting a school of mackerel using sound. **a)** Amplitude spectrum of stimuli. **b)** Echogram showing a school of mackerel (*Scomber japonicus*) swimming up from a depth of about 70 m to about 10 m or even closer in response to sound. Copy from Maniwa, 1976.

ches through acoustic attraction. Many attempts have been successful, but very few modern fishing operations make use of such results. It is unclear why this is the case. It is possible that there have been problems in implementing the results from successful experiments into real fishing operations, but such experiences are sadly not reported in the literature.

General problems on acoustic herding and attraction

Surprisingly few of the studies examined in this report have dealt with the well-known fact that fish can become habituated to sound stimuli. In addition, the response of the fish to sound usually varies greatly between different trials, which may indicate differences in behaviour due to the behavioural and physiological state of the fish (e.g. Nelson and Johnson, 1976).

Many physiological techniques use the readiness of fish to be acoustically conditioned. This may create an opportunity as well as a problem in acoustic fishing. Fish may be conditioned to assemble at a feeding station, where later they are caught (Abbott, 1972; Olsen, 1976). On the other hand, fish which are not successfully caught during acoustic herding and attraction may become conditioned against any future attempts to catch them. It may be necessary to vary the nature of the sounds used in these techniques more than has been previously assumed.

Considerations on efficient sound production

According to previous studies, fish may be herded and attracted by sound. To increase the effectiveness of present fishing operations by using this information, more behavioural data on fish reactions to sound are needed. It is also important to develop an efficient and practical sound source for the frequencies and intensities of interest. Most systematic studies have used very expensive (though high quality) transducers, but such equipment is neither economic nor practical (due to its size) for use in fishing operations.

Depending on the fishing method used, we are looking for a sound transducer with the characteristics listed in Table 7.

The problem of obtaining such transducers is not easily solved: we have to face some physical constraints imposed by sound production.

First, at wavelengths longer than the dimensions of the transducer, the efficiency of sound production is seriously limited due to the changing acoustic impedance in the near field region of the source (Figure 10; Beranek, 1996). Most sound producing mechanisms may be modelled either as a *monopole* (such as a pulsating sphere) or a *dipole* (e.g. an un-baffled loudspeaker). Due to acoustic short-circuiting between the high and low pressure sides of a dipole, the radiated sound intensities at low frequencies are much less than for a monopole (Figure 10). According to Table 7, acoustic herding would need transducers generating

Table 7. Desired physical characteristics of acoustic transducers to be used in fishing operations.

Technique	Frequency (Hz)	Sound level (dB re 1 μ Pa)	Directionality
Herding	<10	>160	Desirable
Attracting	<100 – >1000	>120	Optional

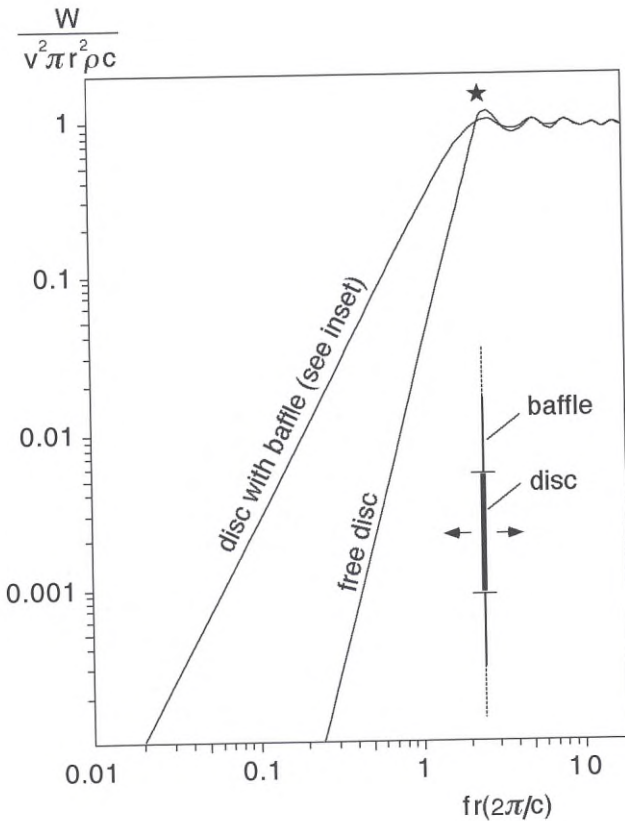


Figure 10. Sound producing efficiency of a monopole (disc with baffle) and a dipole (free disc) as a function of emitted frequency. W =emitted sound power, v =velocity of motion of disc (rms), r =radius of disc, ρ =density of the medium, c =sound velocity of the medium, f =frequency. From: Michelsen, 1983.

wavelengths of hundreds of meters. To be efficient, the transducer therefore has to be as large as possible.

Second, as wavelengths increase beyond transducer dimensions the directional characteristics of the transducer become poorer. Parametric techniques, making use of second-order effects in acoustic field interference patterns, can overcome these problems (Urlick, 1967). Present parametric systems are designed for frequencies over 100 kHz, but it is not clear if it is feasible to construct systems for the long wavelengths of interest to fisheries.

To sum up, we are looking as big a transducer of as possible. For the fisherman, the largest object at hand is his boat.

To see if a fishing boat may be modified to generate high intensity infrasounds, I did some practical trials. A 3 hk (approximately 2.1 kW) outboard engine with no propeller was mounted on an 11 m long research vessel. Weights were attached eccentrically onto the flywheel of the engine to make it vibrate. The vibrations were translated to the hull of the boat, which secondarily could be expected to work as a dipole sound radiator. Measurements were taken with different eccentric weights and at various flywheel revolution frequencies. The highest intensities (more than 155 dB re 1 μ Pa @ 1 m) and lowest frequencies (20 Hz) were found with a large eccentric weight (about 150 g) and a low revolution frequency. The highest sound pressure level obtained corresponds to a radiated acoustic power of about 25 mW, several orders of magnitude below the power obtained from the engine. One may wonder where most of the efficiency is lost. Calculating the product on the x axis of Figure 10, we obtain $f \cdot r \cdot 2\pi / c = 20 \cdot 11 \cdot 2\pi / 1500 = 0.9$. At this x value, then sound power emission efficiency of a dipole is about 10 dB below the theoretical maximum (Figure 10). Thus, one order of magnitude of intensity is lost due to the low *wavelength/boat size* ratio, whereas the rest is lost as heat through the engine and the boat vibrations. Modifying the engine to produce vibrations more efficiently seems to be promising for producing higher intensities and lower frequencies.

Acoustic attraction has a more modest demand of low frequencies and intensities (Table 7). Thus, it should be possible to use smaller transducers. We have tested several transducers:

- 1) A University Sound UW-30 underwater *loudspeaker* has a frequency response ranging from less than 100 Hz

to above 10 kHz. Its efficiency varies between 110 and 120 dB re 1 μ Pa re 1 V @ 1 m. Sound pressure levels up to 140 dB re 1 μ Pa @ 1 m can be generated. One problem with these loudspeakers is that they do not work in water more than a few metres deep.

A *piezoelectric beeper* (Elfa model COS-20BL) contained in a plastic bottle filled with oil can also generate intense sounds. The frequency range, however, is limited to the resonance frequencies of the crystal, starting at 2.5 kHz. The efficiency at the resonance frequency is about 114 dB re 1 μ Pa re 1 V @ 1 m. A larger crystal would generate lower frequencies of similar intensities and could be well-suited to acoustical attraction experiments. Also, a coil may be used to lower and broaden the resonance peak of the transducer since the transducer itself essentially acts as a capacitance in the electric circuit.

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Appendix A. Active acoustic herding (and scaring) of fish

Obs No	S/F *	Fish species	Order	Hearing ability	Type of gear	Sound-producing mechanism	Sound character	Source Level [dB re 1 μ Pa @ 1 m]	SPL at fish [dB re 1 μ Pa]
1	f	mackerel (<i>Scomber sp</i>)	Perciformes	nosp	observing behaviour	sounds of motor boat			
2	s	mackerel	Perciformes	nosp	observing behaviour	vessel noise playback	"broad-banded; peak at 300 Hz"	126	
3	s	yellowtail, young	Perciformes	nosp	observing behaviour	vessel noise playback	"broad-banded; peak at 300 Hz"	136	142
4	s		Perciformes	nosp	observing behaviour	playback of Risso's dolphin			
5	s	flounder	Pleuronectiformes	nosp	seine	hitting the water surface with a rod			
6	s	juvenile salmon (<i>Salmo sp</i>)	Salmoniformes	gen	observing behaviour	acoustic tube and loudspeaker	tone, 10 Hz	170	167
7	f	juvenile salmon (<i>Salmo sp</i>)	Salmoniformes	gen	observing behaviour	acoustic tube and loudspeaker	tone, 150 Hz	204	204
8	s	salmon smolt (<i>Salmo sp</i>)	Salmoniformes	gen	observing behaviour	acoustic tube and loudspeaker	tone, 10 Hz	177	167
9	f	salmon smolt (<i>Salmo sp</i>)	Salmoniformes	gen	observing behaviour	acoustic tube and loudspeaker	tone, 150 Hz	176	196
10	f	small salmon	Salmoniformes	gen	irrigation canal	noise-making device			
11	f	trout (<i>Salmo sp</i>)	Salmoniformes	gen	hydropower plant		60 Hz–70 kHz		
12	f	king salmon (<i>Oncorhynchus sp</i>)	Salmoniformes	gen	steam plant	hammer hitting metal			
13	s	trout, whitefish	Salmoniformes	gen	nets	engine			
14	s	trout, whitefish	Salmoniformes	gen	observing behaviour	playback, vibrating door	5–500 Hz	128	
15	s	silverside (<i>Atherina sp</i>)	Atheriniformes	gen	observing behaviour	vessel noise playback	broad-banded, peak <100Hz		110/Hz
16	f	killifish (<i>Fundulus sp</i>)	Cyprinodontiformes	gen	observing behaviour	sounds of motor boat, shotgun			
17	s	cod (<i>Gadus sp</i>), capelin (<i>Mallotus sp</i>) etc	Gadiformes	gen	observing behaviour	boat			
18	s	cod (<i>Gadus sp</i>), saithe (<i>Pollachius sp</i>), etc	Gadiformes	gen	observing behaviour	loudspeaker	noise frequency peak=10–380 Hz, BW=10–300 Hz	130	
19	f	cod (<i>Gadus sp</i>)	Gadiformes	gen	observing behaviour	"playback of tones, noises; vibrating trawl"	"100 Hz–15 kHz; 1 Hz"		
20	f	saithe (<i>Pollachius sp</i>)	Gadiformes	gen	observing behaviour	airgun			
21	f	scup (<i>Stenotomus sp</i>)	Perciformes	gen	observing behaviour	sounds of motor boat and gun			
22	f	kingfish (<i>Menticirrhus sp</i>)	Perciformes	gen	observing behaviour	sounds of motor boat and gun			
23	f	cunners (<i>Tautoglabrus sp</i>)	Perciformes	gen	baited lines	sounds of motor boat and gun			
24	f	bar jack (<i>Caranx sp</i>)	Perciformes	gen	observing behaviour	playback of feeding sounds from <i>C. latus</i>	stridulatory		
25	s	grey mullet	Perciformes	gen	raft fishery	noise			
26	s	jewfish (<i>Sciaenidae</i>)	Perciformes	gen	Purse seine?	striking pole with a ring of shells and tin			
27	f	bluefish (<i>Pomatomus sp</i>)	Perciformes	gen	observing behaviour	sounds of motor boat			low intensity
28	s	delah (<i>Caesio ssp.</i>)	Perciformes	gen	Japanese drive-in net	rattle of rings			
29	f	killifish (<i>Fundulus ssp</i>) etc.	Perciformes etc	gen	observing behaviour	iron ball striking end of tank			
30	s	herring (<i>Clupea sp</i>)	Clupeiformes	spec	gill net	engine			

* (s=successful, f= failure)

<i>Signs of habituation?</i>	<i>Daytime/ nighttime fishing</i>	<i>Geographical area</i>	<i>Source</i>	<i>Comments</i>
			Parker 1911	Sounds failed to alter behaviour
		fish culturing net in Chiba, Japan	Maniwa 1971	Vessel noise created an obvious fright reaction
		fish culturing net in Chiba, Japan	Maniwa 1971	Fish dispersed by vessel noise
			Hashimoto & Maniwa 1966	Fish driven into stationary net
		Netherlands	Weijs 1993	Stated to herd flounder into the center of the seine
y	tank		Knudsen <i>et al.</i> 1992	"Fish reaction; wild fish dove, hatched fish turned away from sound source"
	tank		Knudsen <i>et al.</i> 1992	No reaction
n	river		Knudsen <i>et al.</i> 1994	"Fish swam away from sound source; no habituation observed"
	river		Knudsen <i>et al.</i> 1994	No reaction observed
		Mill Creek, Tahama County, US	Radovich 1955	Fish disregarded sound device, both alone and together with an electric screen
y		Columbia River, Oregon, US	Burner & Moore 1953	No indications of fish reacting to sound
		San Joaquin River, California	Kerr 1953	No effective results
		Höga Kusten, Sweden	H. Frimansson (pers.comm.)	Disturbing for the general public.
n			Vanderwalker 1966	Response only for frequencies below 280 Hz
		Chiba, Japan	Maniwa 1971	Fish descended when vessel noise was applied
	cage		Parker 1911	"Boat noise failed to alter behaviour; shotgun caused momentarily startle"
		Norway	Olsen <i>et al.</i> 1982	Fish dove and swam away dispersed in response to passing boat
y		lake, Scotland	Chapman 1976	"Avoidance response; next year tests showed an attraction at lower BWs! "
	tank		Chapman 1963	"Occasionally turned away at the onset of lf sounds; tendency to avoid vibrating structures"
y		Norway	Olsen 1976	Fish habituated almost immediately
			Parker 1911	Sounds failed to alter behaviour
			Parker 1911	Sounds failed to alter behaviour
			Parker 1911	Fish ceased feeding while running boat stood six feet away
y		net pen, Bermuda	Moulton 1960	Initially movement away from sound source, but failed to respond after some minutes
		Russia, Mediterranean, Madagascar	v. Brandt 1964	Fish scared to jump into rafts
		Malaysia	Parry 1954	Fish is meant to be scared into purse seine pocket
			Parker 1911	Fish ceased feeding on close passage of the boat
		Singapore	Burdon 1954	Rings and white cloth carried by divers herd fish into trap
	tank		Parker 1910	Fish sank to bottom in random distribution or swam away from source
		Gothenburg archipelago, Sweden	Anon. pers. comm. 1995	Fisherman stated a significant increase in catches

Appendix A. Active acoustic herding (and scaring) of fish (cont.)

Obs No	S/F *	Fish species	Order	Hearing ability	Type of gear	Sound-producing mechanism	Sound character	Source Level [dB re 1 μ Pa @ 1 m]
31	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	purse seiner	engine		
32	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback	various pure tone and noise signals	25 dB ab amb noise
33	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	loudspeaker	pure tones and noise signals, 3–5000 Hz	
34	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	airgun		
35	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	vessel noise		
36	f	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback of pure tones, noises	100 Hz–15 kHz	
37	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	vibrating trawl warp	1 Hz	
38	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback of vessels and synthesized sounds	0–3 kHz	112
39	f	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback of natural sounds (eg killer whales)	<100 Hz–20000 kHz	
40	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	vibrating obstacles	5–15 Hz	
41	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	trawling	boat engine		
42	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	train passing bridge	peak at 64 Hz	
43	s	herring (<i>Clupea sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	boat		
44	s	hog-mouth fry (<i>Anchoviella sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback of predatory feeding sounds	stridulatory	
45	s	blueback herring (<i>Alosa sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback	110–140 kHz	180
46	f	blueback herring (<i>Alosa sp</i>)	<i>Clupeiformes</i>	spec	observing behaviour	playback	0.1–1 kHz	175
47	s	alewife, (<i>Alosa sp</i>)	<i>Clupeiformes</i>	spec	power plant	playback	pulse: peak at 60 Hz	180
48	s	alewife, (<i>Alosa sp</i>)	<i>Clupeiformes</i>	spec	power plant	playback	110–150 kHz	
49	s	<i>Spratelloides sp</i>	<i>Clupeiformes</i>	spec	observing behaviour	vessel noise playback	broad-banded, peak <100Hz	
50	s	scabbardfish			purse seine	striking pole with a ring with shells and tin		
51	f	striped bass (<i>Roccus sp</i>)				steam plant	steel barge with air hammer	
52	s				drive-in fishery		""frightening line""	
53	s				drive-in fishery		noise, beating the water	
54	s				raft fishery		noise	
55	s				seine		splashing the water	
56	s				seine		noise, hitting the water	
57	s				nets		noise	
58	s				gill net		percussive devices	
59	s					unknown	pounding on deck and detonating explosive	
60	f				observing behaviour		500–3000 kHz	

* (s=successful, f= failure)

A review of the literature on acoustic herding and attraction of fish

SPL at fish [dB re 1 μ Pa]	Signs of habituation?	Daytime/ nighttime fishing	Geographical area	Source	Comments
		daytime	Tysfjord, Norway	F. Ugarte pers.comm.	Fisherman states a significant increase in catches
			net-aquarium in the sea	Olsen 1971, Hering 1968	"LF interrupted or pulsed signals scared most efficiently; brake up school, swim away from source"
94/Hz	y		closed net	Olsen 1976	"Distinct avoid resp; LF gave stronger resp. rapid discont incr in stim level incr reaction"
	y			Olsen 1976	Increased swimming speed and turn away from source
			Atlantic	Mohr 1971	"Flighted and dove at a distance of up to 150 m from ship; in Skagerrak flight upwards from trawl"
			tank	Chapman 1963	No consistent reaction
			tank	Chapman 1963	Tendency to avoid vibrating structures
	y		tanks, pens, open water	Schwarz & Greer 1984	Avoidance response increased with lower frequencies
			pen	Schwarz & Greer 1984	No reaction
140	n		aquarium	Blaxter & Batty 1985	Strong avoidance
			Otofjord, Norway	Ona & Toresen 1988	"Boat influenced movement; sugg. pair trawling more efficient because of herding effect"
150			Denmark	Westerberg 1996	Fish dove in response to passing train, but continued on original course
			Norway	Olsen <i>et al.</i> 1982	Fish dove and swam away from vessel and dispersed in response to passing boat
			Bermuda	Moulton 1960	School showed tendency to divide and clear the area beneath the transducer
151	n		confined area and open water	Nestler <i>et al.</i> 1992	School gathered and swam away from sound source
	y		confined area and open water	Nestler <i>et al.</i> 1992	Only short-term startle responses
			net, Lake Ontario	Haymes & Patrick 1986	Repelling fish
163	y		rock quarry, NY	Dunning <i>et al.</i> 1992	Broad-banded sounds repelled more easily
110/Hz			Chiba, Japan	Maniwa 1971	Fish descended when vessel noise was applied
			Malaysia	Parry 1954	Fish is meant to be scared into purse seine pocket
			California	Kerr 1953	No effective results obtained
			Phillipines	v. Brandt 1964	Fish scared by (proposedly) the sound from rattling line
			Russia	v. Brandt 1964	Fish scared by sound
			Malta	v. Brandt 1964	Fish scared to jump into rafts
			Lake of Constance, African lakes	v. Brandt 1964	Fish scared toward the bag
			Mediterranean, 200 A.D	Sahrhage & Lundbeck 1992	Fish scared towards gear
			China	Sahrhage & Lundbeck 1992	Fish scared towards gear
			Ryukyu area, Polynesia	Anonymous 1948	"Fish are efficiently scared out of hiding places into net; visual and/or acoustical cues"
				Radovich 1955	Fish is proposed to 'light up' the bioluminescence.
			reservoir, Pennsylvania	Smith & Andersen 1984	No reactions seen

Appendix B. Passive steering of fish by (proposed) acoustical or hydromechanical cues

<i>Obs</i> <i>No Fish specie</i>	<i>Order</i>	<i>Hearing</i> <i>ability</i>	<i>Type of</i> <i>gear</i>	<i>Proposed</i> <i>soundproducing</i> <i>mechanism</i>
1 salmon <i>Salmo salar</i>	<i>Salmoniformes</i>	gen	trap net	poles driven into mud
2	<i>Salmoniformes</i>	gen	salmon trap net	leader
3	<i>Anguilliformes</i>	gen	eel trap net	leader
4 American shad <i>(Alosa sapidissima)</i>	<i>Clupeiformes</i>	spec	drift gill net	gill net
5			offshore palisade trap	poles in tidal stream
6			trap net	poles or fence
7			trap net	leader

<i>Daytime/night-time fishing</i>	<i>Geographical area</i>	<i>Source</i>	<i>Comments</i>
	Sumatra, Indonesia	Westenberg 1953	Spaces between poles wide enough for fish to pass if they wished;proposes Aeolian tones
	Baltic Sea	Westerberg 1982b	Fish turns away from leader before being able to visually observe it; proposes acoustical cues
	Lake Hjälmaren, Sweden	Westerberg 1982a	Fish turns away from leader before being able to visually observe it.
	North America	Leggett & Jones 1971	Avoided net during night; proposes hydromechanical cues (during light visual cues)
	Singapore	Burdon 1954	Fish is turning away from pole barrier, even though it is physically possible to go between poles
best at night-time with no moon	Indonesia	Westenberg 1953	For daytime fishery, the water should not be too clear. Proposes aeolian tones.
	Japan, Alaska, Baltic Sea, Mediterranean	v. Brandt 1964	Leader increase catches significantly

Appendix C. Acoustical attraction of fish

Obs No	S/F *	Fish species	Order	Hearing ability	Type of gear	Sound-producing mechanism	Sound character	Source Level [dB re 1 μ Pa @ 1 m]
1	s	sharks (<i>Carcharhinus</i> ssp., <i>Triaenodon obesus</i>)	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	playback	"25–100 Hz filt. noise; pulse rate 10 Hz"	156
2	f	sharks	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	playback	50 Hz sine and square wave 10 Hz modulated	156
3	s	sharks	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	spearing fish	sounds of struggling speared fish	
4	s	sharks	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	fish vocalization		
5	s	sharpnose shark (<i>Rhizoprionodon</i> sp)	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	playback	irregularly pulsed 55 Hz 'overdriven' sine waves	
6	s	sharks (<i>Carcharhinus</i> ssp)	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	playback	10–20, 20–40 and 40–80 Hz bands 0.3–3 pulses/s	135–155
7	s	lemon shark (<i>Negaprion brevirostris</i>)	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	playback	sounds of struggling fish etc., BW:20–640Hz	80–105
8	s	sharks	Class <i>Elasmobranchiomorphi</i>	nonsp	observing behaviour	loudspeaker	BW 25–50 Hz and 100–200 Hz noise 0.1–5 pulses/s	120
9	s	sharks	Class <i>Elasmobranchiomorphi</i>	nonsp	local fishing	shark-attracting rattle of coconut shells		
10	f	flounders (<i>Platichthys</i> sp etc.)	<i>Pleuronectiformes</i>	nonsp	observing behaviour	electric bell, buzzer, motor horn		
11	s	yellowtails	<i>Perciformes</i>	nonsp	observing behaviour	feeding and swimming sounds		>117
12	f	yellowfin tuna	<i>Perciformes</i>	nonsp	observing behaviour	playback	0.1–70 kHz	
13	s	yellowtail (<i>Seriola</i> sp) mackerel (<i>Scomber</i> sp. etc.)	<i>Perciformes</i>	nonsp	observing behaviour of conspecifics	bait eating and swimming sounds	<100 Hz–3 kHz	>120
14	s	tuna (<i>Katsuwonus</i> sp., <i>Neothunnus</i> sp.)	<i>Perciformes</i>	nonsp	hooked	"splashing water; throw out fish as bait"		
15	s	tuna (<i>Euthynnus affinis</i> C., <i>Neothynnus rarus</i>)	<i>Perciformes</i>	nonsp	hooked by trolling	lure made of feathers on line		
16	s	<i>Scomber neglectus</i> , <i>S. kanagurta</i>	<i>Perciformes</i>	nonsp	netting	rope with coco-palm leaves		
17	s	mackerel and jack mackerel	<i>Perciformes</i>	nonsp	observing behaviour	tonal sounds?		
18	s	squid (<i>Todarodes pacificus</i>)	<i>Ph Mollusca</i>	nonsp	angling	playback and higher	pure tone 600 Hz	160
19	s	deep sea queen crab (<i>Chioniceles japonicus</i>)	<i>Ph Crustacea</i>	nonsp	observing behaviour	playback of bait-eating sounds	2–5 kHz	>118
20	s	<i>Gadus</i> sp., <i>Pollachius</i> spp)	<i>Gadiformes</i>	gen	observing behaviour	"loudspeaker; diver's aqualungs"	30–110 Hz tones, continuous and pulsed	124 and 133
21	s	cod (<i>Gadus morhua</i>)	<i>Gadiformes</i>	gen	observing behaviour	trawling noise	0–250 Hz	90/Hz
22	s	barracuda (<i>Sphyraena barracuda</i>)	<i>Perciformes</i>	gen	observing behaviour	playback of feeding sounds of <i>Caranx latus</i>	stridulatory	
23	s	carangids (<i>Decapterus</i> spp), <i>Selar</i> spp.	<i>Perciformes</i>	gen	netting	rope with attached coco-palm leaves		
24	s	labrids and <i>Platypoecilus</i>	<i>Perciformes</i>	gen	harpooned	nail moving over stem under water	broad-banded 1–10 kHz	100
25	s	predatory reef fish	<i>Perciformes</i>	gen	observing behaviour	loudspeaker	BW 25–50 Hz and 100–200 Hz noise 0.1–5 pulses/s	120

* s=successful, f=failure (col. 1)

A review of the literature on acoustic herding and attraction of fish

<i>SPL at fish [dB re 1 μPa]</i>	<i>Signs of habituation?</i>	<i>Daytime/nighttime fishing</i>	<i>Geographical area</i>	<i>Source</i>	<i>Comments</i>
			Polynesia	Nelson & Johnson 1976	Attracted to noise; species and area differences in response due to unknown reason
			Polynesia	Nelson & Johnson 1976	No reaction
			Polynesia	Nelson & Johnson 1976	More intense attraction with larger fish
			Polynesia	Nelson & Johnson 1976	Sharks attracted by fish sound
			Bahamas	Myrberg <i>et al.</i> 1969	Highly attracted
			Florida	Myrberg <i>et al.</i> 1976	Low frequency sounds more attractive; repetition rate had to be 3 Hz for attraction
			Florida	Banner 1972	Sharks attracted or startled, detection distance about 1 m
			Bahamas	Richard 1968	Especially higher frequencies attracted sharks
			Indonesia	Westenberg 1953	Successfully attracting sharks
			aquaria and pens	Moorhouse 1933	No consistent reaction
>84			fishing grounds and net, Japan	Hashimoto & Maniwa 1966 & 1971	Fish ascended towards sound projector and increased in speed, apparently searching for bait
			tank	Miyake 1951 (in: Tester 1959)	Indications of attraction by complex sounds of low frequency; inconclusive results
117,122			fish culturing net and fishing grounds	Maniwa 1976	Fish swim up from the bottom towards the projector near the surface; attempts to feed
			Indonesia	Westenberg 1953	Proposed to attract fish acoustically; immediate detection of bait splash
			Indonesia	Westenberg 1953	Proposed to attract fish acoustically
			Indonesia	Westenberg 1953	Attracts fish before netting; proposes Aeolian tones
				Kleerekoper & Chagnon 1953	Fish conditioned; moved toward strongest sound source
123		nighttime with lamps	fishing grounds	Maniwa 1976	600 Hz clearest response; squid swam upward; more squid caught, also light attraction
118			tank	Maniwa 1976	Induced food-seeking behaviour; tests with other species failed
			Scotland	Chapman 1976	Fish attracted by especially 40 Hz tone; response increased if tone was pulsed; fish attracted to divers
			Canada	Buerkle 1974	Increased catches of cod in presence of noise; attraction or stimulated locomotor activity
			Bahamas	Moulton 1960	Came abruptly to a spot about 8 feet from transducer and lay quietly facing it for about 3 minutes
			Indonesia	Westenberg 1953	Attracts fish before netting; proposes fish attracted by produced Aeolian tones
			Senegal, Niger	Busnel 1959	Suggested acoustical attracting, complemented by other stimuli
			Bahamas	Richard 1968	Different species attracted to different sounds

Appendix C. Acoustical attraction of fish (cont.)

Obs No	S/F *	Fish species	Order	Hearing ability	Type of gear	Sound-producing mechanism	Sound character	Source Level [dB re 1 μ Pa @ 1 m]
26	f	herbivorous reef fish	<i>Perciformes</i>	gen	observing behaviour	loudspeaker	BW 25–50 Hz and 100–200 Hz noise 0.1–5 pulses/s	120
27	s	butterfish (<i>Poronotus tricanthus</i>)	<i>Perciformes</i>	gen	observing	loudspeaker behaviour	2 kHz tone	
28	s	young <i>Caranx</i> sp	<i>Perciformes</i>	gen	observing behaviour	playback of swimming sounds and tooth rasps		
29	s	<i>Perca</i> sp	<i>Perciformes</i>	gen	anecdotal fish behaviour			
30	s	<i>Perca</i> sp, <i>Acerina</i> spp, <i>Lucioperca</i> sp	<i>Perciformes</i>	gen	net, 'Klapperfischerei'	various impulse sounds with rods etc	40–250 Hz pulses	
31	s	sea bream (<i>Pagrus</i> sp)	<i>Perciformes</i>	gen	angling	throwing lead weights into the water	broad banded >124 with peak at 300 Hz	124
32	s	black pomfret (<i>Stromateus</i> sp)	<i>Perciformes</i>	gen	encircling with net	boys singing 'ooh' with bamboo stick in water		
33	f	Rock cod (<i>Sebastes</i> sp)	<i>Perciformes</i>	gen	observing behaviour	electric bell, buzzer, motor horn		
34	s	sea robin (<i>Printus</i> spp)	<i>Perciformes?</i>	?	observing behaviour	iron ball striking end of tank		
35	f	surf perch (<i>Cymatogaster aggregatus</i>)	<i>Perciformes?</i>	?	observing behaviour	electric bell, buzzer, motor horn		
36	f	<i>Semotilus atromaculatus</i>	<i>Perciformes?</i>	?	observing behaviour	underwater loud speaker	100 Hz–70 kHz tonal?	
37	f	Sculpins (<i>Oligocottus</i> sp and <i>Leptocottus</i> sp)	<i>Scorpaeniformes</i>	gen	observing behaviour	electric bell, buzzer, motor horn		
38	s	clupeid (<i>Brevoortia</i> sp)	<i>Clupeidae</i>	spec	observing behaviour	loudspeaker and pure tones	1–20 kHz warble	155–187
39	s	<i>Clupea</i> spp	<i>Clupeidae</i>	spec	netting	rope with attached coco-palm leaves		
40	s	<i>Silurus glanis</i>	<i>Siluriformes</i>	spec		hitting surface with stick		
41	s	carp	<i>Cypriniformes</i>	spec	observing behaviour	bait eating sounds		

* s=succesful, f=failure (col. 1)

A review of the literature on acoustic herding and attraction of fish

<i>SPL at fish [dB re 1 μPa]</i>	<i>Signs of habituation?</i>	<i>Daytime/nightime fishing</i>	<i>Geographical area</i>	<i>Source</i>	<i>Comments</i>
			Bahamas	Richard 1968	Herbivorous reef fishes not attracted even though abundant
	y		tank	Moulton 1963	Fish moved into region of highest intensity
	y		aquarium	Moulton 1960	Initiated feeding reaction; subsided after several minutes
			Sweden	Jansson 1995	Fish proposed to be attracted to the sound created when making a hole in the ice
			Germany	Wolff 1967, Jansson 1995	Fish attracted and / or scared by sound
			fish culturing net and fishing grounds	Maniwa 1976	Changed swimming direction and approached sound projector
			Java	Westenberg 1953	Fish flock around singer, and sometimes even jump in his face of excitement
			aquaria and pens	Moorhouse 1933	No consistent reaction
			tank	Parker 1912	Fish concentrated at the end toward the sound source
			aquaria and pens	Moorhouse 1933	No consistent reaction
			concrete tank and pool	Miyake 1952	Some possibility of orientation toward the sound of exhaust from a motor boat and a 200 Hz signal.
			aquaria and pens	Moorhouse 1933	No consistent reaction
	y		tank	Moulton 1963	Moved to area of highest intensity, frenzied swimming; response decreased above 15 kHz
			Indonesia	Westenberg 1953	Attracts fish before netting; proposes fish attracted by produced Aeolian tones
		before sunrise, during summertime	Serbia	Busnel 1959	Sounds attract fish
			pond, Japan	Hashimoto & Maniwa 1966	Fish gathered around projector; higher intensities frightened the fish

<i>Geographical area</i>	<i>Comments</i>	<i>Source</i>
Hanöbukten, Sweden	Eels tended to swim away from the power plant when it was in function	Westerberg 1994
North of Norway	Sensitive to visual and acoustic stimulation during feeding periods, but not during spawning season	Olsen 1971
	Review of chemical, acoustical, visual and electrical attraction	Tester 1959
	Evidence of fish orienting to the echo of its own call	Griffin 1950
Bermuda	Description of swimming sounds	Moulton 1960
	Catches less by steel vessels than by wooden vessels	Maniwa 1971
Bermuda	Description of swimming sounds	Moulton 1960
	Underwater explosions possible affects fish life	Hubbs & Rechnitzer 1952
	Herding fish with air-bubble curtains	Smith 1963
aquarium	Studies of blinded fish school	Moulton 1960
Bermuda	Description of swimming sounds	Moulton 1960
Labadi District, Gold Coast	Finding fish through listening with paddle	Moulton 1960
	Catches less by diesel engine trawler than by steam engine	Maniwa 1971
	Classification of fishing gear	Brandt 1971
	Discussing herding and attracting fish; many unrealistic suggestions	Alverson & Wilimovsky 1963
	suggests the use of sounds to steer fish	Maniwa 1971
several locations	Passive listening for fish, with blade or head dipped in water	Westenberg 1953
	Discussing herding in trawling	Chapman 1963
	Review of acoustic attracting and repulsing	Blaxter 1988
	Discussing difference in response to infrasound between sharks and teleosts	Enger <i>et al.</i> 1993
	Discussing effects on fish migration due to infrasound generation in bridges	Westerberg 1993
Kelantan and Tenganu, Malaysia	Fish attracted to shade under coconut fronds	Parry 1954
Kelantan and Tenganu, Malaysia	Finding fish through listening for 'croaks and chuckles'	Parry 1954

Visual ecology of fish – a review with special reference to percids

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Summary	47
Introduction	49
From the sun to the fish cornea, visual conditions of aquatic environments	50
Light absorption in water	51
Seasonal and diel patterns of visual conditions in aquatic environments	53
Vision in fishes	55
Morphology and function of the fish eye	55
Visual localisation of objects in water	59
Visually associated adaptations for aquatic living	63
Characteristic features of vision in percids	64
The percid retina	65
Changes of the visual system in early life	66
Additional sensory mechanisms of percids	69
Impacts of visual conditions	71
General patterns in the impacts of turbidity	71
Influence of daylength	72
Impacts of visual conditions during early development	73
References	76

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Summary

The function and morphology of the fish visual apparatus is in many respects similar to terrestrial vertebrates. Light passes through a cornea, is concentrated by a lens and absorbed by photoreceptors in the retina, which sends nervous signals via the optical nerve to the brain for interpretation. But there are also some important dissimilarities. Instead of changing the shape of the lens, fish accommodates by moving its lens in relation to the retina. Fish has no air–cornea interface, which deprives it of nearly 80% of their optical power compared to terrestrials. Fish as a group has also a more diverse set of visual pigments than terrestrial vertebrates since they have adapted to a large number of different light environments.

The light environment in water is depending on both above surface, at surface and below surface conditions. The proportion of light transmitted through the surface depends on the angle of the incident light and whether the surface is still or rough. The more dislocated the angle is from the perpendicular the more light is reflected. A rough surface reflects more light than a still. Once light has entered the water column it is absorbed and scattered by the water itself and dissolved and particulate substances. Depending on the composition of different substances in the water, light of different wavelengths is more or less diminished. There are four major agents absorbing light in aquatic environments. 1) The water itself, which absorbs most of the light in the ultraviolet, green and red parts of the spectrum 2) Dissolved organic substances (so called Gelbstoffe) absorbing maximally in the UV, violet, blue and green part of the spectrum 3) Phytoplankton, which absorbs light depending on pigment composition. Chlorophyll, the dominating pigment group absorbs most light in the blue and red part of the spectrum. 4) Particulate inorganic substances absorbing light of different wavelengths

in a more even fashion. The absorbance characteristics of these substances nevertheless may vary between different types.

Percids can be grouped into two major classes by their visual adaptations for foraging in different light environments. Pikeperches (*Stizostedion* sp.) mainly and ruffe (*Gymnocephalus* sp.) feed crepuscularly or nocturnally, and are thus equipped with a visual apparatus designed for light sensitivity. These species has a so-called *tapetum lucidum*, a reflective layer of the retina consisting of a substance called 7,8-dihydroxyanthopterin. The arrangement induces extra reflections of light back and forth between the rods with additional absorptions at each reflection. Perches (*Perca* spp.) are instead diurnal feeders, foraging in bright light. They lack a *tapetum lucidum* and have instead a visual physiology enhancing visual acuity in bright light.

Larval perch are equipped with UV-sensitive cones. These are believed to be supportive when they feed on zooplankton in the pelagial. When the perch larvae go through metamorphosis and switch habitat, from the pelagial to the benthic littoral, the UV-sensitive cones are regressed.

As with most other freshwater fishes, the retina of percids absorbs maximally in regions of the spectra slightly deviating from the regions where water transmits maximally. This is believed to be advantageous when detecting objects underwater. Since light reflecting off an object usually contains larger portions of light in regions spectrally deviating from the background, which nearly eclipses the regions where light transmission in the particular water is maximum. Having a retina that absorbs more light of such wavelengths will increase the perceived contrast between the object in particular and the background. For deep-sea fishes on the other hand there seems to be a clear match between the spectral characteristics of their visual pigments and

the spectral region of maximum transmission in water. This is probably due to the fact that the only light that reaches down to their ambient environment is in the regions of the spectrum where light transmission in seawater is maximal.

The importance of contrast for prey recognition has been demonstrated for many freshwater fishes. For percids it has been studied at early developmental stages. Both for perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) larvae, contrast seems to be an essential factor for prey recognition.

One important factor affecting the light environment in aquatic environment is turbidity. Increasing turbidity decreases the distance of a fish's visual field, increases luminosity, affects contrasts, defocuses and depending on type, selectively changes the composition of wavelengths of light transmitted through the water. All these factors influence a fish's foraging ability. Not necessarily negative. By changing the colour of the background light it may actually enhance the contrast of certain prey items. It will also affect the light attenuation with depth. High levels of turbidity will decrease the maximum distance of light penetration thus imposing spatial constraints on fish foraging.

Introduction

The visual system of fishes is adapted to their lifestyle and the constraints of their ambient environment. Since fishes occur in a very wide spectrum of light environments the magnitude of diversity in visual adaptations is of considerable range. The diversity of visual pigments for example, exceeds that of all other vertebrates collectively (Nicol, 1989).

The deep-sea fishes are examples of one extreme, adapted for vision in environments with very low light intensity and their visual apparatus is thus designed to meet the demands of these conditions. Some species of deep-sea fishes even generate light by themselves to visualise their surroundings (Randall, 1993). The surface living fishes at the other extreme forage in bright light and have very high visual acuity in the visible field, in some species even combined with the ability to visually detect the UV-portion of the light spectra (Lythgoe, 1979).

The visual conditions can influence both predator-prey interactions and behavioural patterns of fish (Hanson & Walton, 1990; Gregory, 1990; Barrett *et al.*, 1993) thus having the potential to significantly influence aquatic ecosystems. When analysing these mechanisms it is of fundamental importance to understand the general relationships between visual conditions, the function of fish vision, species adaptations, and fish behaviour.

Numerous anthropogenic activities and associated environmental disturbances can affect the visual conditions of aquatic habitats. Eutrophication often results in increased turbidity caused by algal blooms and suspensions of sediment particles. Dredging, boat-traffic and other mechanical disturbances can cause strong turbation of sediment particles also increasing the turbidity in affected areas. The impacts of altered turbidity on fish depends largely on the visual adaptations and life-strategy of the concerned species influencing their capability of performing in environments of varying turbidity.

The objective of this literature review is to portrait the current understandings of the influence of visual conditions on fish biology, with special reference to percids. Main emphasis will be on describing the physical mechanisms influencing visual conditions in natural waters, the function of fish vision, visual adaptations of different species of percids with comparisons to their lifestyle and behaviour and conclusively the influence of visual conditions on fish performance.

From the sun to the fish cornea— visual conditions in aquatic environments

Light impinging on earth originates from the sun, either directly or indirectly when it reflects on the moon, and the stars. From a view of strict physical semantics light is "a part of the radiant energy of the electromagnetic spectrum" (Wetzel, 1983). Thus being a type of energy, light can be transformed to other energetic forms, predominantly heat. The electromagnetic spectrum is expressed in frequency (in Hz) and in wavelength (λ), usually in nanometer, nm.

The solar flux of energy ranges in wavelength from 100 nm to 3 000 nm (Fig. 1). The visible part of the spectrum ranges from 400 nm to 760 nm (Rüttner, 1963). The maximum energy flux, both extraterrestrially and at ground level lies in the visible field of the spectrum or more precisely in the green and blue portions, at approximately 480 nm. Light is filtered by means of selective absorption by various agents before entering the water column. Shorter wavelengths, especially the ultraviolet portion, is strongly absor-

bed in the atmosphere by ozone and oxygen. Longer wavelengths, especially the infrared section, are absorbed by water vapour, ozone and carbon dioxide (Wetzel, 1983; Lythgoe, 1979; Nicol, 1989).

The photons are reflected, refracted and to some extent polarised at the water surface. Thus, due to reflection, only some portions of the photons penetrate the surface and become available for animal vision below. The portion of light entering through the surface depends on if the surface is still or rough (Fernald, 1993) and with which angle the solar radiation hits the water surface (Wetzel, 1983) (Fig. 2). Reflection increases with increasing distance from the perpendicular. More light penetrates a still surface. Hence, the visual environment of aquatic habitats is partially depending on surface conditions.

Once light enters the water column it is scattered, or redirected, due to reflection, refraction and diffraction (Valiela, 1995). This process can determine how

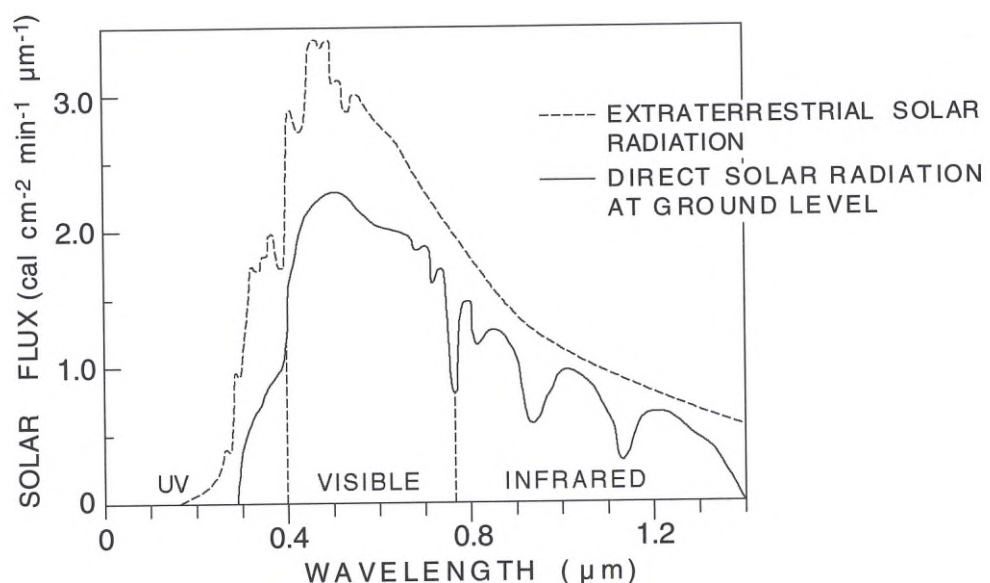


Figure 1. Spectral composition of solar radiation, extraterrestrially and at ground level. Modified from Wetzel (1983).

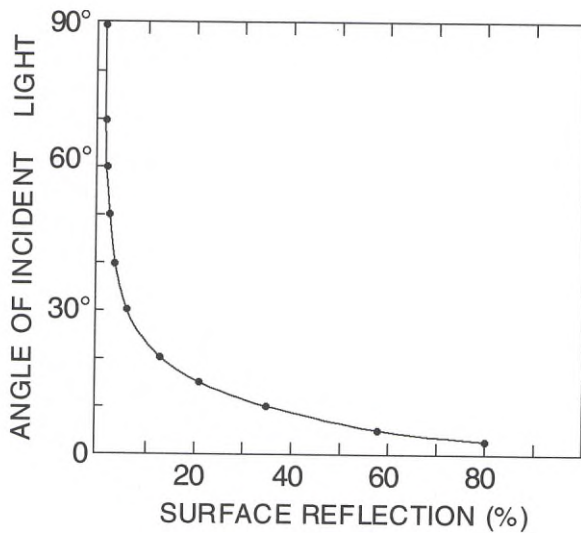


Figure 2. Surface reflection as a percentage of total solar radiation at cloudless conditions and at angles of incidence varying from the horizontal. From Wetzel (1983).

light forms images on an animals retina. The process of scattering decreases the penetration of light in water and diminishes the directionality of light, hence eliminating directionality cues (Marcotte & Browman, 1986). Light reflecting on an image is, of course, also scattered, reducing the available information about the image. Upwelling light, with other words light scattered, comprises only 4 to 5% of the downwelling (Lythgoe, 1984)

Light absorption in water

Light absorption is defined as the transformation of light leading to diminution increasing with depth. When light penetrates the water surface it is absorbed by the water itself and also by dissolved and particulate substances. Different substances absorb different parts of the light spectra. Distilled water absorbs much of the light in the red and the infrared (>575 nm), violet and ultraviolet (UV) region (<400 nm) of the spectra and very little in the middle regions, especially in the blue section (400–450 nm) (Fig. 3a) (Wetzel, 1983).

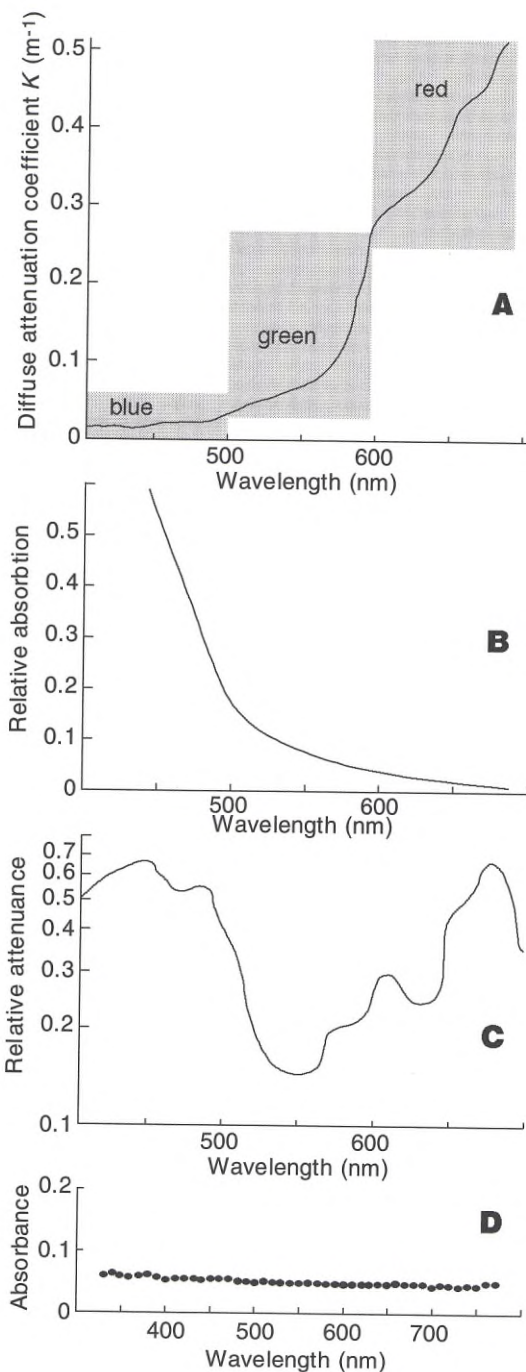


Figure 3. The four major absorbing agents in natural water: a) the water itself b) stable products of organic decay (Gelbstoffe) c) Phytoplankton, in this case the chlorophyll-dominated attenuation spectrum of a suspended green algae d) suspended matter, in the example a clay solution. a)–c) from Lythgoe (1979) and d) from Bristow et al. (1996).

Different particulate or dissolved substances have varying absorptive characteristics. Dissolved organic material has its absorbance maximum in the lower wavelengths, absorbing most of the UV, violet, blue and green light (Fig. 3b) (Fernald, 1993). Especially humic particles greatly increase the absorption of the blue and green wavelengths (Wetzel, 1983). Particulate suspensoids on the other hand do not show the same selective absorption as dissolved organic material (Wetzel, 1983). Absorbance varies more between different substances, and they generally absorb different sections of wavelengths in a more even fashion (Fig. 3c). The type and amount of absorbing agents in water

also influence its colour, or more precisely, how a human observer perceives its colour. Natural water has a colour that matches the portion of the spectra that is maximally transmitted. Clear water therefore has a blue appearance, and most freshwater lakes, where algae, particles and dissolved substances dislocate the maximum transmission point upward in the spectrum has a green outlook.

Light passing through a watercolumn is thus progressively diminished. The attenuation of light can be approached in many ways. One of the most straightforward is to describe light attenuation or in this case light intensity at a given depth I_z as a function of surface intensity (I_0)

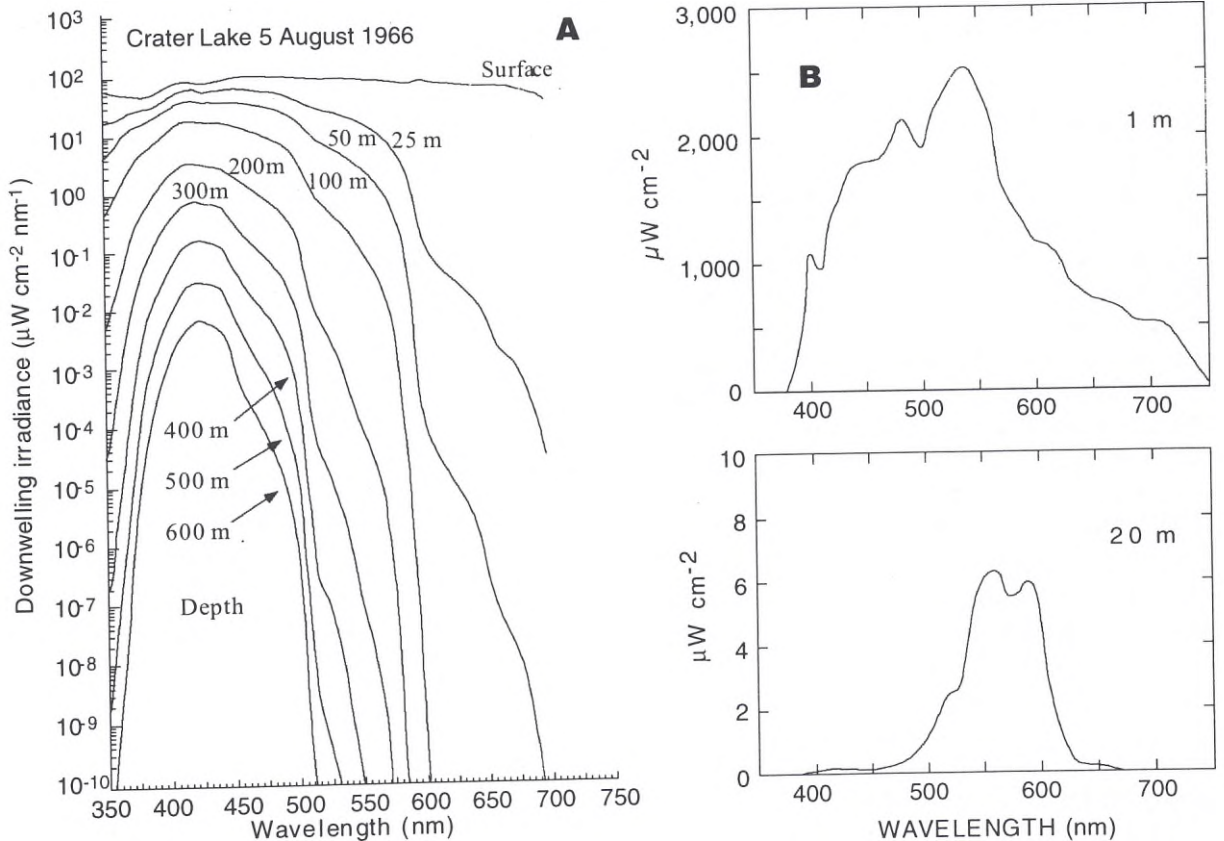


Figure 4. a) Downwelling irradiance in the extremely pure water of Crater Lake. (From Lythgoe, 1979) b) Comparison of spectral distribution in Gull Lake, Michigan at 1 and 20 m depth. Note how the spectral composition at larger depths differs between "pure" water and the water of a mesotrophic lake (From Wetzel, 1983).

and the logarithm of the negative extinction coefficient (k) times the depth in meters (z) according to the formula (Nicol, 1989):

$$I_z = I_0 e^{-kz}$$

The extinction coefficient (k) is affected by the magnitude and composition of different dissolved or particulate substances in the water (Fig. 4a & b). Simply expressed as the sum of the extinction coefficient of the water itself (k_w), of absorbing particles (k_p) and of dissolved coloured compounds (k_c) (Wetzel, 1983):

$$k = k_w + k_p + k_c$$

Seasonal and diel patterns of the visual conditions of aquatic environments.

The amount of solar radiation that is received by the water surface is mainly a function of the angular height of the sun incident to the earth and is thus greatly influenced by time of day, latitude and season (Blaxter, 1975). In temperate and arctic areas daylength changes considerably with season (Gates, 1962) (Fig. 5). During the winter season the bright part of the day is short and the angle to the

sun during daytime is small. This relationship does not only affect the climate in temperate and arctic regions but also influences the light conditions in the waters. The more the angle with which the sun impinges on the water surface is dislocated from the perpendicular the larger is the part of the solar radiation reflected at the surface (Lythgoe, 1975). Thus, visual conditions in aquatic environments are strongly influenced by winter conditions.

Visual conditions at dawn and dusk are characterised by shorter wavelengths (Fig. 6). The reason for this is that light arrives to the surface at a lower angle after a longer atmospheric path (Munz, 1971). When the spectral composition of daylight changes during the day, from short wavelengths at noon to longer wavelengths at dawn and dusk, naturally the downwelling irradiance changes accordingly.

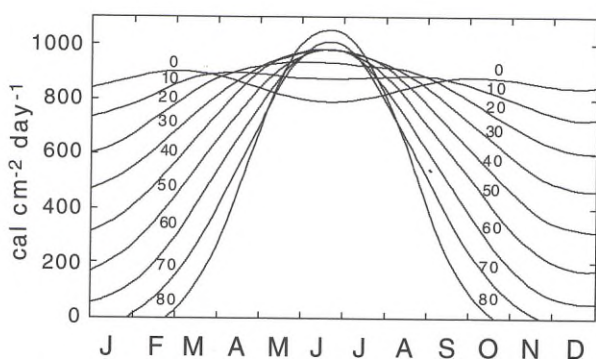


Figure 5. Daily totals of the undepleted solar radiation received on a horizontal surface for different geographical latitudes as a function of the time of year (solar constant $1,94 \text{ cal cm}^{-2} \text{ min}^{-1}$). From Gates (1962).

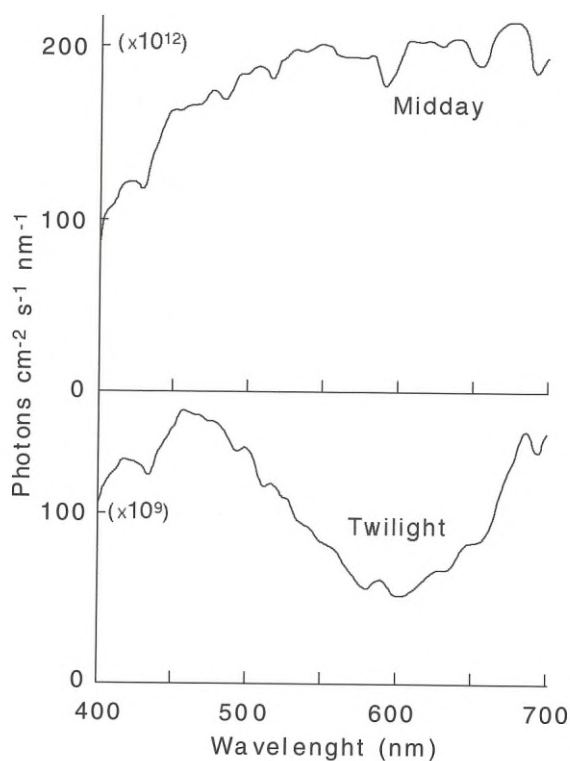


Figure 6. Spectral irradiance during midday and twilight at the Einewetok Atoll. From Lythgoe (1979).

Another seasonally occurring feature of temperate and arctic regions that has impacts on the visual conditions of aquatic organisms is the formation of ice. The percentage of light transmission through clear colourless ice is not that different from water. But if the ice is coloured or cloudy, attenuation of light greatly increases. With the addition of snow on the ice surface light transmission is nearly depleted. In conditions with both ice and snow it is not unusual that light is entirely attenuated already at one meters depth (Wetzel, 1983).

Summary:

- the maximum energy flux of solar radiation lies in the visible field of the spectrum, at approximately 480 nm.
- light reflection on the water surface is depending on with which angle the solar radiation hits the surface and whether the surface is still or rough.
- once light enter the watercolumn it is scattered, refracted and absorbed by the water itself and by dissolved and particulate substances.
- different particulate and dissolved substances in the water absorbs different parts of the light spectra and thus influences the attenuation of light of different wavelengths.
- the intensity of solar radiation and the spectral composition of the light impinging on the water surface is greatly influenced by time of day, latitude and season.

Vision in fishes

The visual system of fish is in many respects designed in a fashion similar to most terrestrial vertebrates. The eye collects light that is concentrated by a lens forming a focused image for analysis on the retina. Besides these fundamental similarities, fish as a group display a more diverse set of visual adaptations compared to terrestrial vertebrates. As a result of the large number of various dissimilar habitat types that fish inhabit they have developed a broad variety of visual adaptations. The set of visual pigments in fishes is for example by far more diverse and variable than in other groups of vertebrates (Lythgoe, 1986). Munz (1971) stresses that the evolution of diverse sets of pigments in fish is probably a necessity in the selection for adaptive abilities in aquatic environments.

Morphology and function of the fish eye

The fish eye grows throughout the entire life. Therefore the morphologic adaptations of its visual system must satisfy both immediate and future needs of vision (Nicol, 1989; Loew & Wahl, 1991; Fernald, 1993).

The fish eye is located in an orbital cavity formed of connective tissue, cartilage and bone and is surrounded by a thick fibrous coat, the sclera (Nicol, 1989) (Fig. 7). Its transparent part at the front of the eye is called cornea. Light passes through the cornea and is refracted on the lens and then concentrated to parts of the innermost tunic of the eye cavity, where photoreceptive cells form a light sensitive layer, the so-called retina. The light is concentrated to a part of the retina, the fovea, where the abundance of photoreceptors is greatest resulting in a more resolved image.

The optics of fish is different from terrestrial animals in one fundamentally important respect. There is no air-cornea interface, a feature that provides significant optical power to terrestrial vertebrates. The refractive index of the cornea

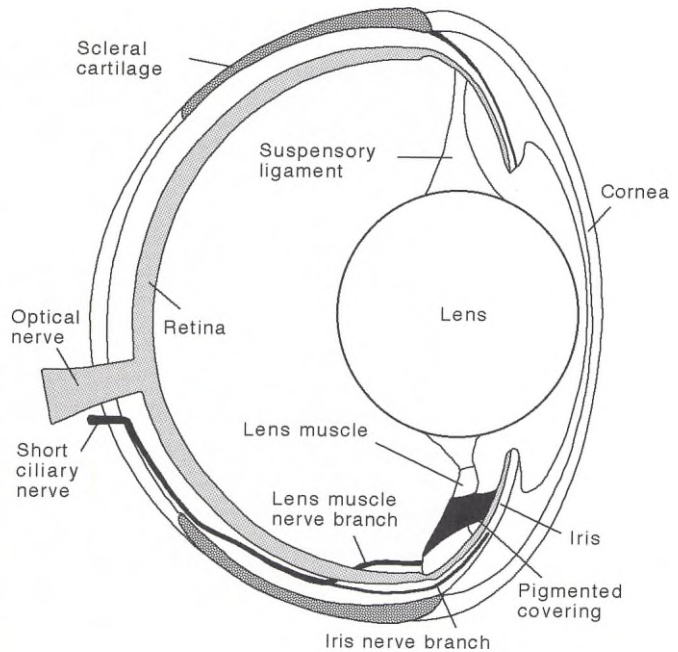


Figure 7. Vertical cross-section of a fish eye. From Nicol (1989).

of fish is similar to the surrounding water, hence it is more difficult for them to focus objects. This feature deprives fish of nearly 80% of their optical power compared to terrestrials making it more difficult for them to focus when the lens must provide all the dioptric strength (Easter, 1975).

In order to attain their hydrodynamical body form, fish must have a short focal length of their lens. But the lens of fish must, as discussed earlier, provide all of the optical strength and therefore fish face the trade-off between maximizing the size of their lens and good swimming capacity (Fernald, 1993). In order to meet both these constraints a spherical lens with very high refractive power has developed in fish (Fernald, 1993) (Fig. 8).

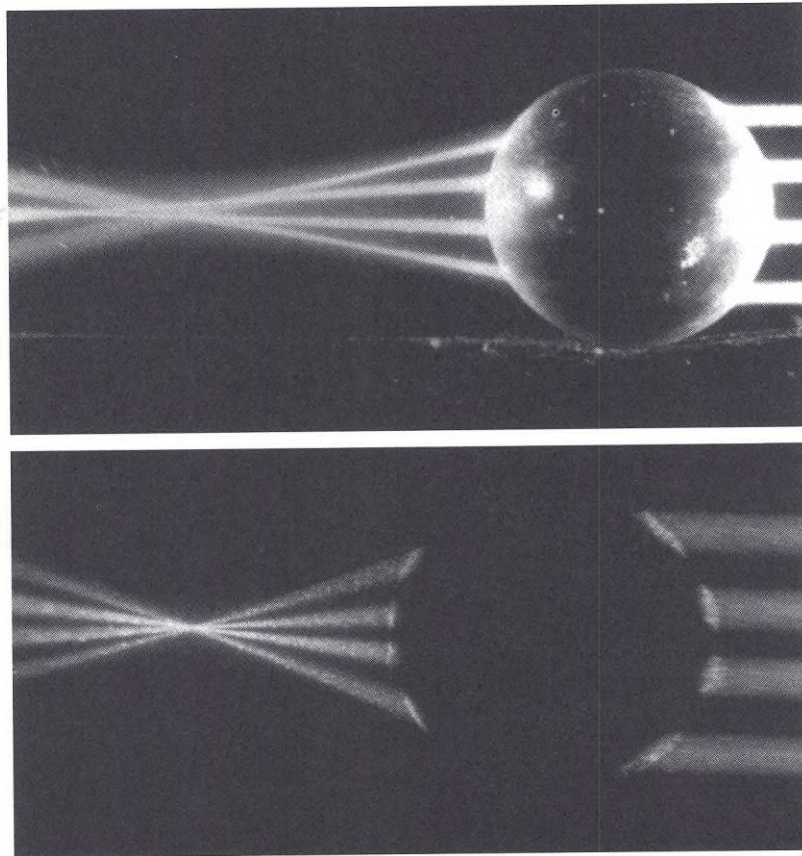


Figure 8. Fish lenses have evolved a very high resolving capacity. The figure shows the difference between a glass sphere (top) and a fish lens (bottom) of equal size focusing four argon laser beams (494 nm). From Fernald (1993).

Besides offering better possibilities for visual acuity large eyes also gather more light. Deep-sea fishes have enlarged eyes that enable them to detect light more efficiently (Fig. 9). Fishes living close to the surface on the other hand depend more on the intensity of illuminating light for their retinal luminance and accordingly the advantage of larger eyes does not compensate for lost swimming abilities (Fernald, 1993).

Instead of changing the shape of the lens as for example humans do, fish accommodate by changing the distance from the retina to the lens. All fish, with exception of lampreys, have this ability (Nicol, 1989).

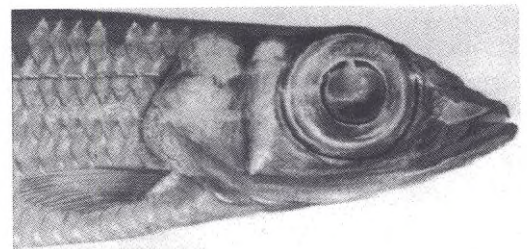


Figure 9. The visual apparatus of deep-sea fishes are adapted for enhancing light-sensitivity. One feature common in deep-sea fishes improving their light sensitivity, is large eyes. The figure shows the large eye of the great silver smelt (*Argentina silus*) living at depths of 150 to 1000 m. From Muus & Dahlström (1965).

Some fish species have coloured corneas. Cornea colorations can be useful firstly to filter light that disturbs an image and secondly to compensate for camouflage illumination of fishes swimming above making them appear as shadows against the light background (Lythgoe, 1979; Fernald, 1993). Especially surface-living, diurnal fishes have this type of configuration usually coloured yellow (Nicol, 1989). Yellow coloured corneas reduce short-wavelength light that is the most scattered and hence can degrade an image the most (Fig. 10). Some nocturnal species even have corneal chromatophores filtering light at day-time and becoming virtually transparent at night (Fernald, 1993).

The retina of fishes, a thin laminar structure located at the back of the eye, is constituted by seven major cell types: photoreceptors, bipolar, horizontal, interplexiform, amacrine, ganglion and Müller cells. The fundamental parts of the fish retina do not significantly differ from ter-

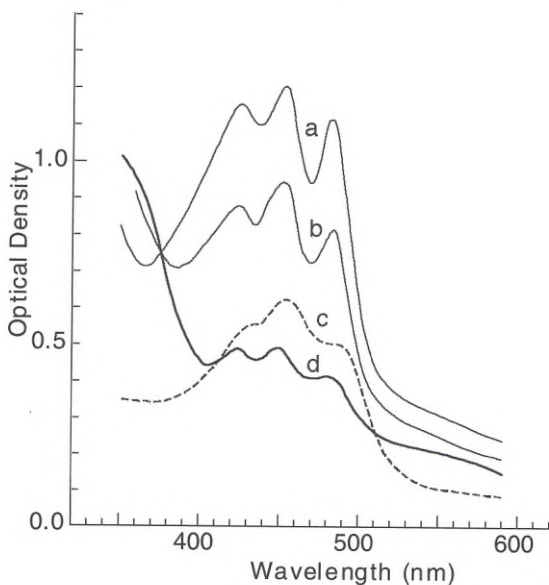


Figure 10. The spectral absorption curves of the yellow cornea of four fish species, a) the green wrasse (*Labrus viridis*), b) the rainbow wrasse (*Coris julis*), c) the perch (*Perca fluviatilis*) and d) the peacock wrasse (*Thalassoma pavo*). From Lythgoe, 1979.

restrial vertebrates but the structural configuration of the retinal mosaic can vary considerably.

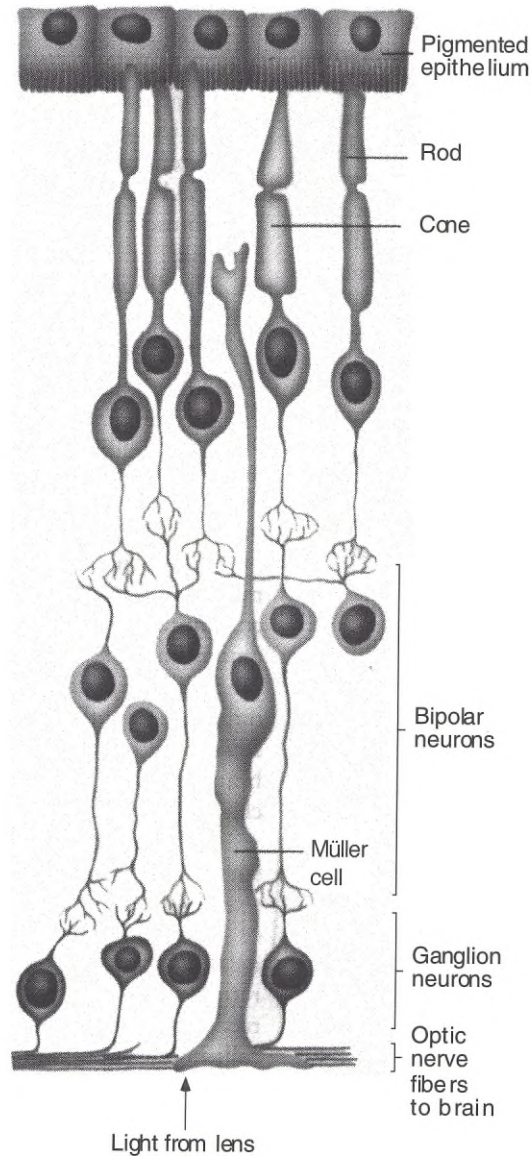


Figure 11. Illustration of a cross-section of the human retina. Light passes through all of the cell layers in the retina and is absorbed by photoreceptor proteins in the rods and the cones. The axons of the photoreceptor cells synapse with the bipolar neurons. These in turn synapse with the ganglion neurons whose axons run through the optic nerve to the brain. Müller cells function as supportive tissue and constitutes much of the retinal space. From Lodish et al., 1995.

Photoreceptors situated on the retinal surface absorb photons and transmit the received energy to electrical signals transported and interpreted by the nervous system, which then is further transported to the brain via the optical nerve. There are two types of photoreceptors, the rods and the cones. The rods have elongated cylindrical outer segments while cones usually have short cone-like outer segments (Fig. 11). Already in the middle of the nineteenth century Müller observed and described the two types of photoreceptors. Only a decade later Schülze discovered that the cones functioned daytime in bright light and the rods during the night in dim conditions (Munz, 1971). Vision in bright light is termed *photopic* and in dim light it is called *scotopic*.

Cones are often arranged singly, in pairs (double cones) or in small groups in order to facilitate sharp high-resolution vision in bright light (Nicol, 1989). The cones tend for most of the chromatic vision in contrast to rods, which usually only provide low-resolution monochromatic images. Cone length is associated to spectral sensitivity. The shorter the cone the shorter the absorbed wavelengths (Lythgoe, 1979). The rods function best in dim light and are aggregated in larger groups to accentuate light sensitivity.

As most other vertebrates fish have the ability to adapt their retinal configuration to the "current" light environment. At daytime when light intensity is high and the fish retina is set for photopic vision the cones constitute most of the visual power of the fish, but when light

Dark-adapted	←—————→	Light-adapted
Low intensity scotopic vision by rods		High intensity photopic vision by cones
High sensitivity		Low sensitivity
More sensitive in the blue (though not seen as a colour)	← Purkinje shift →	More sensitivity in green-yellow
No colour vision		Colour vision
Low acuity (much summation)		High acuity (less summation)
Low frequency for flicker-fusion		High frequency for flicker-fusion
←————— Changes in many behaviour patterns —————→		

Table 1. Physiological differences between the dark- and light-adapted eye. From Blaxter (1975).

intensities decrease the retinal mosaic undergoes structural changes "switching" to scotopic vision. The cones are drawn back, and the rods are elongated and moved forward. This mechanism is called retinomotor response (Guma'a, 1982) (Tab. 1).

The retinal organisation may differ greatly among different species of fish depending on their habitat preference and lifestyles. Fishes foraging nocturnally, crepuscularly, at large depths or at high turbidity have a retinal organisation that emphasises light sensitivity (Munz, 1982). Consequently the retina of diurnal surface living fishes is organised in order to emphasise visual acuity.

Do fish have the ability to distinguish different colours? In 1964 Marks and McNichol, Jr. conducted spectrophotometric measurements on single cones of the goldfish (*Carassius auratus*) and concluded, that it had three distinct types of retinal cones with different absorptive characteristics absorbing blue, green and red respectively (Eckert *et al.*, 1988). Following behavioural experiments provided more evidence. The goldfish seemed to have the ability to distinguish between green, blue and red objects supporting the theory of trichromatic vision (Ingle, 1971). More recent research in this area further implies, that fishes have the ability to distinguish different colours or more precisely perceive the difference between two radiances by hue alone (Fernald, 1993). The photoreceptors only signal of receiving a stimuli, their signal does not contend any information of colour. The interpretation of colours are made by the brain co-ordinated with the retina comparing the outputs of photoreceptors with their different spectral sensitivity (Lythgoe, 1986).

Visual localisation of objects in water

Visual detection of underwater objects by fish is influenced by a number of factors all associated to the unique features of the visual environment in aquatic habitats.

The fish visual volume, i.e. the irregular sphere in which the fish can see objects, is one factor that obviously affects a fish's ability to visualise its surroundings (Fig. 12). The fish visual volume is expanded upwards due to the fact that the intensity of downwelling light is normally about twenty times greater than the scattered upwelling light. It is therefore often advantageous, to strike prey from beneath. The visual volume increases with increasing light intensity and decreases with increasing turbidity.

The foraging pattern of particulate feeding fish, like percid larvae for example, are determined by prey visibility and size, visual acuity and mouth structure. Hessen (1985) suggests that prey selection of juvenile roach was mainly determined by varying pigmentation of the prey. In groups of *Bosmina rongirostris*, the mean diameter of the pigmented eye decreased significantly in groups where high abundances of roach was present, suggesting that the fish selectively eat individuals easier to detect.

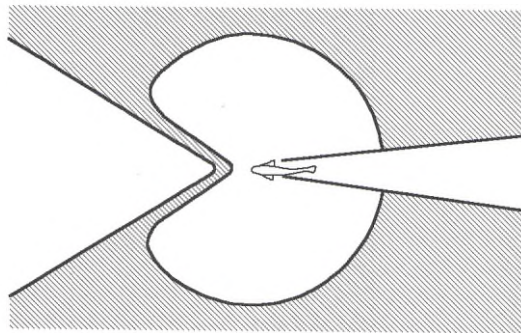


Figure 12. Diagrammatic representation of the visual field of a fish seen from above with its eyes unaccommodated. The triangular open area in front of the fish lies beyond the "far point", for a resolved image of an object closer than the far point, the fish need to accommodate or else it would be "near-sighted". The circular open areas on the sides are within the locus of the "near point", posteriorly disturbed by the shadow of the fish's body. From Munz (1981).

To maximise light uptake, the spectral characteristics of the visual pigments of fish should be in accordance with the spectral composition of light in their environment. For deep-sea fishes there seems to be a very clear match between these two parameters, but in many surface-living fishes this has proved not to be the case. The absorbance properties of fresh water and coastal fish visual pigments instead has a peak a bit offset the spectral peak of the ambient illumination (Fig. 13). This puzzling relationship led Lythgoe (1975) to emphasise the importance of visual contrast as the main selective agent for the evolution of different adaptations of the visual system in fish with accordance to their environment. His explanation of why fresh water and coastal fish would have a peak absorbance slightly deviating from their aquatic environment

was that it accordingly would enhance contrast detection of underwater objects.

When light is reflected by an object, it travels a shorter distance than the scattered light behind it, before it reaches the eye of the fish giving light from the object a different chromatic composition than the background (Munz, 1981) (Fig. 14). The wavelength maximum of the light reflected from the object is closer to the spectral region dominating at the surface, while the wavelength maximum of the background is closer to the maximum transmission point of the water (Lythgoe, 1986). Therefore the maximal absorption of freshwater and coastal fish eyes is at a wavelength somewhat removed from the transmission maximum of the surrounding water in order to enhance the visual contrast between the object and the background (Lythgoe, 1986). Freshwater and

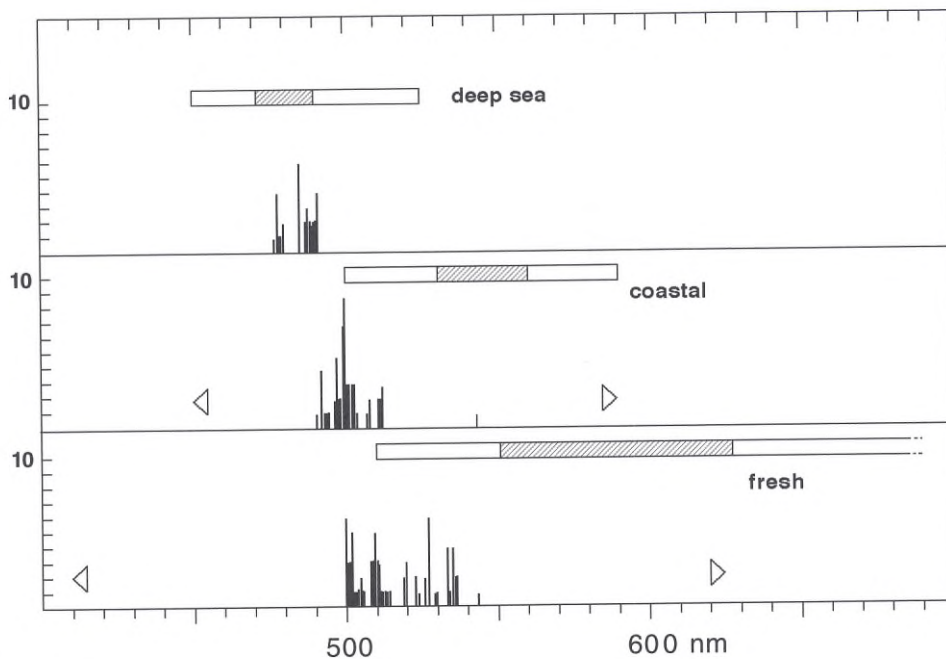


Figure 13. Histograms of the number of fish species containing visual pigments with a known absorption maximum. The horizontal bars above show the possible range of spectral absorption maxima of visual pigment that would give optimal light sensitivity in each type of environment. The shaded areas show the most likely absorption maxima. The open triangles represent the most extreme absorption maxima measured in fishes inhabiting each water type. Note how coastal and freshwater species deviate from what would be expected for optimal enhancement of light sensitivity. From Lythgoe (1979).

coastal fish species forage at comparatively lower depths than deep sea fishes. Therefore the loss of light sensitivity by not having maximal absorbance at the least attenuated wavelengths is not as costly. The distance between visual λ_{\max} and the transmission λ_{\max} must be balanced not to lose sufficient light sensitivity.

Collyer (1997) also recognises the importance of contrasts in the localisation of underwater objects. He demonstrates

how contrasts are "exaggerated" by the visual system of fish and states that:

"Perception goes beyond simple copying even in the way light is registered by the eye itself. Fish vision concentrates on the contrasts between object and background. Hence the most important part of the pattern of an underwater scene that is portrayed by the retina is the edge between the object and the background."

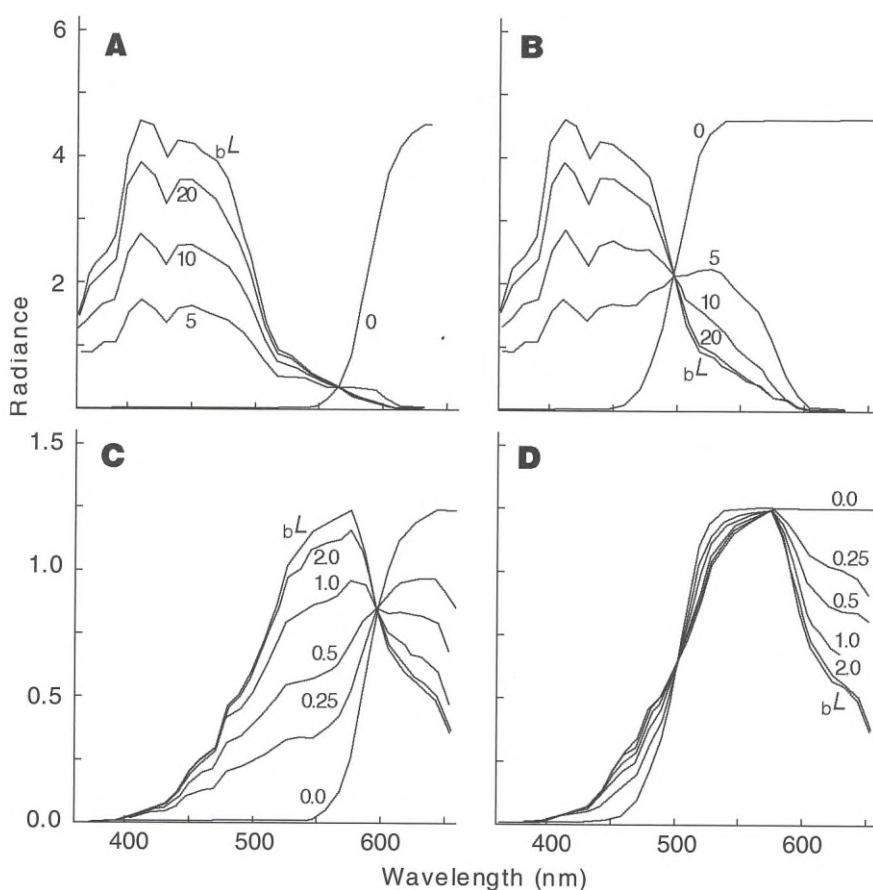


Figure 14. The changes in spectral radiance of a yellow and red object as they recede horizontally from the beholder's eye in blue (the Gulf Stream) and green water (a typical freshwater). The distances are given in meters. a) A red object in blue water b) yellow in blue water c) red in green water and d) yellow in green water. Note how the object radiance and the spectral radiance remains distinctly different in b) and c) and thus will appear different in hue at a much longer distance than in a) and d). This phenomenon may be one reason for that fish signalling colours in freshwater usually are red (e. g. the pelvic and anal fins of the perch [*Perca fluviatilis*]) and why similar signalling sets are yellow in marine fish. From Lythgoe (1979).

Predation of fish consists of a series of discrete steps. The first step in the predation sequence, reaction to prey is largely limited by the reactive distance, the maximum distance at which a fish reacts to its prey (Link & Edsall, 1996). Besides external conditions, light intensity and level of turbidity, the reactive distance is heavily affected by prey size and visibility and the visual acuity of the fish. The visual acuity of a fish is a function of lens diameter and the density of retinal cones (Breck & Glitter, 1983). A larger lens is accompanied by a larger retina. As the fish grows the retina is continuously receding from the lens which will increase the so called retinal magnification factor. A given object at a given distance will thus cast a larger image in a larger eye thereby improving the visual

acuity of the object portrayed (Hairston *et al.*, 1982). Due to the fact that lens diameter increases with fish size it is probable that, if retinal cone density does not decrease with size, the visual acuity of fish enhances with increasing fish size (Fig. 15). This hypothesis was tested by Breck & Glitter (1983) and Hairston *et al.* (1982) for bluegill sunfish (*Lepomis macrochirus*). Both groups found that visual acuity indeed was improved with increasing fish size. The largest size classes though showed a slight decline in acuity. This was suggested to be an indication of a slight descent in cone density with increasing size (Fig. 16). Conclusively, larger fish can perceive a larger volume of space, which will allow them both to see more prey than small fish but also to detect predators earlier.

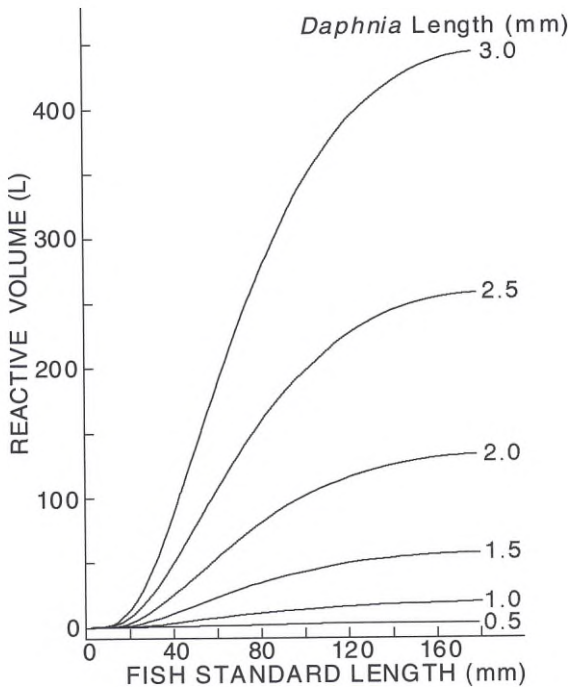


Figure 15. Predicted visual volume of bluegill (*Lepomis macrochirus*) versus standard length for various sizes of *Daphnia*. From Breck & Glitter (1983).

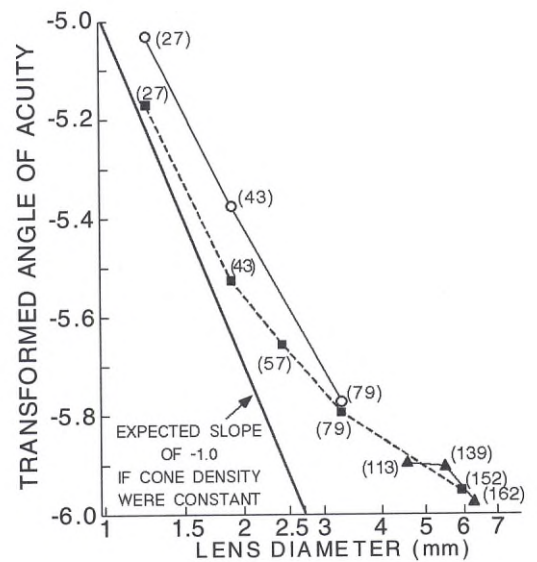


Figure 16. Transformed angle of acuity (the lower the value the higher the acuity) versus logarithm of bluegill (*Lepomis macrochirus*) lens diameter, calculated from the results of a foraging experiment with two types of prey, *Daphnia galeata* (open circles) and *Daphnia magna* (filled circles). Fish lengths (mm) are shown in parentheses near each data point of their lens diameter. From Breck & Glitter (1983).

Visually associated adaptations for aquatic living

Besides adapting their visual system to the aquatic light environment fish have developed many morphological and behavioural adaptations. The coloration of fishes is often perfectly designed for camouflage against predators or to avoid prey detection. Examples of such colour patterns occurring in most fishes are the dark dorsal surface making the fish harder to detect from above against the dark background beneath, and a light ventral surface running into the light surface background. Many fishes have also colorations that give them camouflage in vegetation or on rocky spots. Some fish have even developed ventral photophores that generate light obscuring their silhouette (Fernald, 1993). Coloration and colour patterns also have an ethological significance in the mutual recognition of conspecifics. Mainly involved in signalling aggression, attracting mates or communicating with their young (Fujii, 1993). Fishes have the ability to rapidly change their hue and colour by effectively controlling their chromatophores, i. e. the pigment cells in their skin (Fujii, 1993).

Summary:

- As a consequence of the large number of dissimilar light environments that fish inhabit, they have evolved a diverse set of visual adaptations.
- Fish have a spherical lens that provides all of the optic strength, and they accommodate by changing the distance between the lens and the retina.
- Many fishes have coloured corneas that filter light that may disturb an image.
- The retina of fish, similar to other vertebrates, has two types of retinal photoreceptors, the rods and the cones. The cones function in bright light (photopic vision) and the rods in dim light (scotopic vision).
- Fish can adapt their retinal configuration to the current light environment, the so-called retinomotoric response.
- The contrast between an object and the background seems to be of great importance for the vision of coastal and freshwater fish species. The photoreceptors of these species have an absorption peak in a spectral region slightly deviating from the region where most light is transmitted. This is believed to be advantageous when detecting an object. Mainly because light reflected against an object has its spectral maximum in other regions than the background illumination which spectrally eclipses the regions where the ambient water transmit maximally.
- The reactive distance, i.e. the maximum distance at which a fish reacts to its prey, is affected by light intensity, turbidity, prey size and visibility as well as the visual acuity of the fish.

Characteristic features of vision in percids

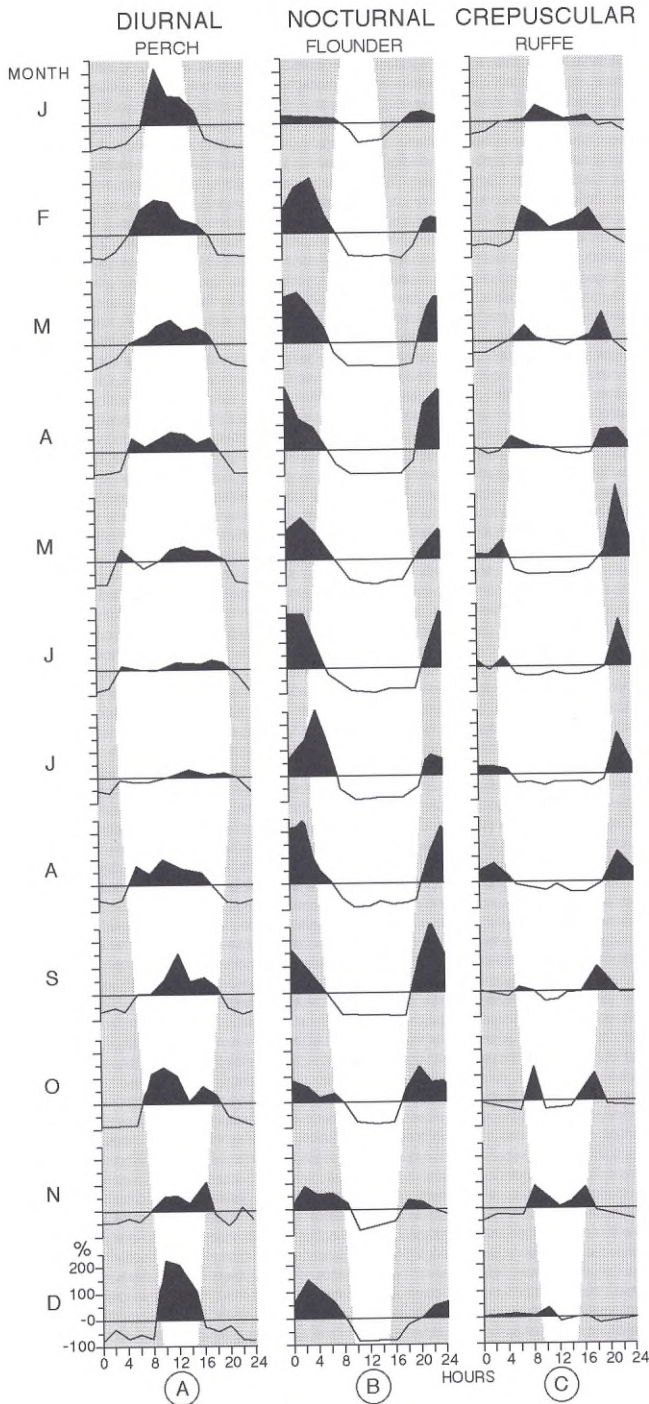


Figure 17. Diurnal (perch), nocturnal (flounder) and crepuscular (ruffe) patterns of locomotor activity. From Westin & Aneer (1987).

The visual systems of both *Perca* spp. and *Stizostedion* spp. are in the most respects relatively well studied. Unfortunately that is not the case with the *Gymnocephalus* spp. where many of the visually related properties still remain unexplored. Consequently, this description will concentrate on the former.

Parallel to the considerable variation among the teleosts there is also some variation among the family of *Percidae* in adaptations for different visual conditions. The differences among the *Percidae* relate to the differences in behaviour and lifestyle of the species in question. There are two general directions of visual adaptations among the adult *Percidae* both clearly reflecting the lifestyle and activity pattern of the species in question:

(1.) Species equipped with a visual apparatus adapted for feeding at low light intensities in turbid environments or, in more clear waters, nocturnally and crepuscularly (Fig. 17) (Collette *et al.*, 1977). Examples of species belonging to this category are the members of the *Stizostedion* genus, e. g. pikeperch (*Stizostedion lucioperca*), walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadensis*) (Ahlbert, 1973; Westin & Aneer, 1987; Ryder, 1977; Craig, 1987; Collette *et al.*, 1977) and the members of the *Gymnocephalus* genus, e. g. ruffe, which also rely on a highly developed lateral-line organ, advantageous when feeding in environments with dim light and high turbidity (Disler & Smirnov, 1977; Hay & Adams, 1997).

(2.) Diurnal, day-active species (Fig. 17) that depend largely on high visual acuity at moderate or high light intensities and forage in the upper part of the water column, e. g. perch (*Perca fluviatilis*) and yellow perch (*Perca flavescens*) (Ahlbert, 1973; Collette, 1977; Huusko *et al.*, 1997; Westin & Aneer, 1987; Craig, 1987 and Wahl *et al.*, 1993).

The percid retina:

There are only small differences in the absorptive characteristics of the pigment epithelium in percids (Fig. 18) (Ali *et al.*, 1977). The differences in visual performance instead originate mainly from the differences in photoreceptor structure and organisation.

The cones of *Perca* spp. are of moderate size and oriented in a fashion that enhances visual acuity with most of the cones placed near the optic nerve. The rods are relatively large and uniformly distributed over the retina (Ali *et al.*, 1977). Sauger, walleye, pikeperch and most other *Stizostedion* spp. species differ from *Perca* spp. in this respect, having voluminous cones, which are more evenly dispersed over the retina and small rods arranged in groups. This arrangement is more adapted to light sensitivity than visual acuity (Guma'a, 1982).

The cone mosaic arrangement of adult *Stizostedion* spp. has two different types of cones, midwave with a maximum sensitivity of about 530 nm and longwave with a maximum sensitivity of 605 nm (Ali & Anctil, 1977). Similarly both adult Eurasian perch and yellow perch also have two types of cones arranged singly or in pairs (double) in a square retinal cone mosaic. The double cones form the corners of a square surrounding a central single cone. Double cones have a maximum sensitivity at 620–630 nm and the single cones at 535 nm, in other words nearly similar to the absorbance maxima of *Stizostedion* spp (Fig. 18) (Loew and Wahl, 1991).

Both the *Stizostedion* spp. and the *Gymnocephalus* genus have a special structure of their retina, the *tapetum lucidum*, a reflective layer situated in the pigmented epithelium layer of the retina, that enhances light sensitivity in dim conditions. The *tapetum lucidum* optically isolates groups of rods and consists of a substance adding reflective capacity, called 7,8-dihydroxyanthopterin (Sone-

sten, 1991). This arrangement induces extra reflections of the light back and forth between the rods with additional absorption at each reflection. The arrangement and the distribution of the *tapetum lucidum* in percids differ somewhat among species largely depending on their lifestyle. Within the *Stizostedion* genus the sauger (*S. canadensis*) is probably the species with the most developed *tapetum lucidum*, uniformly distributed over the entire retina (Ali & Anctil, 1977). Most

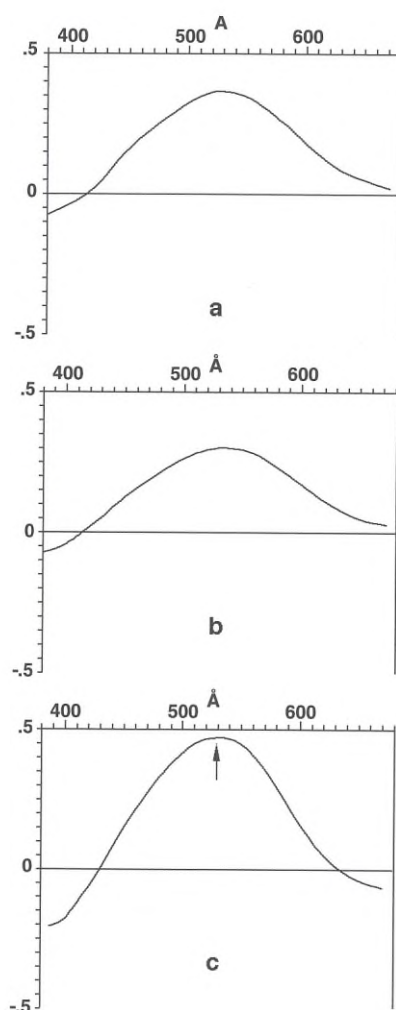


Figure 18. Optical density of retinal patches at different wavelengths in a) walleye, b) sauger c) yellow perch. Note the similarities between different species. From Ali *et al.*, (1977).

other species, like for example the pikeperch and the ruffe, have only the *tapetum lucidum* in the dorsal two thirds of the retina. Ventrally, where most of the light is concentrated, these species have instead a higher density of single cones than sauger assuring increased visual acuity in the more light dominated part of the retina.

Perhaps reflecting their day-active life style, the members of the *Perca* spp. have much larger concentration of the pigment melanin than the *Stizostedion* spp. Melanin, which absorbs maximally at about 500 nm absorbs much of the light that otherwise might traverse the retina, thus hindering backscattering and image deterioration (Nicol, 1989).

The visual system of fish has a certain plasticity in the retinal structure that enables the fish to adapt to variations in the light environment. This function is termed retinomotor response. It can be described as the concentration of masking pigments in the retinal epithelial cells and the expansion and contraction of rods and cones in response to changes in the ambient light (Guma'a, 1981). In adult *Perca* spp., both cones and rods are mobile

and function in the retinomotor response. When adapting to darkness, perch cones migrate from the light path, and the rods elongate. In the opposite situation, the cones migrate back to their original site, and the rods are drawn back. In *Stizostedion* spp., the cones are immobile and very small and have no function during the retinomotor response. Instead their retinomotor response only consists of the rods extending or being drawn back.

Changes of the visual system during the larval and juvenile periods.

Perches (*Perca* spp.) undergo a fundamental ontogenetic change during their first year of life. They change from a pelagial lifestyle, foraging on planktonic organisms, to a demersal, eating mainly macroinvertebrates. Pikeperches (*Stizostedion* spp.), on the other hand, remain pelagial throughout their life. It is quite unclear whether ruffe larvae are pelagial or demersal during their early ontogeny. Rösch *et al.* (1996) declares that the larval distribution of ruffe is unknown, while Disler and Smirnow (1977), without referring to any specific data or investigation, suggests the ruffe to be benthic as larvae.

Table 2. Comparison of the visual characteristics of different percids.

	Sauger (<i>Stizostedion canadensis</i>)	Walleye (<i>Stizostedion vitreum</i>)	Pikeperch (<i>Stizostedion lucioperca</i>)	Ruffe (<i>Gymnocephalus cernua</i>)	Perch & Yellow perch (<i>Perca fluviatilis</i> & <i>P. flavescens</i>)
activity pattern in clear water	nocturnal	nocturnal	nocturnal/ crepuscular	nocturnal/ crepuscular	diurnal
Tapeta lucidum	distributed over entire retina	distributed over entire retina except area retinae	distributed dorsally in two thirds of retina.	distributed dorsally in two thirds of retina.	lacking
single- double cone ratio	low	low	moderately low	unknown	medium
retinomotor response	only rods involved, cones immobile	only rods involved, cones immobile	only rods involved, cones immobile	unknown	including both rods and cones
retinal organisation	photoreceptors aggregated in groups	photoreceptors aggregated in groups	photoreceptors aggregated in groups	unknown	photoreceptors evenly dispersed

Morphologically all percid larvae gradually transform from a transparent appearance to the adult coloration and outlook. This transformation is termed metamorphosis and naturally also involves changes in the visual apparatus.

Percid larvae showcase a positive phototactic behaviour during the first weeks after hatching. They gradually become less phototactic. About the time of metamorphosis the larvae of some species, predominantly of the *Stizostedion* genus, instead develop a negative phototactic response (Craig, 1987).

Guma'a (1981) found that the larval retina of perch only consisted of single cones and that double cones and rods developed at the time of metamorphosis. Contrary to those findings, Ahlbert (1973) has reported the presence of rods already at hatching. These discrepancies in results have been explained by Wahl *et al.* (1993) as a consequence of using slightly different techniques, thus supporting Ahlbert's findings of rods. Rods may develop very early, but they only occur in low densities in perch larvae as opposed to single cones, that are the dominating photoreceptors.

The retina of perch larvae contains two types of single cones. There are single cones of the same type as earlier described for the adults, and there is a type of UV-sensitive small cones not found in the adults (Fig. 19 and Fig. 20) (Loew & Wahl, 1991). The UV-sensitive larval cone cells are smaller and morphologically distinct from other types of percid cones (Loew & Wahl, 1991). Detection of short-wavelength light can be advantageous at shallower depths where the intensity of short-wave light still is significant. These shorter wavelengths are highly scattered, which, if the retina is capable of detecting it, may enhance the contrast between the planktonic organisms and the background. The result is then a more effective high-resolution localisation of prey organisms. Besides offering a tool for better contrast in visual detection UV-sensitive mechanisms also give the larval perch increased opportunities of selecting prey (Loew & Lythgoe, 1978). Observations of planktonic prey in UV-light demonstrate an array of characteristic patterns for most groups of prey items, that could play a role in larval prey selection.

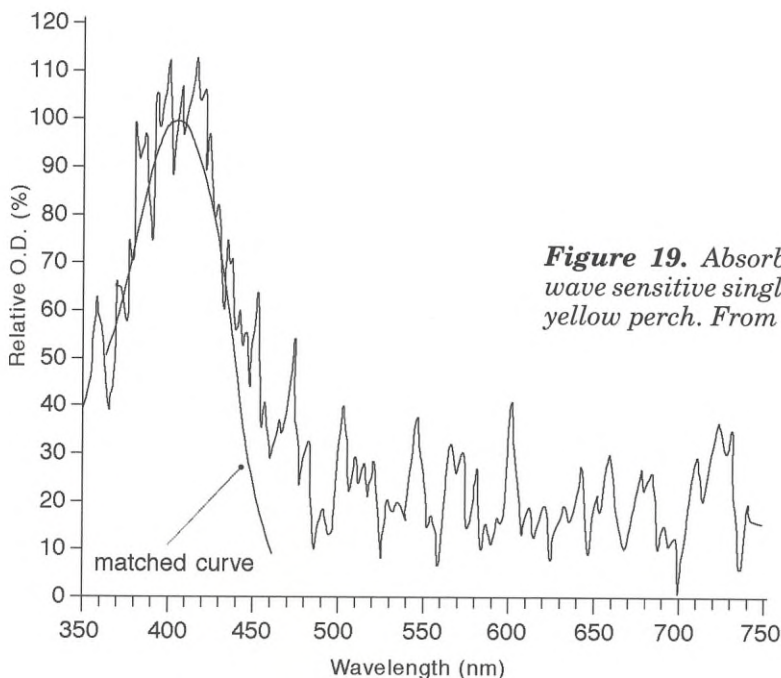


Figure 19. Absorbance spectra of a short-wave sensitive single cone of a 25 mm juvenile yellow perch. From Loew & Wahl (1991).

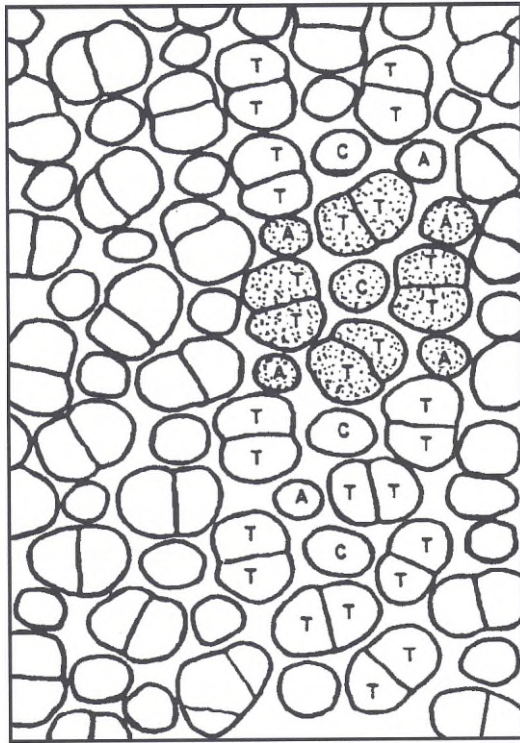


Figure 20. Tangential section of the retina of a 15 mm juvenile perch showing the cone organisation. T: Twin cones (or double cones), C: central single cones and A: Short UV-sensitive corner cones. From Loew & Wahl (1991).

The retina of perch is believed to successively refine during development of the fish eye becoming increasingly similar to the adult (Wahl *et al.*, 1993). The density and size of rods increase (Fig. 21b), and at about 15 mm length another type of cones, the twin oriented or double cones, starts to appear. Double cones are believed to be more efficient in detection of movements (Ahlbert, 1973). The cone density as opposed to rods decreases with increasing fish size (Fig. 21a). The cone mosaic successively develops a more regular pattern (Fig. 20), similar to the adults, starting at the first appearance of double cones. A regular cone mosaic pattern normally enhances visual acuity at the expense of light sensitivity (Ahlbert, 1973).

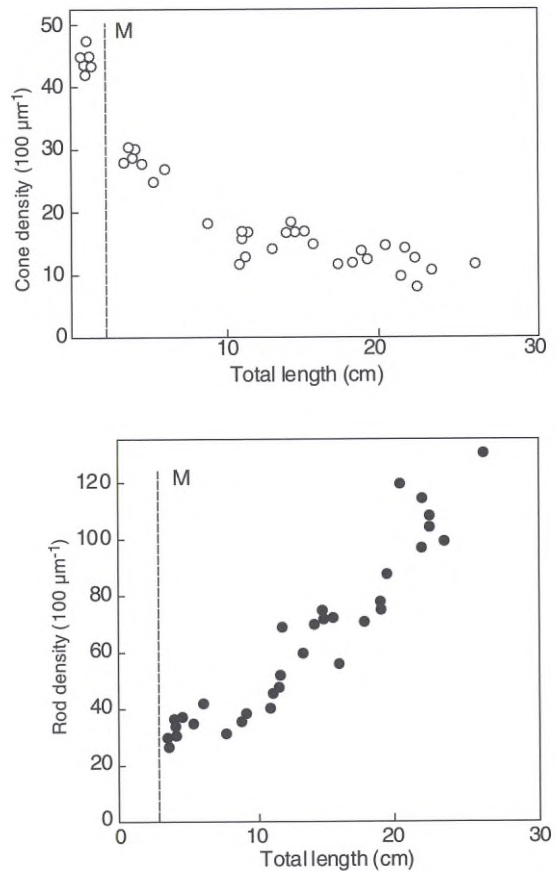


Figure 21. a) Changes in the density of cones (both twin and single) in the retina of perch during development. b) Changes in the density of rods in the retina of perch during development. The dotted line indicated with an M, shows approximate time of metamorphosis. From Guma'a (1981).

When the juvenile perch switches habitat and starts demersal feeding, its visual acuity, increasing successively during the early ontogeny, nearly equals that of adults (Fig. 22) (Wahl *et al.*, 1993). The increase of visual acuity is also accompanied by adaptations for feeding and living in more dim conditions. At or slightly after the time of metamorphosis, the first signs of a retinomotor response commence, and the number and size of rods are increased (Guma'a, 1982).

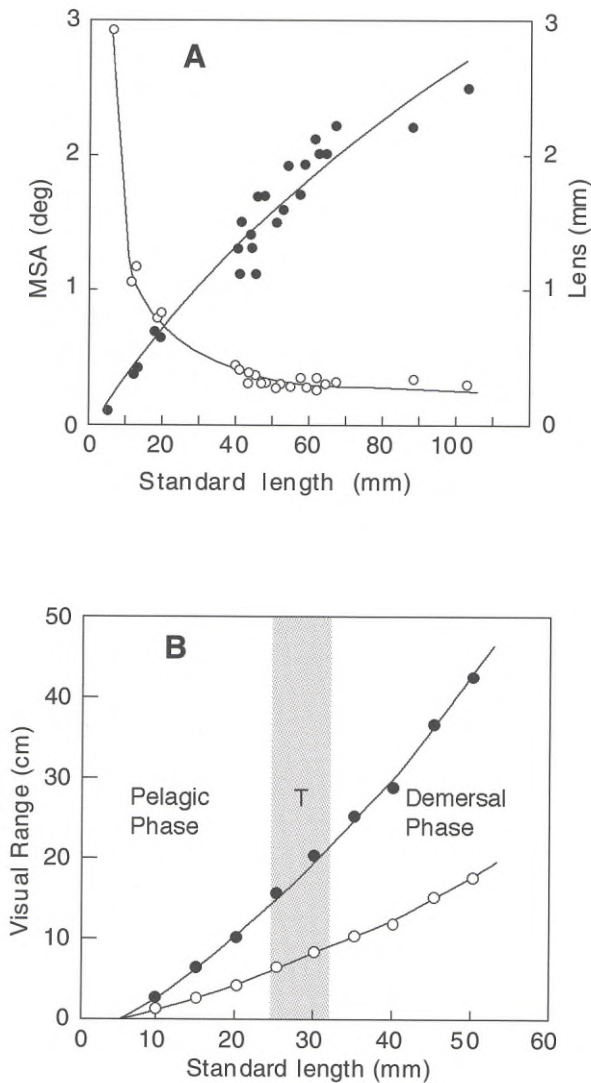


Fig 22. a) Regression of the visual acuity (MSA), the lower the value the higher acuity, and lens diameter against standard length of young-of-the-year yellow perch (*Perca flavescens*). Open circles indicate MSA (minimum separable angle) in degrees and solid circles indicate lens diameters. b) Visual range versus standard length of young-of-the-year yellow perch. Solid circles indicate values for the average minimum sized prey eaten and open circles maximum sized. The shaded areas indicate the range of standard lengths at which yellow perch in Lake Oneida switched from a pelagic to demersal habitat. From Wahl et al. (1993).

When feeding at larger depths, the use of an UV-sensitive mechanism loses its function. Subsequently the short-wavelength sensitive cones are lost, when the perch juveniles convert from living in the pelagial to the benthos. The ultraviolet portion of the light spectrum is effectively reduced at depths exceeding one meter (Williamson, 1997).

Additional sensory mechanisms of percids

Besides extracting visual signals fish perceive their surroundings with the mechanoreceptor organs of the lateral line system, by hearing and by smelling. These organs act as complements to vision when a fish senses its surroundings and may be of some importance in environments where visual abilities are limited (Hara, 1971; Lowenstein, 1971; Tavalga, 1971).

The lateral line system, situated longitudinally, on each side, is constituted by cutaneous sensory cells, the mechanoreceptor organs, that register movement and sound waves in water.

The Eurasian perch, yellow perch and the members of the *Stizostedion* genus depend mainly on vision when sensing their environment. The lateral line-system appears to be less insignificant. In contrast to *Perca spp* and *Stizostedion spp.*, the *Gymnocephalus* genus has a very sensitive lateral-line system combined with highly developed sensory organs placed on the external walls of their head canals (Fig. 23) (Disler & Smirnov, 1977). The advantage of a developed lateral line organ can be illustrated with an experiment by Bergman (1988). She tested the foraging ability of ruffe and perch at different light intensities including very low light intensities and darkness. In trials with low light intensity and darkness ruffe fed more efficient than perch probably because of the extra guidance that their developed lateral line organ provided them with.

Summary:

- There are two general directions of visual adaptations among the adult *Percidae* both clearly reflecting the lifestyle and activity pattern of the species in question:

1) pikeperch, walleye, sauger and ruffe are equipped with a visual apparatus adapted for feeding at low light intensities in turbid environments or in more clear waters, nocturnally and crepusculary.

2) the diurnal, day-active perches depending largely on high visual acuity at moderate or high light intensities foraging in the upper part of the water column.

- There are small differences in the absorptive characteristics of the retina of percids. The differences in visual capacity instead originate from the differences in photoreceptor structure and organisation.

- Both the *Stizostedion* and the *Gymnocephalus* genus have a special structure of their retina, the tapetum lucidum, a reflective layer situated in the pigmented epithelium layer of the retina, that enhances light sensitivity in dim conditions.

- Only rods are involved in the retino-motor response of pikeperches as opposed to perch, where both rods and cones are involved.

- Perch larvae have small, single, short-wave-sensitive cones. These cones, sensitive to UV-light, disappear shortly after metamorphosis. The UV-sensitive cones are believed to be advantageous when foraging close to the surface, where the intensity of UV-light, still is relatively high.

- The visual acuity of young-of-the-year percids is successively enhanced with increasing size following the parallel increase in lens diameter.

- Besides visual cues, the ruffe also rely on a highly developed lateral line organ when feeding in environments with dim conditions.

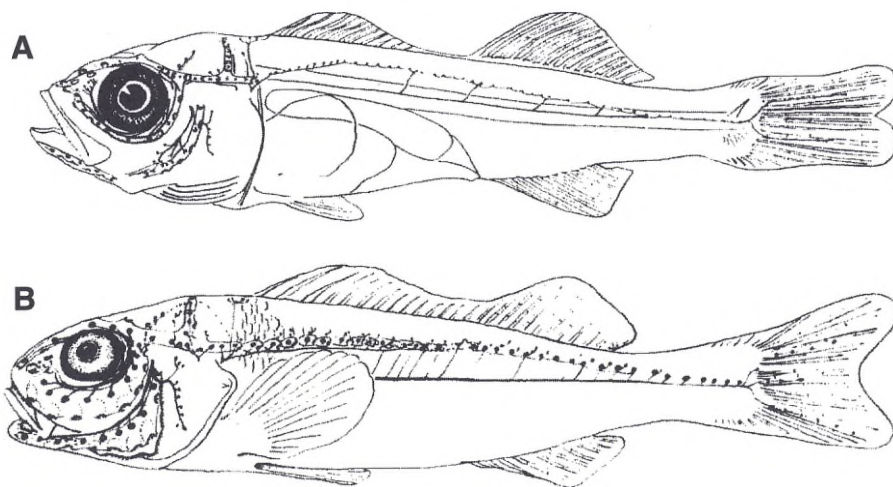


Figure 23. The lateral line system in perch and ruffe fry. A) perch (20 mm) and B) ruffe (22 mm).

Impacts of visual conditions

Varying visual performance of fishes affects the detection of prey, predators and conspecifics. As described earlier, the visual performance of fish is dependent on light intensity, turbidity, visual adaptation of the species in question, size and development of the fish and the size and colour of the prey items. Of the ambient factors varying between different environments, turbidity and latitude are the most relevant to discuss in this context.

General patterns in the impacts of turbidity

Turbidity decreases the distance of a fish's visual field, increases luminosity, affects contrasts, defocuses and, depending on type, selectively changes the composition of wavelengths of light transmitted through the water (Marcott, 1983). All these factors influence the ability to see distant objects, judge pursuit distances and behavioural mechanisms of fish. Turbidity also determines a fish's perception of the size, shape and colour of prey items and potential predators.

A spontaneous conclusion of the effect of increasing turbidity is usually that it always has negative impacts on a fish's ability to detect and acutely portrait objects. This is nevertheless a truth with considerable modifications. As discussed earlier, one important factor determining the visual performance of fish is the contrast between an object and the background. Particulate and dissolved substances in the water determine how the light spectrum of the background light is composed. Depending on the object and the type of turbidity the visual contrast of an object can actually be enhanced by increasing turbidity (Lythgoe, 1979; Ryder, 1977). Also important to mention is that different species of fish have different adaptations to turbid environments. The exact effects of turbidity, are therefore both dependent on the type of turbidity, a factor with infinite variation, and species.

Increased turbidity of aquatic systems is often associated with eutrophica-

tion. The responses of the limnic fish community to eutrophication generally involves an initial shift from a dominance of coregonids to percids and with proceeding eutrophication yet a dominance shift to cyprinids (Hartmann, 1977 and Leach *et al.*, 1977). An example of how different percid fish respond to a shift in eutrophy is the Lake Volkerak-Zoom in the Netherlands. A rapid change to a more eutrophicated state coincided with a marginal decline of the perch population and a significant increase of the ruffe and pikeperch populations taking advantage of the deteriorating visual conditions (Breukers *et al.*, 1997). Similar observations have been made by Leach *et al.* (1977) also implying that perch are less tolerant and ruffe and pikeperch are more tolerant to eutrophication.

Eutrophication has, besides increasing turbidity, a number of other large-scale effects on aquatic communities. The increased productivity of eutrophicated systems may influence size-structured dynamics (Persson, 1991), lead to changes in pH and levels of dissolved oxygen (Leach *et al.*, 1977). It may alter the composition of both planktivore and benthivore prey and lead to deteriorating structural complexity, mainly due to reduced abundance of submerged macrophytes (Persson, 1991; Leach *et al.*, 1977). All these aspects may have profound consequences on the composition of the fish community and may explain the dominance shifts.

The effects of turbidity in eutrophicated systems may thus be hard to isolate from other impacts of eutrophication. Nevertheless, the eventual constraints of turbidity on the visual capacity of different species of fish could provide complementary knowledge on the influence of eutrophication on fish communities.

Dredging, boat-traffic and other mechanical disturbances may cause turbation of sediment particles also increasing the turbidity in affected areas. During the process of dredging, when sedi-

ment is removed from the bottom, there is always some quantity of the sediment lost to the watercolumn. The amount of sediment suspended during a dredging operation is mainly depending on the type of dredging effort (type of technology, operational control etc), the character of the sediment and the morphometry of the given site (La Salle, 1990).

Besides increasing turbidity, and hence changing the visual conditions, dredging can also induce other chemical and physical alterations of the aquatic environment. Suspended sediments may effect the levels of dissolved oxygen. Suspended sediments have also, in some extreme cases, had direct toxic effects on fish in the vicinity of the dredging site. The main cause is usually hypertrofi and necrosis caused by particle aggregation on the fish gills (Simenstad, 1990). Most percids occur in waters with medium or high turbidity, evidently competing well in turbid environments. Both *Stizostedion* spp. and *Gymnocephalus* spp. have visual adaptations that help them overcome the problems of seeing in turbid water. This is, however, not the case with *Perca* spp., that are better suited for living in clear or slightly turbid environments. Being one of the most wide spread freshwater species in the northern hemisphere, *Perca* do also occur in turbid environments however.

Investigations on effects of turbidity on percid fish are relatively few and mainly focused on the early developmental stages. Turbidity related studies on other species of fish can, at least superficially, appear quite contradictory. Some studies show that turbidity reduces feeding rates and growth (Barrett *et al.*, 1993; Hanson & Walton, 1990; Emmett *et al.*, 1990; Nakamura & Matsuike, 1988 & Sigler *et al.*, 1984) while others show no effect at all (Breitburg, 1988, Hayes *et al.*, 1992), and some even show positive effects (Boehlert & Morgan, 1985). Other related studies on the effects of turbidity on fish report increased emigration rates (Sigler *et al.*,

1984; Westerberg, 1996), increased locomotory activity (Barrett *et al.*, 1993), and changes in behaviour (Berg & Northcote, 1985) and in coloration (Seehausen *et al.*, 1997).

The diversity of fish responses to turbidity naturally depends on the simple fact that different species of fish are differently equipped to cope with poor visual conditions. But the levels of turbidity may also differ greatly among different studies and different developmental stages may respond differently. Generally the most negative impacts are reported when predators relying on high visual acuity are exposed to extreme levels of turbidity.

McMahon & Holanov (1995) demonstrated how turbidity combined with varying light intensity may put both temporal and spatial constraints on the foraging of fish. They conducted laboratory feeding trials to determine how light intensity affected foraging success by a visual piscivore, the largemouth bass (*Micropterus salmoides*). The results illustrate how differences in the light environment can have influence on fish foraging. In different water clarities (0.5, 2.0, and 4.0 m Secchi depth), estimated depth limits for feeding during the day ranged between 5.5 and 44 m and from 1.6 to 13 m at night during full moon. At starlight, light intensity rapidly attenuated to a level below the feeding threshold within 0.5 m of the surface at all water clarities. The depth of the water column available for feeding in low clarity water (0.5 m secchi depth) was 67 and 75% less than at moderate and high water clarities.

Influence of daylength

Depending on the type of diel locomotor activity pattern and thus also foraging strategy, the variations in daylength will influence the time per day when light is sufficient for consumption. Daylength varies with date and latitude. Especially for diurnal species, like perch, the daylength restricts the time per day for effi-

cient consumption (Karås & Thoreson, 1992). Nocturnal and crepuscular species, like ruffe and pikeperch, avoid intensive light during the day by migrating to deeper areas (Ryder, 1977). Another seasonally related phenomenon in temperate areas is the occurrence of ice, which decreases light intensity, hence substantially reducing the feeding capacity of diurnal fishes.

Impacts of visual conditions on early developmental stages of percids.

Since the visual acuity of fish generally increases with size, young fish can be more sensitive to poor visual conditions (Ali, 1975; Wahl *et al.*, 1993). Investigations on larval bluegills have showed, that both very intense and very low light intensity can decrease larval growth and survival.

Does this also include larval percids? Hinshaw (1985) tested the influence of prey contrast on survival, growth and feeding of larval yellow perch in different light intensities. Highest survival and growth were derived in treatments that combined high light intensity and high prey contrast. In treatments with high prey contrast and low light intensity, larval survival was significantly higher than in treatments with high light and low contrast. Lowest growth, survival and consumption were recorded from trials with both low light intensity and low contrast. The experiment shows that both light and contrast are important for larval foraging, but that prey contrast is more important for survival and growth of yellow perch larvae than absolute light levels (Fig. 24).

The importance of contrast for feeding of perch larvae was further explored by Loew & Mills (1997) who tested the preference of larval yellow perch for two copepod species with varying coloration lit with different colours. The fish preference for the two prey species was, when tested individually, influenced by the colour of the light, selecting the species

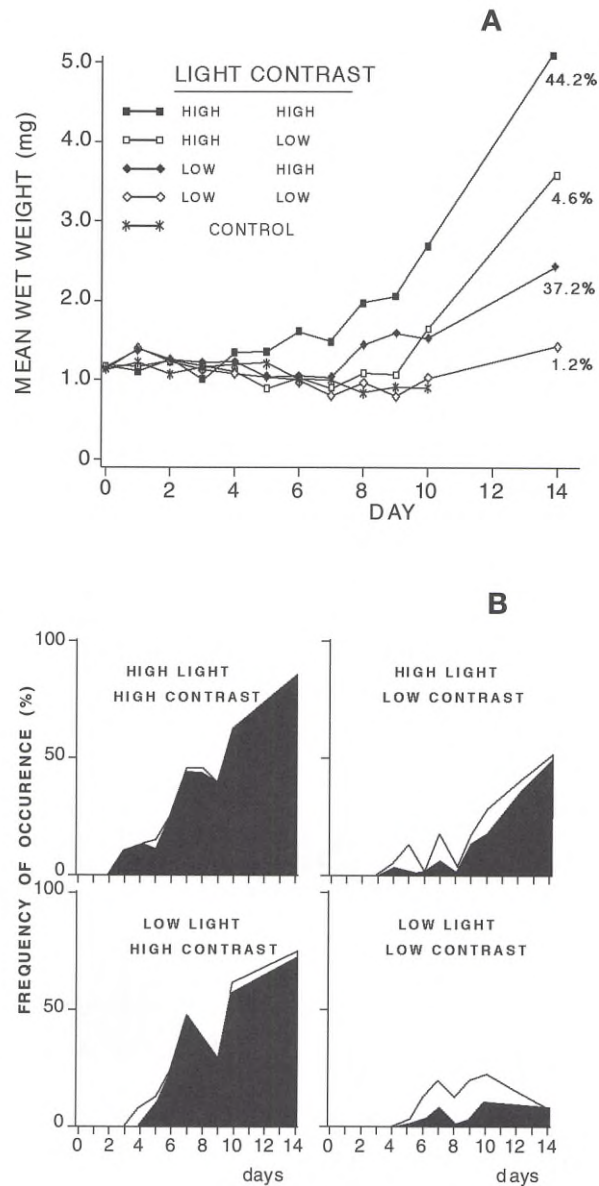


Figure 24. a) Mean wet weights (mg) of larval yellow perch from hatching to 14 days later. Each sample represents a total of 40 fish from two samples of 20 each. Percent survival is listed at day 14. Note that fish in trials with high contrast had a much higher survival than in trials with no contrast. b) Occurrence frequency of food items in the guts of larval yellow perch from the same experiment as in a). The white area represents fish that only ate brine shrimp cysts. The solid area represents fish that ate both cysts and nauplii. From Hinshaw (1985).

with the greatest contrast. However this pattern was not as clear when tested in larger groups. Young yellow perch have also been shown to feed selectively on ephippial, egg bearing, *Daphnia* due to their greater visibility compared to individuals not bearing eggs (Mellors, 1975). Also walleye fingerlings' and larval bluegills' ability to detect prey objects seems to increase when the preys contrast against the background increases (Masterson & Garling, 1986; Miner & Stein, 1993)

Contrary to the findings on perch larvae, experiences from culturing show that pikeperches do not eat at high light intensity and that high mortality will occur under such conditions (Hilge & Steffens, 1996). This is further supported by Bristow *et al.* (1996) who studied the performance of larval walleye (*Stizostedion vitreum*) in clear, coloured and turbid water in

order to investigate the eventual advantages of turbidity (Fig. 25). Increased turbidity had positive effects on the survival of the larvae due to minimised aggregation of larvae along the light reflecting tank walls during the phototactic stage. This was thought to lead to minimised cannibalism, higher consumption and less competition. There is also a possibility that the contrast may have increased in the turbid waters, facilitating prey localisation.

Because of their pelagial lifestyle percid larvae should have some opportunity to distribute themselves vertically in order to compensate for some of the eventual visual limitations caused by extreme turbidity or varying light intensity. Wang (1994) found that perch larvae, with a mean total length of 24.4 mm (± 3.5 mm), when exposed to vertical temperature gradients, selected the specific depths where the temperature requirements for growth were optimal. The larvae always choose the uppermost layer with the preferred temperature. In trials with no vertical temperature gradient, most larvae stayed in the uppermost layer of the aquaria. Presumably, larvae will aggregate close to the surface during the first weeks after hatching, when there is a stage of positive phototropism (Urho, 1995). After the short stage of positive phototaxis, the pikeperch larvae successively develop a negative phototactic behaviour and will probably reside in deeper waters (Ryder, 1977).

Even if the larvae can find depths where the light intensity is sufficient for their foraging, extreme turbidity can still have an impact on their performance. High turbidity can minimise the visual volume of the larvae and affect the contrast between the prey and the background. In the worst case the edges between the prey item and the background will be erased making it harder for the fish to detect the prey.

Perch larvae selectively feed on prey

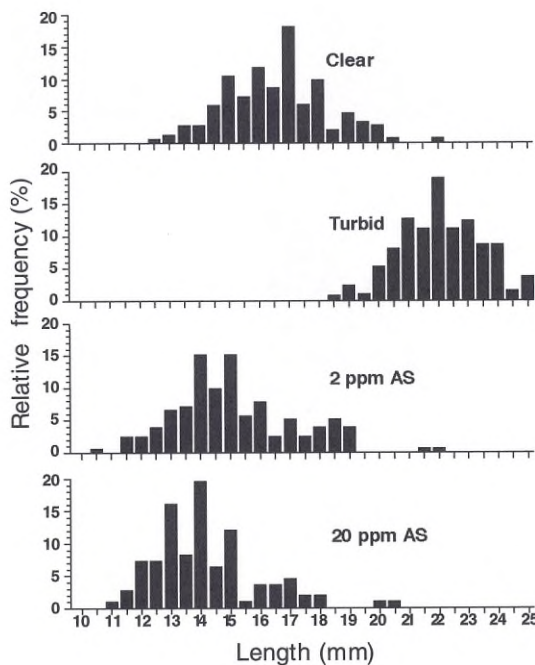


Figure 25. Length frequency distributions of 21-day old walleyes (*Stizostedion vitreum*) in clear water, turbid water and water containing two concentrations of the colouring agent Aquashade (AS). From Bristow *et al.* (1996).

of considerably smaller size than what they are capable of (Fig. 26). This behaviour is in opposition to both mechanistic and optimal foraging models. Both models predict that the largest prey a fish can rapidly handle and digest would be the most preferable. These models have predicted the foraging modes of adult fish quite accurately. Why do young planktivorous fish not select prey in accordance with these models? Mills *et al.* (1984) suggest that the return per handling time might be higher for smaller prey. Young fish pass prey through their digestive tract intact. Small prey can pass faster through the digestive system and their surface to volume ratio is higher than that for larger prey. Consumption of small prey may thus maximise the assimilable energy for growth. Smaller prey items are harder to detect than larger ones (Breck & Gitter, 1983). When visual conditions are poor it will be even harder to detect small prey

items. Hence it is plausible that the negative correlation between size and and prey selection may be reduced when visual conditions are poor (Mills *et al.*, 1986). It may thus be harder for the larvae to forage entirely on their most favorable prey items.

The minimum consumption rate necessary for maintaining standard metabolism increases with temperature (Post, 1990). If poor visual conditions limit the consumption rate of the larvae, increasing temperature will at some point become high enough to increase mortality due to starvation and also increase vulnerability to predators due to poor condition of the larvae.

Extreme turbidity will obviously make it difficult for fish to detect predators but it will also make it harder for them to detect their prey. The situation could be described as a matter of "blinded hiding". Naturally, species adapted to turbid environments, like the ruffe and the pikeperch, will have an advantage both when foraging and avoiding predators.

Summary

- Effects of turbidity on fish performance differs among species and with the level and type of turbidity.
- Eutrophication and draining are two examples of anthropogenically derived disturbances that alter the turbidity of aquatic environments.
- Turbidity, combined with light climate can put both temporal and spatial constraints on fish foraging efficiency.
- Contrast is the single most important factor for visual prey detection of young-of-the-year percids.

- Perch forage more efficiently in high light intensities and less efficiently in low light intensities while pikeperch foraging may be inhibited by intense light.

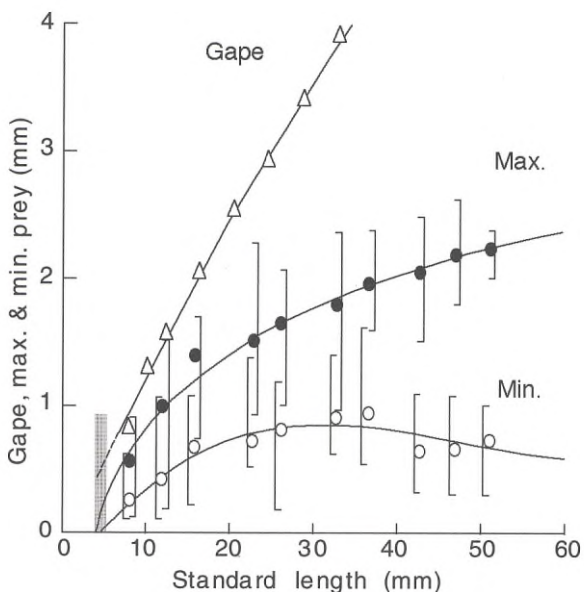


Figure 26. Perch larvae feed on substantially smaller prey than they are capable of. The figure shows the interrelationships between mouth size and the maximum and minimum prey size consumed by different sizes of young-of-the-year yellow perch. From Wahl *et al.*, (1993)

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Reproduction biology of the viviparous blenny (*Zoarces viviparus* L.)

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Innehåll

Abstract	83
Introduction	84
Materials and methods	85
Results	87
Diskussion	92
References	95

Abstract

Reproduction biology was studied in a Kattegat population of the viviparous blenny (*Zoarces viviparus* L.). The females attained maturity at the age of 1+ or 2+ and the males at the age of 1+. Fertilisation of the females took place within 2-3 days. At spawning time the feeding activity of females decreased or stopped until the second half of October when it was resumed and increased up to mid-January when the study was finished. The condition factor was lowest in December.

Size and age of the females did not influence egg size or the duration of the development of eggs and larvae. Length and weight growth rate of larvae was synchronous within and between broods. The mortality of larvae during intra-ovarian development varied between females, and reproduction success was slightly lower in the younger females. High mortality in some broods led to increased

growth rate of surviving larvae. This suggests that relative fecundity may influence larval growth and that growth rate is limited by the maternal supply of energy.

Theoretically, viviparous blenny may maximise reproduction by producing a high number of protoplasmic oocytes, and during later gametogenesis and intra-ovarian offspring development reduce functional fecundity by stepwise mortality. Such a reproductive strategy would ensure a sufficient growth rate of surviving larvae, a maximal number of larvae fully developed to leave ovary, and an optimal parturition time. This hypothesis was verified by observations suggesting that compared to other species of fish the viviparous blenny produces high numbers of abnormal oocytes and larvae with serious malformations, which are dying during pregnancy.

Introduction

The viviparous blenny or eelpout (*Zoarces viviparus* L.) occurs in coastal areas of the North Atlantic Ocean up to the White Sea and in the brackish waters of the Baltic. The species is generally found in littoral areas, where the benthic vegetation provides shelter and feeding habitats. In the Baltic, however, the viviparous blenny also occurs in deeper waters, e.g. in the Gulf of Riga where it is fished commercially by bottom trawls.

During the past decade many data which relate to the biology of this species have been obtained, partly in connection with its use as an indicator of effects of toxic substances (Jacobsson, *et al.*, 1986; Jacobsson & Neuman, 1991; Jacobsson *et al.*, 1993). The female viviparous blenny has one single ovary in which the oocytes are fertilised immediately after ovulation. The embryological development is 2–3 weeks long, and the larvae stay in the ovary after hatching for a period of about 3–4 months before parturition. Although the eggs are comparatively large and yolk is available for the first larval development, the larvae are dependent on a transfer of maternal nutrients for their growth. Some aspects of maternal-embryonic relationships have been studied: the nutritive role of the embryotrophe (Kristofferson *et al.*, 1973; Korsgaard, 1986), vitellogenin, lipid and carbohydrate metabolism during vitellogenesis and pregnancy (Korsgaard & Petersen, 1979; Kristofferson *et al.*, 1974) calcium metabolism in relation to ovarian functions during pregnancy (Korsgaard, 1994) and uptake time – course distribution and elimination of toxic com-

pounds in embryos and ovarian tissues (Joensen & Korsgaard, 1986). There is, however, still little known about many aspects of the reproduction biology, particularly early development and larval growth patterns, malformation frequencies and survival rates of larvae before parturition under natural conditions. Variations in annual recruitment are as well poorly known in this species.

The viviparous blenny occurs as numerous local stocks and races (Schmidt, 1920) with probably different life characteristics, but the reproduction biology of the species is up to now studied only in a few areas in Sweden, Finland, Denmark, Germany and NW Russia (Soin, 1968; Kristofferson & Oikari, 1975; Korsgaard, 1986; Jacobsson *et al.*, 1993, Götting 1976).

As the viviparous blenny is easy to catch, abundant within a large area of distribution, and has a stationary behaviour throughout its entire life cycle, it has been proposed by HELCOM as well as OSPARCOM for monitoring of contaminants and their biological effects. However, the quality assurance process needed before introducing the viviparous blenny in standardised programmes, including a continued research on reproduction biology, is not yet completed. The aim of the present work is to widen the knowledge of its reproduction by analysing maturation, spawning, fecundity, juvenile growth and within-brood competition in a Kattegat population, as well as to document normal mortality patterns before parturition.

Material and methods

All fish were sampled in the Swedish coastal waters of Kattegat (Båtfjorden Bay; salinity 18–22 ppm; Figure 1), between July 8, 1994 and September 11, 1995, using small fyke nets with mesh size 10 mm (Thoresson, 1996). The total number of fish sampled and the different analyses are presented in Table 1.

Length (total length, Tl, mm) and weight (total, Tw, and somatic weight, Sw, 0.1 g) was measured. Otoliths were collected for age determinations. The females were quickly decapitated and the eggs/larvae were immediately dissected out of the ovary, enabling the rate of living/dead juveniles to be estimated. Gonads (total and empty weight in the case of pregnant

females), liver and digestive tract were weighed (0.01 g). Relative gonad size was estimated as the gonadosomatic index, GSI, calculated as gonad weight in percent of somatic body weight. All ovaries from pregnant females were examined using binocular microscope. The eggs/embryos or larvae (after determining if they had died during pregnancy) were counted and random samples of 10–25 were taken for estimating mean lengths and weights. Larvae were blotted on absorbent tissue paper before weighting. Dry weights were measured after freeze-drying during 48 h. Samples of eggs and larvae were fixed in Bouin's solution throughout the period of development.

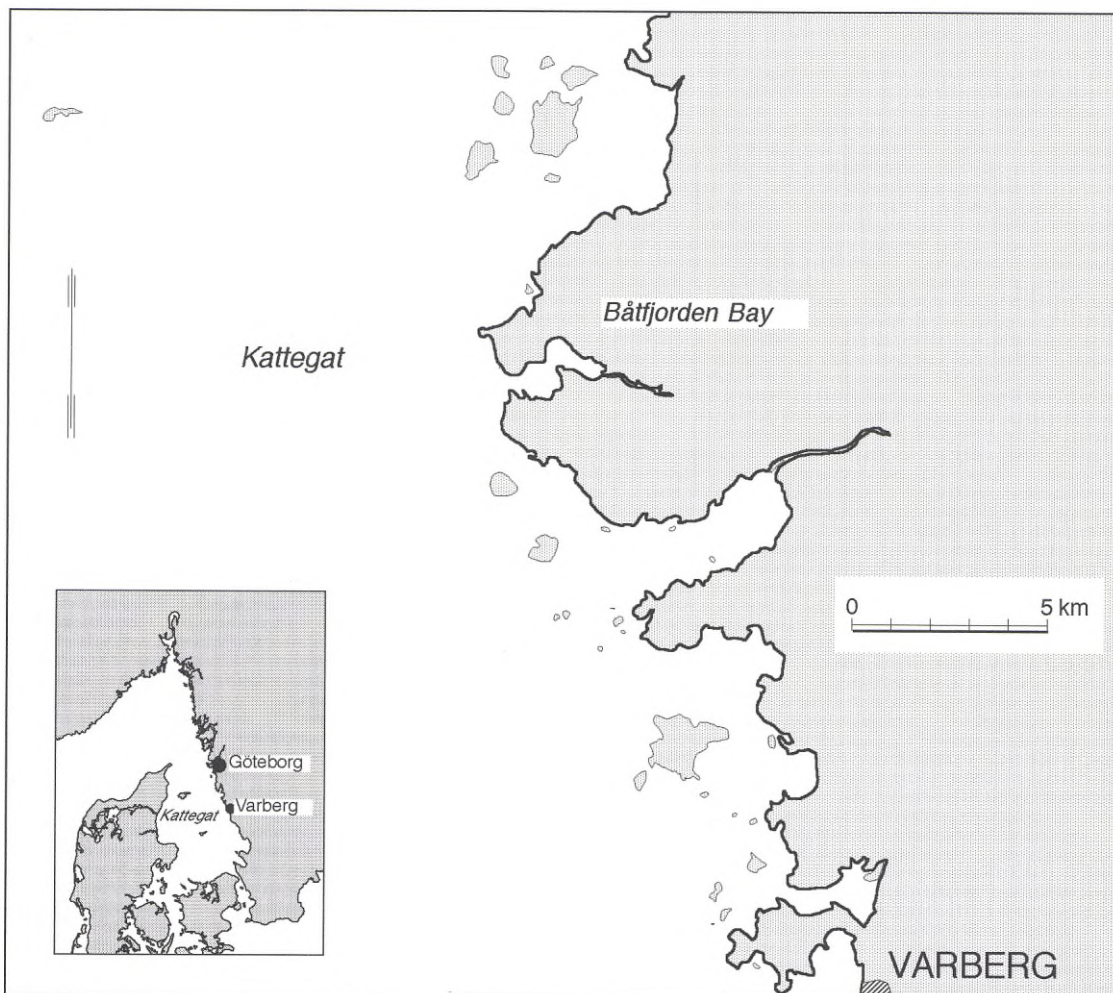


Figure 1. The investigation area.

Table 1 . Catch data.

	Basic analysis	Females Histological study	Egg/larvae dry weight	Males	Juveniles*
1994					
July	17			6	
August	23	11		50	
September	42	21	3	22	
October	63		9	29	
November	19		4	2	
December	34		6	16	
1995					
January	44		2	18	
February	4			3	2
March					10
April	28			11	
August	1			6	
September	36	17		86	

* free-swimming juveniles

After embedding in paraffin wax 8 µm thick sections were produced and stained according to standard histological techniques. Nonfertilized or dead eggs were identified by microscopic analysis. Spawning time was determined by internal examinations of female gonads. Maturity of males was estimated by visual examination and GSI. The limit of maturation was set at GSI=1.

Estimations of mortality were made during all developmental stages. Total mortality (Tm) was defined as:

$$Tm = 100 - (a / b) \cdot 100 ;$$

(a=number of larvae ready to leave ovary; b= number of ovulated oocytes) and was calculated by pooling mortalities during three different periods. Estimations of early egg mortality (embryos dead before epiboly plus ovulated, but not fertilised, eggs) were made during pre-hatching development, because dead eggs vanish soon after the hatching of normal eggs. Estimations of mortality during early post-hatch development were carried out during 2–3 weeks after hatching, as normally developed larvae start to eat dead or retarded larvae during the second half of pregnancy. Accurate estimations of this

mortality component are, however, seldom possible as embryos dying during early development may be disintegrated in the ovarian fluid. However, abnormal embryos (even very extreme ones without head) can stay alive up to parturition and the most likely cause of their disappearance from the ovary is that they are eaten by bigger larvae. Mortality during the second half of gestation was estimated in November–December by counting late-dead larvae.

The growth of larvae was estimated individually from length and weight data. The weight increase of total broods was described by the use of GSI and an embryosomatic index (ESI), i.e. the relationship between the total weight of all young (except ovarian tissue and fluid) and the somatic weight of the female.

The contents of the digestive tract of the analysed females were investigated. Occurrence of food was estimated according to the following classification: 0 – empty; 1 –food fills less than 10% of the digestive tract; 2 –food fills 10–50% of the digestive tract; 3 –food fills more than half of the digestive tract.

Results

Maturation

Most females attained sexual maturity at the age of 1+, during their second summer. Only 30% of analysed 1+ females (n=51) were immature, and all 2+ females (n=31) were mature. The total length of the 1+ females varied between 185 and 250 mm at first fertilisation, with an average of about 220 mm. The smallest mature female was 185 mm long and weighed 27.4 g (Sw 22.9 g). She was caught on October 24 and her ovary contained 16 normally developed larvae. The biggest juvenile female was also caught on October 24 (Tl 222 mm, Tw 37.0 g, Sw 33.9 g, age 1+). Males attained sexual maturity at the age of 1+ and had at their first spawning total lengths between 149 mm (Tw 13.7 g) and 231 mm (Tw 39.1 g) with the average of 205 mm.

Spawning

In 1994, 11 mature females were analysed on August 31. According to histological examinations only one of those had ovulated eggs in the ovary. Two to three females were analysed daily from September 9 up to the end of October. The embryological development among females was found to be synchronous (\pm one day). Estimated from embryological stages and the speed of embryo development, the fertilisation of all analysed females took place between September 3 and 6.

In 1995, daily samplings on the same spawning ground were made from August 26 until September 10 at water depths between 0.5 and 2.0 m. Catch data are presented in Table I and Fig 2. According to the histological study, all females with ovulated oocytes were also fertilised (with the exception of one fish which had dead oocytes in the ovary). Samplings were also made near the opening of the bay at depths of 4–6 m (500 m from the spawning ground) during the same days. Fish were more abundant than on the spawning grounds until September 5, and the shares of females and males were almost

equal in the catches. All females had unovulated oocytes in their gonads. After September 6 no females were found in this deeper place and the number of males decreased rapidly. The observation indicated that spawning of the viviparous blenny in Båtfjorden Bay in 1995 took place at or close to September 5–6, i.e. nearly at the same time as the previous year. Water temperature at spawning was about 18°C in 1994 and about 16°C in 1995.

Eggsize and hatching

The oocyte diameters some days before ovulation varied between 2.2 and 3.5 mm with an average of 2.9 mm and an average wet weight of about 15 mg. The average diameter of the eggs after ovulation and fertilisation (cleavage stage according to histological examination) was 3.1 mm and the average wet weight 21.3 mg.

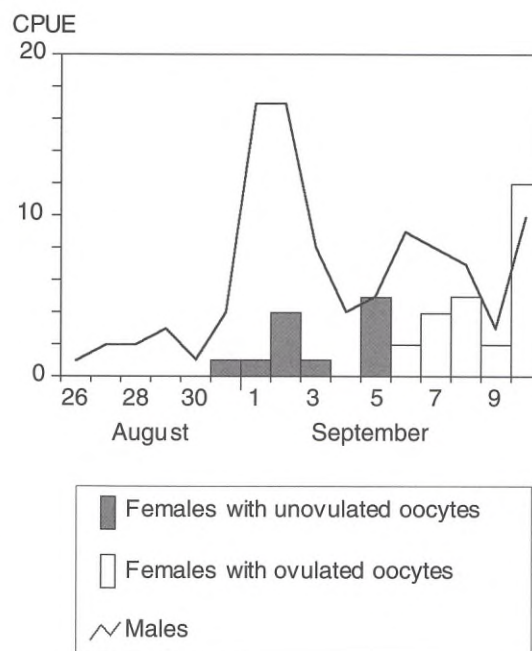


Figure 2. Catch per unit of effort (CPUE) of viviparous blenny during the 1995 spawning season (on spawning grounds).

At the time of fertilisation the gonads in most cases contained a group of smaller but still clearly trophoplasmic oocytes (diameter circa 25% lower than normal) besides the normally developed oocytes. The share of small oocytes varied, but in some cases it reached up to 25% of the total number of eggs. Some of these eggs seemed to develop and hatch.

Egg size of the viviparous blenny was not significantly correlated to female size. However, the smallest oocytes were produced by small females at their first spawning and the youngest females also had the highest shares of abnormally small oocytes. Most of those were atretic at the time of ovulation, but some were fertilised, however usually containing abnormal embryos.

Immediately before hatching the average egg diameter had increased up to 4.8 mm. On three occasions, September 18, 22 and 24, females were analysed on the same day as the hatching of larvae took place (ovary contained both hatched and non-hatched larvae). No hatched larvae were found before September 18 (17 females analysed September 9–17) and no non-hatched larvae after September 24 (23 females analysed during the next 7 days and totally 36 during 14 days, up to October 8). Hatching thus took place during a period of about one week, and hatching synchronicity within the population and within single broods was high. Mean weight of the larvae on the day of hatching was between 30.9 mg (TL 14.7 mm) and 38.3 mg (TL 17.2 mm). Variations between larvae within broods were small, generally ± 1 mg in weight and ± 0.5 mm in length.

Fecundity

Total fecundity was studied during August–September 1995 and on a smaller material collected in 1994 (Fig. 3). Differences between years were rather small. The total number of larvae hatched (abnormal young included; Fig. 4, 5) varied

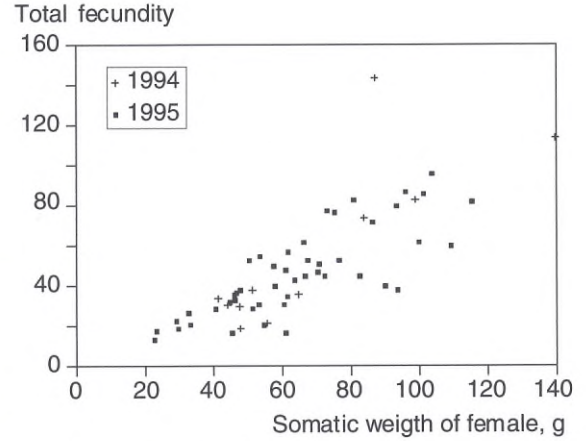


Figure 3. Total fecundity in relation to the somatic weight of viviparous blenny during the 1994 and 1995 spawning seasons.

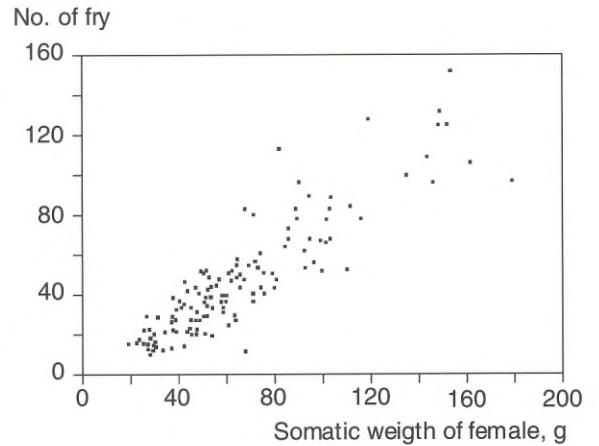


Figure 4. Number of larvae in relation to the somatic weight of females.

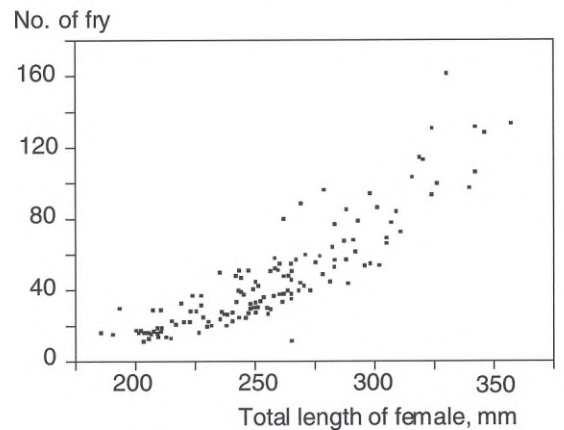


Figure 5. Number of larvae in relation to the total length of females.

from 6 (TL 203 mm, Sw 28.3 g, age 1+) to 161 (TL 330 mm, Sw 153.0 g, age 5+). The somatic weight of the females explained 63% and 80%, respectively, of the total fecundity and the number of post-hatching larvae. The correlation between numbers of larvae hatched and female weight and length was also strong ($r=0.89$ and $r=0.88$, respectively).

Gonadosomatic and embryosomal indici

The development of male gonads was described by changes in GSI from July 1994 to April 1995 (Fig. 6). In the beginning of July male GSI varied between 1.0–3.5. During July and August GSI values grew slowly, reaching a peak (1.5–3.6) at the end of August, when spawning took place. At the end of September male GSI values dropped to 0.2–0.4. Two males captured in December and one in January were found to have abnormally big testes, GSI 2.5, 4.5 and 3.0, respectively, which represent pre-spawning values.

The GSI of adult females increased from September throughout the period of pregnancy and fell down to initial July values in December–January (Fig. 7). The embryosomal index (ESI) followed a similar pattern.

Growth of larvae and parturition

The length growth of larvae (Fig. 8) was documented from the second week of pregnancy (pre-hatching larvae) up to parturition. Parturition began in December and continued to the end of the sampling period, i.e. end of January (Fig. 9). Variations between normally developing larvae appeared to be quite small. A few abnormal and much smaller larvae were seen in almost all broods, in most cases not more than 1–5% of the total number of larvae.

A power function ($y=1.8 \cdot x^{0.46}$) provided the best fit to the length increase curve. During the second half of pregnancy, growth rate decreased and variations in mean lengths between broods increased.

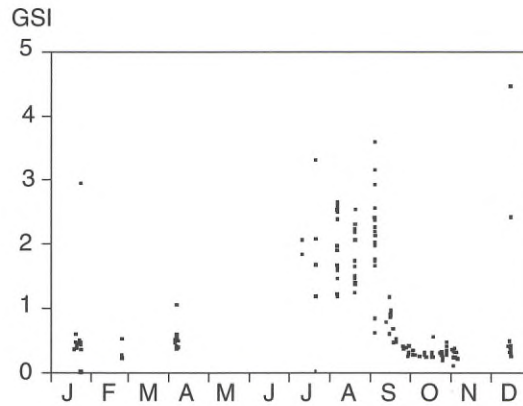


Figure 6. Gonadosomatic index (GSI) of males.

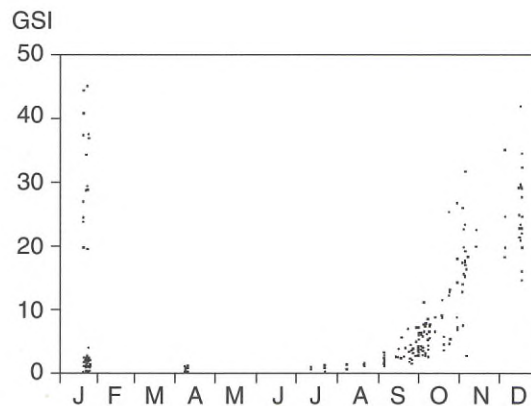


Figure 7. Gonadosomatic index (GSI) of females.

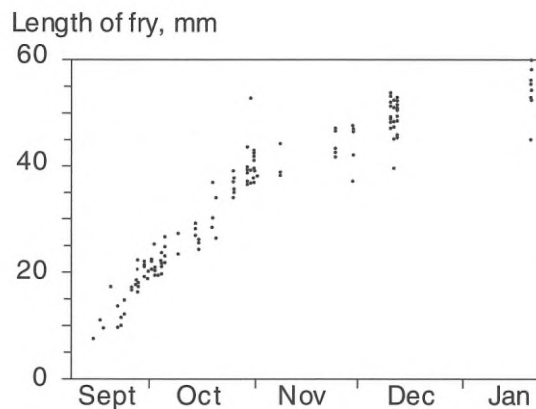


Figure 8. Length growth of larvae.

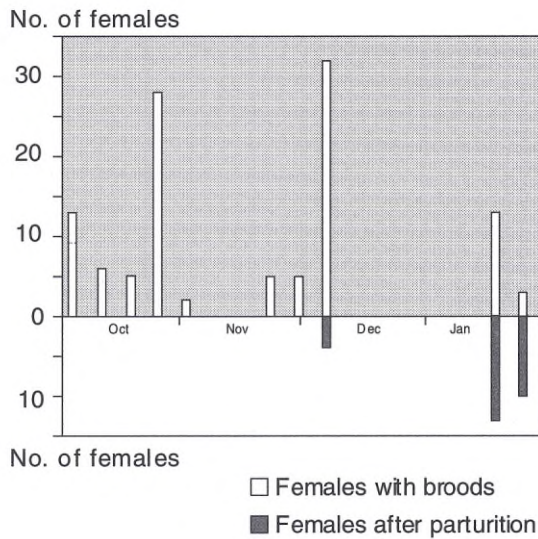


Figure 9. Parturition time indicated by the number of females with or without broods at samplings in Oct–Jan 1994–1995.

Time explained 93% of the variations between broods in average larval length (linear equation) during the first 50 days. During the next (last) 80 days this value was only 44%. For the whole pregnancy period time explained ca 85% of the variations. The average length growth per day was 0.66 mm during the first three months of pregnancy, September–November, when length growth was nearly linear.

In some cases when many of the larvae within broods had died, the growth of the surviving offspring was increased. For example, a 265 mm long female (sampled on October 29), with only 11 young in the ovary (the normal number for such a female is about 50) had unusually big larvae. Normal larvae in the sample had a total length of 34–45 mm (Tw 0.11–0.31 g), but the larvae of this specimen had already attained a length of 51–54 mm (Tw 0.46–0.54 g), which corresponds to normal values at parturition. To estimate the effect of relative fecundity on length growth of larvae, periods during pregnancy were selected when a comparatively high number of samplings were made

during a short time interval. The average length of the larvae (length corrections assuming a daily growth of 0.66 mm were made to minimise the effect of differences in sampling time) was plotted against the number of larvae per unit female somatic weight (i.e. relative fecundity). On one occasion (December 9–11, 29 females) this variable explained only 8% of the differences between larvae. On another occasion (28–30 December, 18 females) the degree of explanation was 53%.

Weight growth of the larvae followed the same pattern as length growth. During the first part of pregnancy differences between broods were small, but close to the end of the pregnancy period growth rate decreased and variations between broods grew. However, differences between individual normal juveniles inside broods were quite small up to parturition.

The weight/length relationship, i.e. the condition factor (Cf), showed some differences between broods (but not inside broods) up to the end of pregnancy. In spite of those small variations in Cf, the average length of larvae explained 98% of the weight differences between broods during the whole post-hatch period.

Based on a study of 24 females the average dry weights of the young (n=10 per female) and the share of dry weight was calculated. Percentage of dry matter increased from hatching (approximately 13%) up to the parturition stage (approximately 19%). In some cases variations in percentage of dry matter between larvae with equal wet weights were quite big and therefore wet weight explained only 67% of the variations in water content.

Mortality before parturition

Egg mortality in 1994 (embryos dead before epiboly plus ovulated, but not fertilised eggs) varied between 0 and 65%. The average value was 14% (14 females analysed). Smaller (younger) females showed a somewhat higher egg mortality

rate, but variations in length explained only 30–36% of the variations in mortality.

Estimations of mortality during early post-hatch development showed that the percentage of surviving larvae varied from 81 to 100, 95% as an average (35 females sampled). Survival rate was higher in the larger broods. Nevertheless, variations in total number of larvae explained only about 30% of the variations in larval mortality during this period and variations in somatic weight of female explained even less. Mortality during the second half of pregnancy was very low, 0–1%.

Total juvenile mortality before parturition varied between 0% and 72% during the 1994–1995 pregnancy period, with an average value of 22%. On some occasions (3 out of 242 females analysed in 1994) reproduction totally failed by some unknown reason. Those three females had developed gonads but no larvae or eggs and they were excluded from the calculations of mortality.

In autumn 1995, the reproduction of the viviparous blenny in Båtfjorden Bay was seriously disturbed. Spawning took place, but in most females studied (15 from 19 sampled fish after September 7) all eggs had died after cleavage. One female carried eggs which had died after epiboly and only three had normally developing embryos (histological study).

Female feeding and condition factor of adults

During July–August most females contained some food in the digestive tract. At spawning time the feeding activity of the females decreased and during an approximately one month long period from mid-September to mid-October almost all females had empty digestive tracts. From the second half of October feeding activity was resumed and remained increasing up to mid-January (Fig. 10).

Cf of females (Fig. 11) and males showed different seasonal patterns. Males

had lowest Cf values in October, approximately one month after spawning, after which Cf started to increase again. Cf of females was highest before fertilisation and decreased up to mid-December.

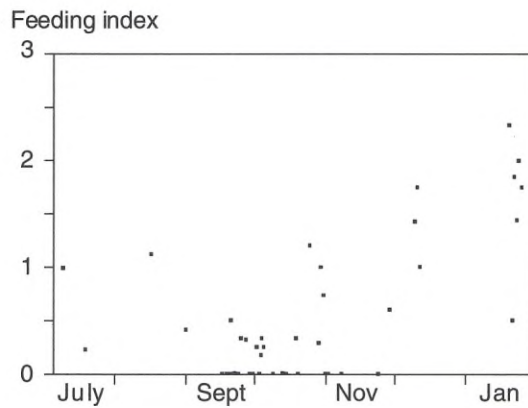


Figure 10. Feeding pattern in females.

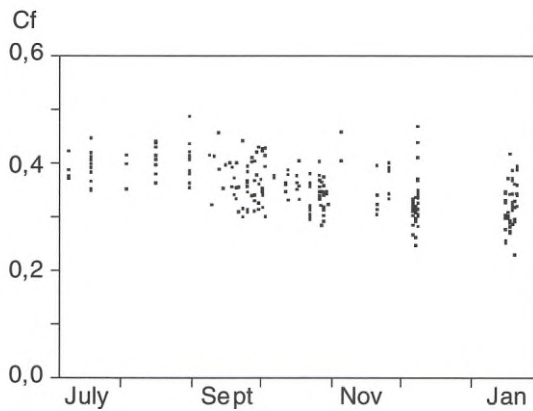


Figure 11. Condition factor (Cf) in females.

Discussion

According to Rass (1949) the viviparous blenny reaches sexual maturity in the second year of life, at a length of 16–17 cm (locality unknown). These data seem to be the only source in literature up to now. Most of the females analysed in the present study were also mature in the second year of life, but they achieved maturity at a bigger size. All 16–17 cm long females sampled were still juveniles. Males, however, matured at a size smaller than 16 cm and an only 15.7 cm long male had the highest GSI value documented during the study.

Spawning in Båtfjorden Bay took place in the beginning of September. A few females were probably fertilised already during the last days of August. Males reached the spawning grounds some days before the females. Synchronicity of spawning in the population was high and the fertilisation took place within 2–3 days. Earlier studies from the Baltic and the North Sea report almost the same spawning time as described in this study. Kristofferson *et al.* (1973) observed, that spawning of the viviparous blenny at Tvärminne, Gulf of Finland, took place in August and September. However, later data from the same area (Kristofferson & Pekkarinen, 1975) suggest (according to internal examination of male gonads) spawning time to be in July–August. Götting (1976) reports that in Helgoland (North Sea) oocytes were ready for fertilisation in July–August, but embryos did not appear in the ovaries of pregnant females until September. In Little Belt, Denmark, spawning takes place in the first decade of September (Korsgaard & Petersen, 1979; Korsgaard, 1986). According to Soin (1968), White Sea blennies mate much earlier, during spring and summer (first parturition already in July–August).

Bretschneider and de Wit (1947), who studied a blenny population in the North Sea near Den Helder, North Holland, found pregnant females at two seasons –

the highest frequency of pregnancy occurred during autumn, but some females carried young from April to July. Later studies from the Baltic Sea (Kristofferson & Pekkarinen, 1975) documented only autumn pregnancies. Neither Korsgaard (1986), who collected females from Little Belt, Danmark, nor Jacobsson *et al.* (1993) sampling viviparous blennies from Skagerrak and the Baltic, found any evidence for two spawnings. Schmidt's report (1920) concerning population genetics in southwestern Kattegat contains a statement that in June gametes are not yet ripe, which indicates that only autumn pregnancy took place. During the present study only 4 specimens showed signs supporting the possibility that also some females in Kattegat can carry young during the spring–summer season. Two males caught in December and one in January were found to have strikingly high GSI values, corresponding to normal pre-spawning values. One female caught in mid-September had an empty gonad filled with remnants from follicular sacks, which is characteristic of the post-parturition period (normally December–February). In spite of those observations two separate pregnancy seasons does not likely occur in the Kattegat.

Hatching of the eggs inside a brood took place almost synchronously, which can be explained by the "chain-reaction" hypothesis. The hatching enzymes released by the first hatched larvae accelerate or even stimulate hatching of others. The idea that hatching enzymes released by one larva may stimulate hatching of others was presented already by Moriwaki (1910) and later confirmed by many authors (Yamagami, 1988; etc). In the viviparous blenny this hypothesis was supported by two observations. Firstly, the hatching of abnormal larvae took place during the same, quite short period of total hatching and even the dead embryos and unfertilised eggs "hatched" or "vanished" from the ovary at the same

time. Secondly, on some extreme occasions when most of the eggs were malformed and only few normal young hatched (this indicates that the concentration of hatching enzymes was too low in the ovary), the rest of the eggs had stayed intact during all the pregnancy period.

The increased percentage of dry matter in growing larvae, recorded during the present study, agrees with data reported by Korsgaard (1986). However, in this area (Little Belt, Denmark), eggs during the cleavage stage were heavier than in Båtfjorden Bay, 27 mg as an average, and the mean weight of newly hatched larvae (45 mg) was also remarkably (circa 10 mg) higher.

Korsgaard and Andersen (1985) described larval weight growth from November to January as nearly linear. According to the present study a power function provided the best fit to both weight and length growth of larvae. In December–January growth seemed to decrease or even stop and variations between broods increased. It is not clear, whether the juveniles had achieved optimal parturition size already some weeks before the real parturition took place or that their growth had decreased in certain broods by lack of food. Neither could it be excluded that after parturition started only those juveniles could be sampled, which belonged to comparatively slow-growing broods.

Fecundity of the viviparous blenny is, as a rule, well correlated with the body size of females (Götting, 1976; Jacobsson *et al.*, 1993). However, fecundity is generally measured during the post-hatching development, when it is too late to detect unfertilised oocytes and eggs dying before the stage of epiboly. Maximum number of larvae in broods documented during the present study appeared to be remarkably smaller than the number reported by Kristofferson *et al.* (1973), who mentioned that in females from the Gulf of Finland the number of larvae was up to 296.

However, those females were very large, maximum TL was 420 mm, and the relative fecundities were not reported.

Differences in ESI values between age groups of females varied more than the differences in average larval length, which were not correlated to size or age of female. Attempts to describe the growth/time relationship of young by the use of larval length and weight is not always satisfying, because growth of the individual larva is closely related to the maternal supply of food (Korsgaard & Petersen, 1979; Korsgaard & Østergaard-Andersen, 1985; Korsgaard, 1986). Some estimates made during this study showed that the number of larvae per unit of female somatic weight during one series of analyses explained more than 50% of the variations between average lengths of broods. In some extreme cases, with only few surviving larvae, the larval growth was extraordinarily rapid. However, ESI values (and also GSI) of such specimens were more close to average.

The normal survival of embryos and larvae between fertilisation and parturition as well as the fertilisation success of the viviparous blenny is not well known. It is generally considered that in most teleost species the mortality is highest during so-called critical periods of early embryological development, and that the fishes are very sensitive to exposures to xenobiotics during these early stages before organogenesis (Wilson, 1973). In viviparous species, however, there is a considerable risk of mortality due to female insufficiencies also during later parts of the pregnancy. In normal environmental conditions, very low mortality of the larvae during late pregnancy has been recorded by Jacobsson *et al.* (1986, 1993), observations supported by the present study. However, when pregnant females were exposed in the laboratory or in the field to effluents from bleached pulp mills as well as chemical industries (Jacobsson *et al.*, 1986; Jacobsson & Neuman 1991;

Vetemaa *et al.*, 1997), increased mortality of larvae in late stages of development were observed as well as reduced larval growth rates.

Why reproduction success of viviparous blenny in Båtfjorden Bay during the autumn 1995 was very low is not clear. However, strong easterly winds caused a temperature decrease from 16.5 °C, which is normal for the season, to 11.5 °C 3–4 days before ovulation. The fact that some females caught in a small archipelago 8 km from the Båtfjorden Bay (Vetemaa, unpublished), where temperature had been more stable, showed better reproduction success (5 of 6 sampled females had normally developing eggs), seems to support the hypothesis that reproduction was disturbed by unfavourable temperature conditions. The temperature in the bay was much more stable in 1994.

There are two observations suggesting the possibility that females have systems to regulate fecundity, i.e. significantly reduce the number of larvae ready to leave the ovary in relation to the number of oocytes which started to grow. Firstly, female viviparous blennies have remarkably higher shares of abnormal oocytes than most other teleost species. This is probably also true when comparing the shares of larvae with serious malformations. It is, however, difficult to estimate malformation rates in non-viviparous species, as the mortality of malformed larvae probably is very high. Secondly, the size of the female was better correlated with the number of post-hatching larvae in the ovary than with the total fecundity. According to the present study the degree of explanation was 80 and 63%, respectively. Earlier estimations (Jacobsson *et al.*, 1993), showed that the somatic weight of females explained 50–75% of the variation in the number of larvae.

Although there are some studies reported on the feeding of viviparous blenny (Larsen, 1936; Aneer, 1975; Urtans, 1992), the annual feeding rhythm of females,

especially during the pregnancy, when the energetic demands are high, is still almost totally unknown. The present study showed that during September–December Cf of females had a tendency to decrease, which indicates that during this period energy input through feeding did not cover the expenditures for larval growth, which may be a cause for competition between larvae. Cf-values in January were higher again, which may be an effect of higher feeding activity and/or decreased juvenile growth. The former hypothesis was supported by the digestive tract analyses.

During the past two decades some data about maternal-juvenile relationships have been published (Kristofferson *et al.*, 1973; Korsgaard & Petersen, 1979; Korsgaard, 1986). However, these authors did not discuss the possibility of food competition between larvae. According to the present study, competition inside broods may have significant effects during October–November, when the growth rate of the larvae is maximal and the females probably suffer from malnutrition. Female muscle fat concentrations are also lowest in October–November (Jacobsson *et al.*, 1993). During this period the number of young per unit of somatic weight of female thus may influence the growth rate of offspring. At the same time the observation that growth rates of all larvae in single broods were almost equal suggests that female feeding and malnutrition does not lead to differences between individual offspring but to limitation of growth of the whole brood.

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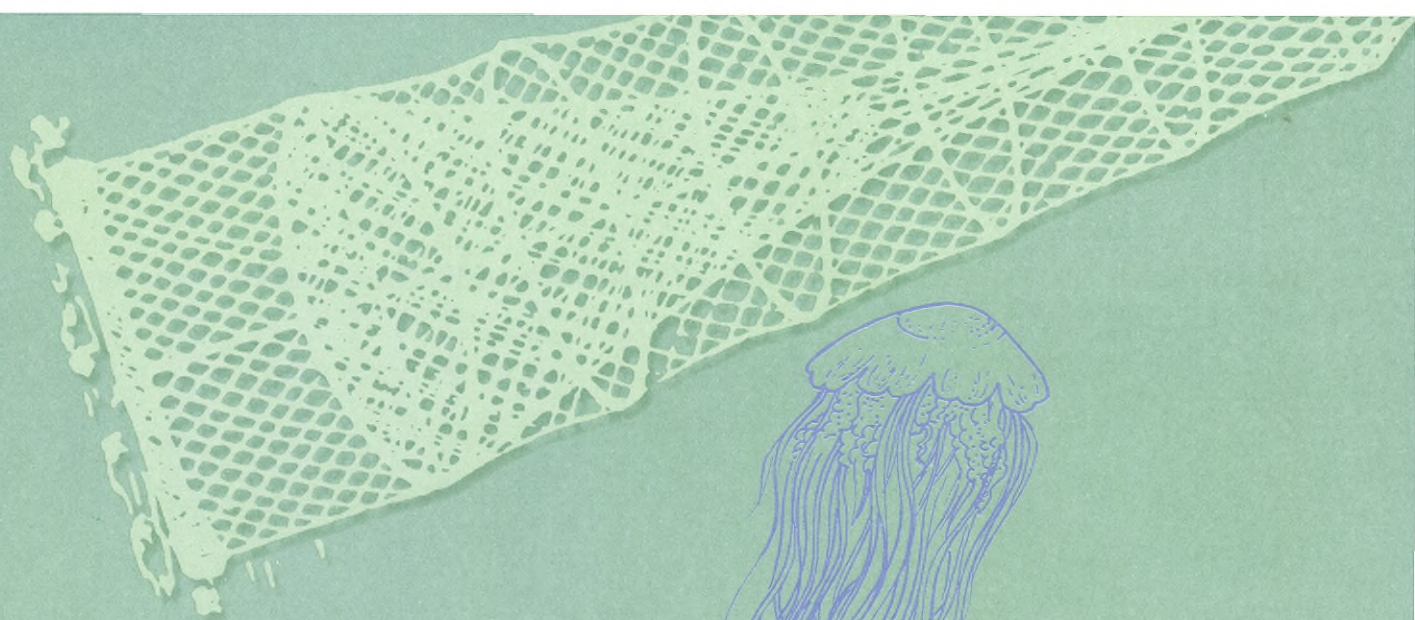
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FISKERIVERKET, som är den centrala statliga myndigheten för fiske, vattenbruk och fiskevård i Sverige, skall verka för en ansvarsfull hushållning med fisktillgångarna så att de långsiktigt kan utnyttjas i ett uthålligt fiske av olika slag.

Verket har också ett miljövårdsansvar och skall verka för en biologisk mångfald och för ett rikt och varierat fiskbestånd. I uppdraget att främja forskning och bedriva utvecklingsverksamhet på fiskets område organiserar Fiskeriverket *Havsfiskelaboratoriet* i Lysekil med *Östersjölaboratoriet* i Karlskrona, *Sötvattenslaboratoriet* i Drottningholm, *Kustlaboratoriet* i Öregrund, två *Fiskeriförsöksstationer* (Älvkarleby och Kälarne) och två *Utredningskontor* (Luleå/Härnösand och Jönköping).



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