

The effects of salinity and temperature on the development and survival of fish parasites

H. MÖLLER

Fischereibiologische Abteilung, Institut für Meereskunde an der Universität Kiel, 23 Kiel, Düsternbrooker Weg 20, W. Germany

(Accepted 15 June 1977)

In brackish water the variety of marine and freshwater parasite species is considerably reduced. The distribution in brackish water of most marine endoparasites is restricted by the salinity tolerance of their hosts, most of the parasite species are more tolerant than their hosts. The influence of salinity and temperature on nine species has been examined; first stage larvae of *Contracaecum aduncum* develop in 0–32‰ salinity; *Cryptocotyle lingua* proved to be infective at salinities down to 4‰. The greatest resistance was found in *Anisakis* larvae from herring *Clupea harengus*, which survived for more than half a year. Parasites in the fish intestines appear to be unaffected by changing water salinities, as the osmolarity in the intestines stays nearly constant. Marine ectoparasites (*Acanthochoondria depressa*, *Lepeophtheirus pectoralis*) survive about three times longer than freshwater species (*Piscicola geometra*, *Argulus foliaceus*) when salinity is 16‰. High temperature increases the effects of adverse salinities on parasites. There is evidence that none of these ectoparasitic species can develop within the range of 7–20‰ salinity.

I. INTRODUCTION

It is known that the number of species of parasites of brackish water fishes is generally lower than that of marine fishes. For example, *Platichthys flesus* from Kiel Bight (ca. 16‰ salinity) carries 13 parasite species (Möller, 1974), and fish from the southern Baltic (7‰ salinity) carry 16 species (Janiszewska, 1938), whereas those from the northern North Sea carry some 20 species (Mackenzie & Gibson, 1970; Markowski, 1938; Möller, 1975*b*; Polyanski, 1955).

There are two reasons for a reduction in the fish parasite species in brackish water; the absence of many marine and freshwater intermediate hosts and ectoparasites that enter brackish water on euryhaline fish are in direct contact with the variations in salinity and most egg stages of endoparasites are also affected by salinity. In addition in some endoparasitic species (*Podocotyle atomon*, *Bothriocephalus scorpii*) the first stage larvae hatch in the open water, and in digeneans the cercaria represents another free living stage.

Experiments on the resistance of fish parasites to salinity and temperature have been few: Bauer (1959) summarized knowledge on the influence of temperature on freshwater fish parasites; Schäperclaus (1954) determined tolerance values for different bacteria causing red disease of the eel *Anguilla anguilla*; and Meyer (1970) examined the seasonal appearance of viral, bacterial and protozoal diseases in connection with changing water temperature. Moreover, previous investigations of the salinity demands of fish helminths either considered only a few temperature changes (Markowski, 1935; Michajlow, 1938; Stunkard & Shaw, 1931) or when examining temperature tolerance, salinity was kept constant (Bauer, 1959; Ronald, 1960).

In this study, the synergistic effect of temperature and salinity on fish parasites was examined to assess the use of fish parasites as natural tags and the extent to which a natural reduction of the parasite fauna in brackish waters might be advantageous for aquaculture.

II. MATERIALS AND METHODS

All endoparasites were taken from fish from Kiel Fjord (Western Baltic); marine ectoparasites were collected near the Marine Biological Station Kristineberg (West Sweden). Freshwater ectoparasites were from a pond near Kiel.

Most experiments were carried out in air-conditioned laboratories with constant temperatures of 0, 5, 10, 15, 20, and 25° C. Maximal temperature deviation was less than 0.5° C. A diurnal rhythm of 16 : 8 h was simulated.

Parasites were kept in covered plastic or glass vessels in water which was originally taken from the Baltic (*ca.* 16‰) and cleaned by deep-freezing and filtering. The salinities were raised by adding artificial sea salt and lowered by adding distilled water. Water of 0‰ means tap water with a pH of 7.6 and hardness as CaCO₃ of 250–255 mg l⁻¹. Water was changed every three days when temperatures were higher than 5° C, otherwise every seven days. Aeration twice a day proved to be sufficient in all cases where parasites were kept without their host fish. No antibiotics were added.

In the experimental series where mortalities from 0–100% could be observed, the $L_{T_{50}}$ has been estimated in accordance to a formula of Spearman-Kaerber (Cavalli-Sforza, 1972):

$$\log L_{T_{50}} = \frac{P_{i+1} - P_i}{100} \cdot \frac{\log x_{i+1} + \log x_i}{2}$$

x_i is the time the parasites spent in the solution, P_i is the respective mortality rate in percentages.

Unless otherwise stated, for each salinity temperature combination 100 animals were used. All endoparasites were directly transferred from their host to the experimental salinity solution. In the case of ectoparasites, at the beginning of the experiment, the water was diluted or concentrated every 4 h by 2‰ towards the final experimental value. Adaptation to the experimental temperatures was 1–2° C h⁻¹.

Additional information on the test procedures is given, where appropriate, in the following accounts of the different experiments. Table I gives information on the life cycles of the endoparasites examined.

III. RESULTS

FREE LIVING STAGES OF ENDOPARASITES

Cryptocotyle lingua (eggs)

Mature trematodes were collected from the intestine of a common gull (*Larus canus*) and kept in sea water. After one day eggs had been released. Salinities from 8–32‰ provoked development of most miracidia within the egg shells. At 4‰ 50% of the eggs developed; no development took place when temperature was 0° C (Fig. 1). At 5° C the development was retarded; after two months miracidia were visible in 60% of the eggs.

Cryptocotyle lingua (cercariae)

Cercariae were obtained from periwinkles (*Littorina littorea*) by slicing the livers and collecting the parasites from the surface of the aquarium. Shedding of the tail was the first visible reaction to a reduced salinity; later the rest of the body swelled

TABLE I. Life cycles of some endoparasites

Trematoda digenea	Egg	Miracidium	Cercaria	Metacercaria	Adult
<i>Cryptocotyle lingua</i>	water	hatches in intestine of <i>Littorina</i> spp.	leaves <i>Littorina</i> penetrates fish skin	encysted in fish skin	in intestine of <i>Larus</i> spp.
<i>Podocotyle atomon</i>	water	penetrates <i>Littorina</i> spp. actively	leaves <i>Littorina</i> penetrates amphipoda	encysted in haemocoel of amphipoda	in intestine of littoral fish
Cestoda	Egg	Coracidium	Proceroid	Plerocercoid	Adult
<i>Bothriocephalus scorpii</i>	water	penetrates plankton copepoda actively	in body cavity of plankton copepoda	in stomach of <i>Gobius minutus</i>	in intestine of <i>Cottus</i> spp., <i>Rhombus</i> spp.
Nematoda	Egg	1 + 2 Larvae	3 + 4 Larvae		Adult
<i>Anisakis</i> spp.	water	in body cavity of euphausiacea	in body cavity of fish (mainly clupeoids)	in intestine of marine mammals	
<i>Contracaecum aduncum</i>	water	in body cavity of benthic and planktonic animals	in body cavity of fish, benthic and planktonic animals		in intestine of most fish species
Acanthocephala	Egg	Acanthella			Adult
<i>Echinorhynchus gadi</i>	water	in body cavity of amphipoda			in intestine of littoral fish

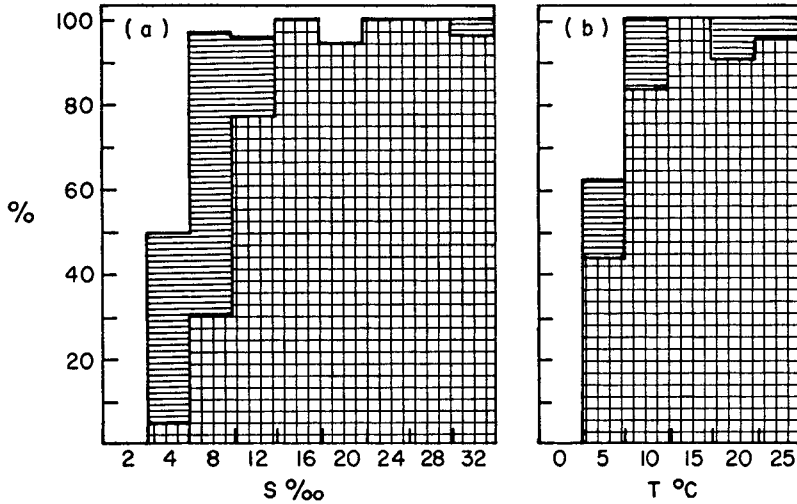


FIG. 1. The percentage of developed miracidia after 45 days culture; horizontal lines: *Cryptocotyle lingua* (miracidia hatched); vertical lines: *Podocotyle atomon* (miracidia mobile within the egg) (a) $T=15^{\circ}\text{C}$, (b) $S\text{‰}=16$.

and movement ceased. Low temperatures with salinities of 8‰ and above prolonged the survival time of free swimming cercariae (Fig. 2). The ability of the cercariae to penetrate fish was tested; flounders (*Platichthys flesus*) of 8–10 cm length (not infected by *Cryptocotyle*) were kept at 0, 10, and 20°C and various salinities. A total of 400–500 cercariae were added to each aquarium and after two days the infestations in the fins were counted. At temperatures of 0°C and salinities of 0 and 2‰ no infections were observed. Flounders kept at 4‰ salinity carried two (10°C) and six (20°C) parasites. No significant differences appeared between 8 and 32‰ (37–52 encysted parasites.)

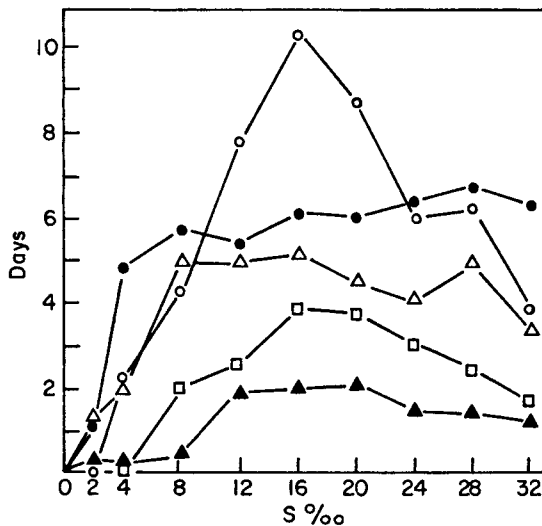


FIG. 2. L_{T50} of cercariae of *Cryptocotyle lingua*; ○, 0°C; ●, 5°C; △, 10°C; □, 20°C; ▲, 25°C.

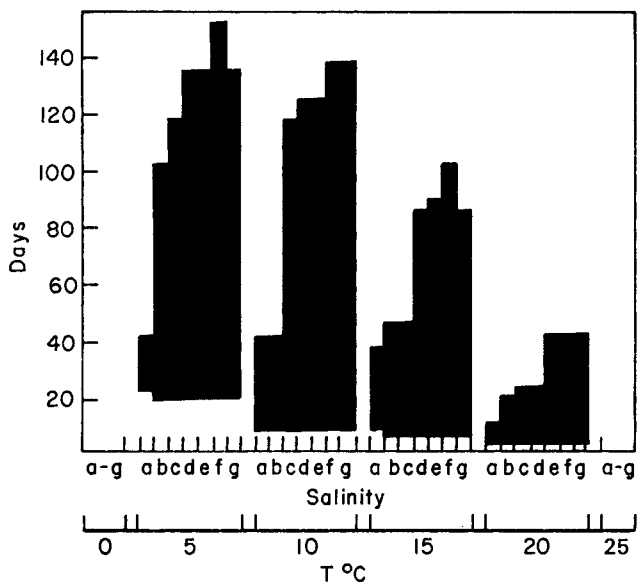


FIG. 3. Development of first stage larvae of *Contracaecum aduncum* (50% of mobile larvae within the egg). a, 0‰; b, 2‰; c, 4‰; d, 8‰; e, 16‰; f, 24‰; g, 32‰.

Podocotyle atomon (eggs)

Mature parasites were taken from the intestines of flounders and kept for two days in sea water, 50 eggs were used for each experiment. Unlike *Cryptocotyle*, the miracidia of *Podocotyle* left the egg actively. The miracidia of *Podocotyle* were more sensitive to temperature and salinity (Fig. 1). At 4‰ only 5% of the eggs developed to miracidia, but all died after hatching.

Contracaecum aduncum

Eggs were obtained from nematodes taken out of the intestines of eelpout (*Zoarces viviparus*). Normal development of the larvae was observed at 5–20° C, their time of survival within the egg was reduced in fresh water. With a water temperature of 5° C and salinities higher than 12‰ the L_{T50} of the larvae was prolonged for 150 days.

INTESTINAL PARASITES

The osmotic pressure of the intestinal contents of a fish has been stated to remain constant, even when the fish migrates between sea and fresh water. To confirm this finding, 35 flounders were each adapted to a particular salinity and a water temperature of 15–17° C. After nine days the fish were killed and their gastro-intestinal tract divided into five sections: stomach; first, second, and third portions of the small intestine; and the rectum. The intestinal contents were clear and needed no filtering. The osmotic pressure was determined by using an electronic osmometer. Values in Fig. 4 represent the average of 25–35 measurements.

The osmolarity of water ingested by the fish appeared to be adapted in the stomach to an average value (about 300 m osmol or 10.5‰ salinity). No differences existed within the different parts of the small intestine and rectum. The posterior parts of the flounder intestines from fresh water contained little or no fluid contents. An

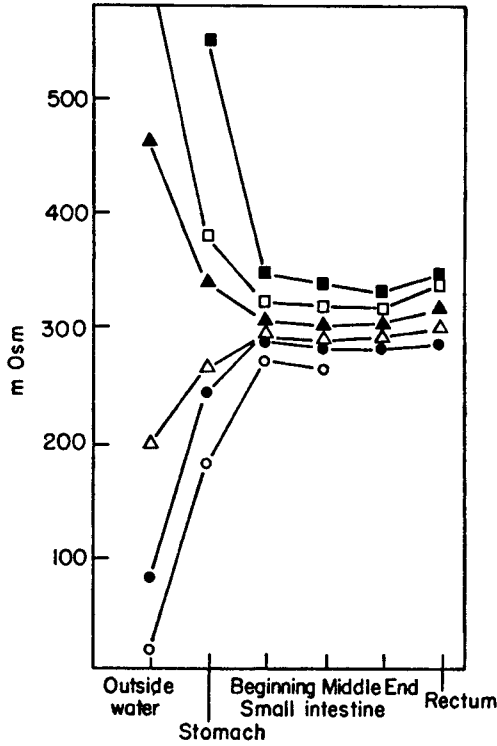


FIG. 4. Osmolarity of the gastrointestinal contents of *Platichthys flesus* after 9 days in different salinities; ○, 0‰; ●, 4‰; △, 8‰; ▲, 16‰; □, 28‰; ■, 32‰.

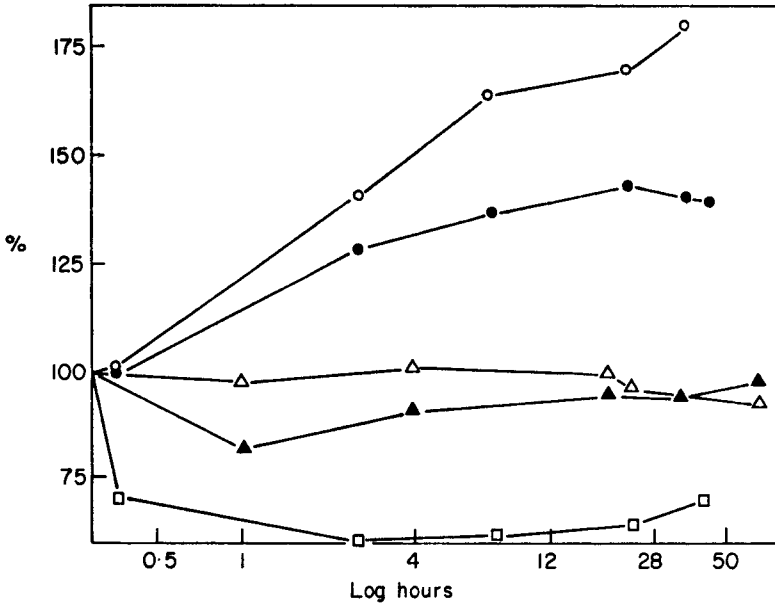


FIG. 5. Deviation of body weight in % of *Contracaecum aduncum* at different salinities; ○, 0‰; ●, 4‰; △, 12‰; ▲, 16‰; □, 32‰.

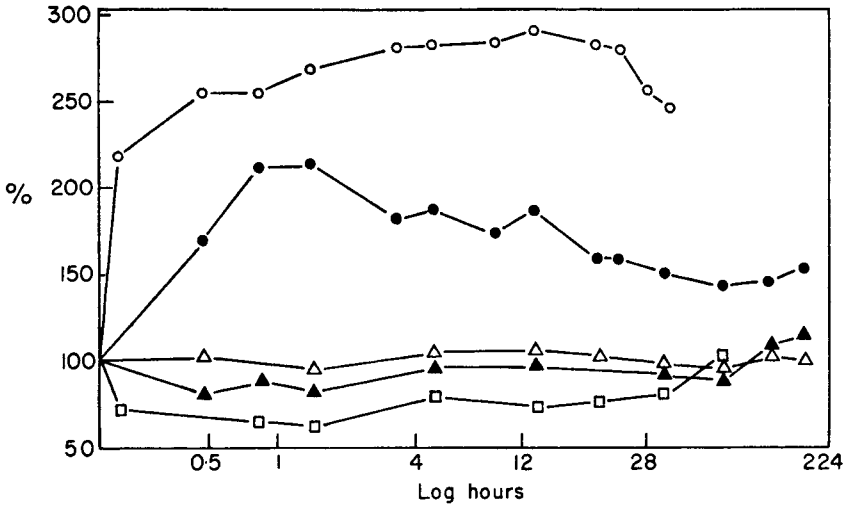


FIG. 6. Deviation of body weight in % of *Echinorhynchus gadi* at different salinities (see Fig. 5).

osmolarity of 300 m osmol is equivalent to the salinity that provides best conditions for intestinal helminths (Figs. 5, 6 and 7).

Figure 5 demonstrates the weight changes of *Contracaecum aduncum* kept at various salinities. Only juvenile nematodes (2.5 mg) were used, and each value gives the average of 6–12 measurements; the water temperature was 18.5–20° C. All the nematodes survived for two days even in 0 and 32‰ water. The weight changes of male *Echinorhynchus gadi* under the same conditions is shown in Fig. 6.

Of all the parasites examined, *Contracaecum aduncum* was the only one able to leave the intestine of the host after the fish had died. The rate of emigration from a

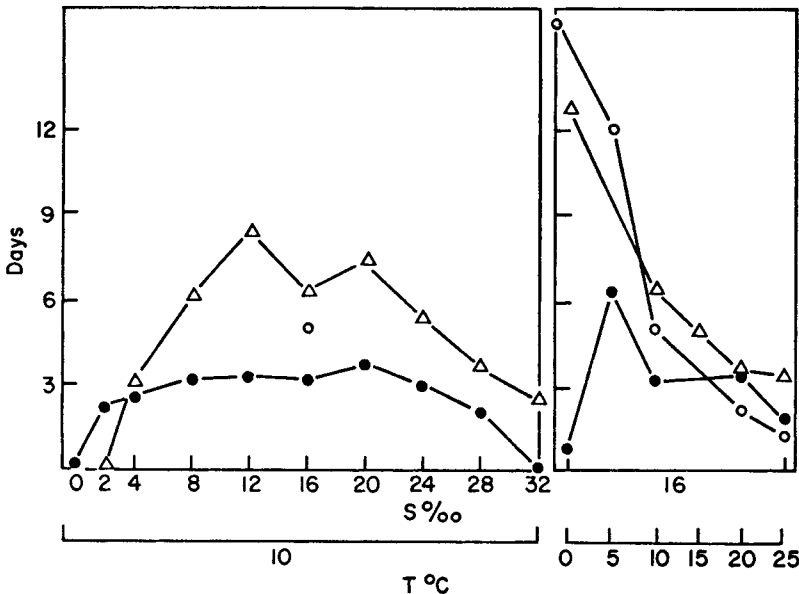


FIG. 7. L_{T50} of some endoparasitic helminths; ○, *Podocotyle atomon*; ●, *Contracaecum aduncum*; △, *Echinorhynchus gadi*.

dead eelpout in relation to air temperatures is shown in Fig. 8. The nematodes left the fish by mouth and anus. The rate of emigration was greatest at 5 and 10° C. Low temperatures kept the nematodes alive for longer times in the dead host but slowed their activity. At 0° C more than half of all parasites survived for 14 days; at 25° C less than 25% were alive after 20 h.

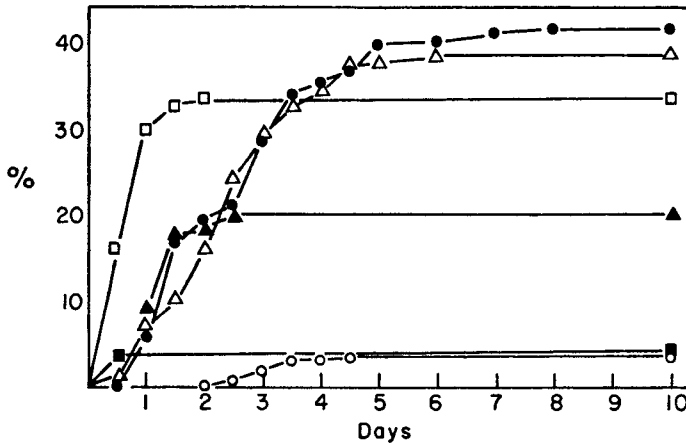


FIG. 8. Percentage emigration of *Contracaecum aduncum* from intestinal tract of dead *Zoarces viviparus*; ○, 0° C; ●, 5° C; △, 10° C; ▲, 15° C; □, 20° C; ■, 25° C.

ENDOPARASITES FROM OTHER ORGANS

Anisakis sp. (larvae)

A total of 360 herring (*Clupea harengus*) containing 2052 *Anisakis* larvae were stored at 0° C (16 days), 5° C (8 days), 10° C (4 days), and 20° C (2 days). After section of the herrings all larvae, except two were still alive; 92% lay free within the body cavity or attached to organs therein, with half of them having escaped from their cysts. Another 5% were encysted in the wall of the peritoneum; 2% were commencing to penetrate the muscle and only three larvae (0.1%) were found within the muscle.

The larvae, when taken out of their cysts, survived for several months in water (Fig. 9). Salinities of 0–24‰ did not result in great differences between survival times. Some parasites stayed alive for longer than six months at temperatures of 0–10° C.

Cryptocotyle lingue (metacercariae)

Twenty cysts each liberated from cod (*Gadus morhua*) were kept in water at 10° C and different salinities for four weeks. After this time no significant difference was observed in the mortalities from salinities of 4–32‰: 30–60% of the larvae died: in fresh water only one larva survived.

ECTOPARASITES

Piscicola geometra

Leeches were collected in early winter from carp (*Cyprinus carpio*). One hundred parasites were kept in aquaria containing 2 l water. Once a week they were fed on

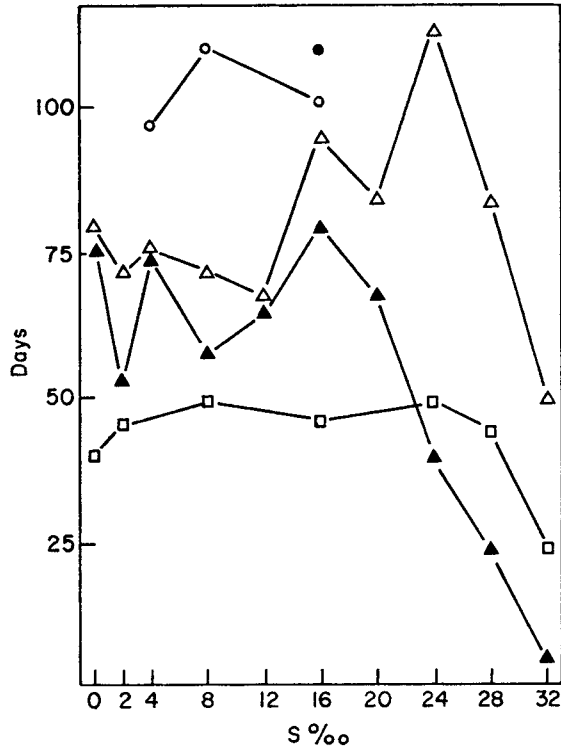


FIG. 9. L_{T50} of *Anisakis* larvae from herring *Clupea harengus* at various salinities; ○, 0° C; ●, 5° C; ○, 10° C; ▲, 20° C; △, 25° C.

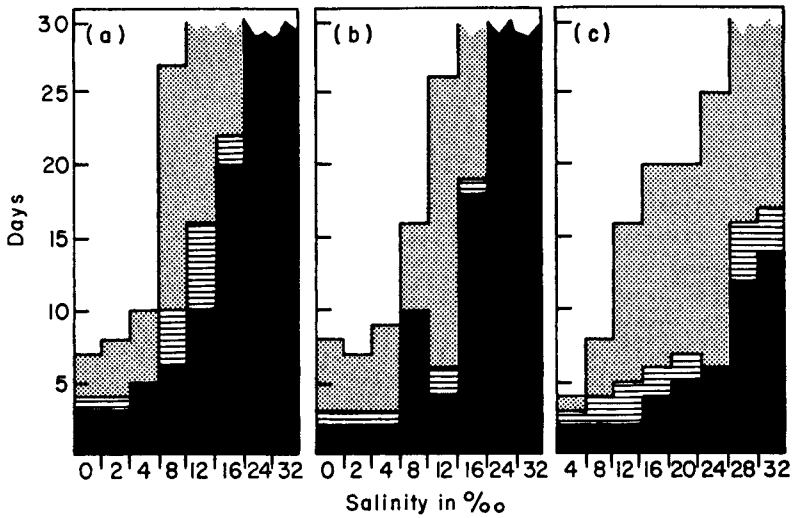


FIG. 10. Time of survival or attachment to the host fish after transfer to various salinities ($T = 14^{\circ}C$), (a) *Lepeophtheirus pectoralis* on flounder *Platichthys flesus*, (b) *Acanthochondria depressa* on flounder, (c) *Acanthochondria depressa* solitary. Black: 75% attached to host (a, b) or survived (c); hatched: 50% attached to host (a, b) or survived (c); dotted: 0% attached to host (a, b) or survived (c).

sticklebacks (*Gasterosteus aculeatus*). The survival of leeches was high at salinities up to 8‰: at 10° C the L_{T50} was reached after four months. No eggs were released at 0 and 5° C (Table II).

Lepeophtheirus pectoralis

Eight flounders each were adapted with their natural parasitic fauna to various salinities ($T=14^{\circ}\text{C}$). Single fish carried 8–27 adult female *L. pectoralis*. For each salinity five flounders were used. Salinity from 0–4‰ prevented the copepods from changing their host or even their place of attachment. Parasites proved to be stenohaline, low salinities caused their death. In Fig. 10(a) the time of attachment to the host is shown; dead copepods took two days to detach.

Acanthochondria depressa

The conditions of capture and cultivation were the same as for *L. pectoralis*. For each salinity, 24–36 mature females, attached to their hosts, were used. The adult copepods did not change their place of attachment. Dead parasites took two days to detach. Salinity tolerance was similar to that of *L. pectoralis* [Fig. 10(b), (c)].

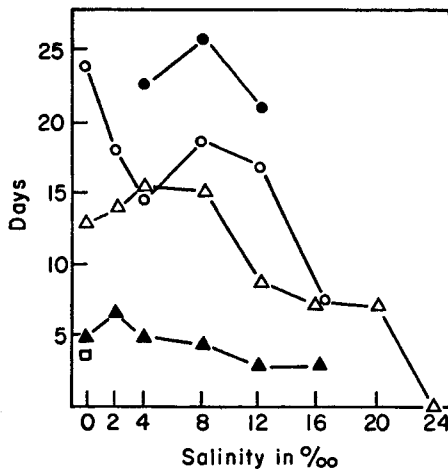


FIG. 11. L_{T50} of *Argulus foliaceus*, ○, 0° C; ●, 5° C; △, 10° C; ▲, 20° C; □, 25° C.

Argulus foliaceus

Conditions of capture, cultivation and feeding were the same as for *Piscicola geometra*. Fifty fish lice were kept in aquaria containing 0.5 l water. Temperatures of 0 and 5° C lowered activity, nevertheless the parasites attacked sticklebacks. Eggs were released as the water temperature exceeded 10° C. Figure 11 demonstrates the L_{T50} in accordance to the varying temperatures and salinities.

IV. DISCUSSION

There are two reasons for reduction of the fish parasitic fauna in brackish water: stenohalinity of the parasite itself and that of the hosts. The first reason explains the lack of ectoparasites in brackish water. The biotope of an ectoparasite, as far as

TABLE II. Survival of adult *Piscicola geometra* expressed as percentages

S‰	1	2	3	5	18	55	120
0° C							
0	100	100	100	100	100	98	98
4	100	100	100	100	100	99	99
8	100	100	100	100	99	99	96
12	100	100	98	95	61	13	0
16	100	84	7	0	0	0	0
10° C							
0	100	100	100	100	96	79	60
4	100	99	99	99	93	76	51
8	100	99	99	98	97	80	48
12	100	100	100	100	62	18	0
16	100	91	78	59	0	0	0
20	100	2	0	0	0	0	0
32	100	0	0	0	0	0	0
20° C							
0	100	100	100	96	94	35	0
4	100	100	97	94	88	49	0
8	100	99	97	88	72	34	0
12	100	98	95	81	62	0	0
16	100	62	26	5	0	0	0

salinity is concerned, is formed by the water which surrounds the parasite as well as the host. Only in cases, as some lernaepod copepods, are ectoparasites resistant to a wide range of salinity. The abdomen of the adult female *Lernaecera* is covered by an uninterrupted cuticle. Mouthparts and legs are buried in the host's body and not exposed to the water (Panikkar & Sproston, 1941; Sundnes, 1970).

Stenohalinity of ectoparasites makes them good indicators for the migrations of their hosts into waters of differing salinities. No European species of parasitic crustaceans or hirudineans is able to survive in salinities between 7 and 20–25‰, (Engelbrecht, 1958; Markowski, 1933; Möller, 1974, 1975a). Ectoparasites found in brackish water indicate that their hosts have immigrated from the sea or from fresh water recently. The resistance of ectoparasites is increased in winter, as low temperatures increase their salinity tolerance (Table II, Figs 10 and 11).

The number of infections with viruses, bacteria and protozoans is reduced with the lack of ectoparasites. Ectoparasites may act as obligatory (in the case of *Trypanosoma* and *Trypanoplasma*) or opportunistic vectors. Furthermore, they cause wounds in the fish skin which may become invaded by secondary pathogens.

The osmotic milieu of endoparasites, unlike that of ectoparasites, is afforded by intestines, blood, gall bladder or tissues of the host. As water salinity changes, parasites from the intestine are usually affected first, as is shown for *Contracaecum aduncum* (Fig. 5) and *Echinorhynchus gadi* (Fig. 6). These parasites are not able to stabilise their water balance when osmolarity of the surrounding medium changes. The end points of the 0, 4 and 32‰ curves in Figs 5 and 6 may be deceptive; there is no adaption to low or high salinities, and an adjustment of weight towards the endpoint (100%) merely signalizes the death of the parasite. In the intestine of fishes, parasites are largely protected from osmotic damage. As shown in Fig. 4, the osmolarity of water ingested by the fish is adjusted in the stomach and the start of the

small intestine to a level which will stay constant throughout the rest of the intestinal tract.

The greatest tolerance of salinity and temperature was shown by larvae of the nematode *Anisakis*. Some nematodes survived for six months at low temperatures (Fig. 9); an important finding since *Anisakis* may become harmful to man. Gustafson (1953) and Houwing (1969) have demonstrated that high concentrations of salt or several hours of deep freezing are needed to kill the larvae in the flesh of a herring.

Free living stages of endoparasites, such as the eggs of most species, are protected by a thick cuticle. Miracidia of *Cryptocotyle* and *Podocotyle* were able to develop even in 4‰ water within the egg (Fig. 1). In the case of *Contracaecum aduncum* the salinity tolerance of first stage larvae proved to be even more pronounced (Fig. 3). The salinity tolerance of the free swimming cercariae of *Cryptocotyle* corresponds with that of their miracidia, and some even succeeded in infecting the second intermediate host at 4‰.

According to the salinity resistance of *P. atomon* and *C. lingua*, the range of these two species within the Baltic should extend to the Finnish Bay and even north to Åland. *Cryptocotyle*, however, does not occur north of Bornholm, where the salinity seldom drops below 7‰, and the most eastern occurrence of *Podocotyle* is the line which joins south Sweden with Rügen (Reimer, 1970). The explanation is given by the geographical limitation of the obligatory first intermediate host *Littorina*. Following Ankel (1936) the eastern limit of *Littorina* in the Baltic is Bornholm. The spread of *Cryptocotyle* in comparison with that of *Podocotyle* is favoured by the more mobile second intermediate (fish) and final (gulls) hosts of the first species.

As is shown in all experiments, a reduction in water temperature increases the salinity tolerance of parasite larvae as well as of adult parasites (Fig. 7) while low temperatures slow down the activity of the parasite (Fig. 8) and reduce the chance of infecting a new host.

Aquaculture will be favoured in brackish water from the parasitological point of view compared with marine or fresh water: the number of parasite species is reduced and so is the possibility of infections through the skin because of the lack of ectoparasites. Furthermore, several endoparasites, among them the highly pathogenic *Cryptocotyle* are less common in brackish water.

This work is part of a thesis, carried out at the Institut für Meereskunde in Kiel. My thanks are due to Professor Dr G. Hempel for arranging the working facilities and for advice during my studies. I also have to thank Professor Dr Llewellyn (Birmingham) for criticising and improving the manuscript.

References

- Ankel, W. E. (1936). Prosobranchia. In *Tierwelt der Nord- und Ostsee* (G. Grimpe & E. Wagler eds), Vol. IXb1. Leipzig: Akademische Verlagsgesellschaft.
- Bauer, O. N. (1959). The ecology of parasites of freshwater fish. *Natn. Sci. Found. Wash. D.C.* 1962, 215pp.
- Cavalli-Sforza, L. (1972). Biometrie. *Grundzüge biologisch-medizinischer Statistik*, 212pp. Stuttgart: G. Fischer Verlag.
- Engelbrecht, H. (1958). Untersuchungen über den Parasitenbefall der Nutzfische im Greifswalder Bodden und Kleinen Haff. *Z. Fisch.* 7, 481–511.
- Janiszewska, J. (1938). Studien über die Entwicklung und die Lebensweise der parasitischen Würmer in der Flunder (*Pleuronectes flesus* L.). *Mém. Acad. pol. Sci. Sér. B* 14, 1–68.

- Mackenzie, K. & Gibson, D. I. (1970). Ecological studies of some parasites of plaice and flounder. *Symp. Br. Soc. Parasitol.* **8**, 1-42.
- Gustafson, P. V. (1953). The effect of freezing on encysted *Anisakis* larvae. *Parasitology* **39**, 585-588.
- Houwing, H. (1969). Het inactiveren van de haringnematode door keukenzout en azijnzuur. *Visserijwereld* **28**, 3 pp.
- Markowski, S. (1933). Die Eingeweidewürmer der Fische des polnischen Balticums. *Archwm Hydrobiol. Ryb.* **7**, 1-53.
- Markowski, S. (1935). Einfluß der Milieueränderungen auf die Entwicklung der Eier von *Bothriocephalus scorpii* (Müller 1776). *Bull. Acad. pol. Sci. sér. sci. biol.* **2**, 49-58.
- Markowski, S. (1938). Über die Helminthenfauna der baltischen Aalmutter (*Zoarces viviparus* L.). *Zoologica Pol.* **3**, 89-103.
- Meyer, F. P. (1970). Seasonal fluctuations in the incidence of disease in fish farms. In *A Symposium on Diseases of Fishes and Shellfishes*, (S. F. Snieszko, ed.), pp. 21-29. Wash. D.C.: Am. Fish. Soc. Spec. Publ. 5.
- Michajlow, W. (1938). Über die Entwicklung der Eier von *Triaenophorus lucii* (Müll.) in Süß- und Brackwasser. *Zoologica Pol.* **3**, 251-259.
- Möller, H. (1974). Untersuchungen über die Parasiten der Flunder (*Platichthys flesus* L.) in der Kieler Förde. *Ber. dt. wiss. Kommn Meeresforsch.* **23**, 136-149.
- Möller, H. (1975a). Der Einfluß von Temperatur und Salzgehalt auf Entwicklung und Verbreitung von Fischparasiten. *Diss. mat. nat. Fak. Univ. Kiel*, 108 pp.
- Möller, H. (1975b). Parasitological investigations on the European eelpout (*Zoarces viviparus* L.) in the Kiel Fjord (Western Baltic). *Ber. dt. wiss. Kommn Meeresforsch.* **24**, 63-70.
- Panikkar, N. K. & Sproston, N. G. (1941). Osmotic relations of some metazoan parasites. *Parasitology* **33**, 214-223.
- Polyanski, Y. I. (ed.) (1955). *Parasites of the fish of the Barents Sea*, 158 pp. Jerusalem: Isr. Progr. Sci. Transl.
- Reimer, L. W. (1970). Digene Trematoden und Cestoden der Ostseefische als natürliche Fischmarken. *Parasit. SchrReihe* **20**, 1-144.
- Ronald, K. (1960). The effects of physical stimuli on the larval stage of *Terranova decipiens* (Krabbe 1878). 1. temperature. *Contr. Dep. Pêche Quebec* **74**, 623-642.
- Schäperclaus, W. (1954). *Fischkrankheiten*, 708 pp. Berlin: Akademie-Verlag.
- Stunkard, H. W. & Shaw, C. R. (1931). The effect of dilution of sea water on the activity and longevity of certain marine cercariae with descriptions of two new species. *Biol. Bull. mar. biol. Lab. Woods Hole* **61**, 242-271.
- Sundnes, G. (1970). *Lernaecera branchialis* (L.) on cod (*Gadus morhua* L.) in Norwegian waters. *Inst. mar. Res. Bergen* 48 pp.