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Mechanisms of co-existence of *Heterocope saliens* (Crustacea, Copepoda) and planktivorous fish

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The simultaneous occurrence of *Heterocope saliens* and a large stock of Arctic char was investigated in the oligotrophic, coastal Lake Selura in SW Norway. Habitat-overlap of *H. saliens* and Arctic char was restricted mainly to June. With increasing temperature, Arctic char disappeared from the littoral and the upper water masses and inhabited the hypolimnion of the lake. The interaction between *H. saliens* and its important predator was minimized and thus a large population of *H. saliens* could be established, primarily in the littoral, but to a minor extent also in the pelagial of the lake.

H. saliens can avoid elimination from lakes with strong pelagic fish predation by staying in the littoral, while both strong littoral and limnetic fish predation probably lead to elimination of *H. saliens*. When fish disappear during acidification, *H. saliens* seems to expand its area considerably and to become a permanent inhabitant of the pelagic zone. The relationship between fish predation and distribution of the other Norwegian *Heterocope* species is briefly discussed.

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INTRODUCTION

The copepod *Heterocope saliens* (Lillj., 1863), has a boreoalpine distribution restricted to the Old World. It must be a relatively early immigrant to freshwater, as no *Heterocope* species are found in salt or brackish water today. *H. saliens* is a large-sized copepod (adult females: 2.2—4.0 mm), conspicuously coloured, that inhabits ponds, and the littoral and pelagial zones of lakes. It is vulnerable to fish predation, and seems to avoid lakes with heavy fish predation (Lindström 1955, Nilsson and Pejler 1973).

Lake Selura, a coastal lake in southern Norway (Fig. 1), had a large stock of stunted Arctic char (*Salvelinus alpinus* (L.)), a moderate stock of freshwater resident brown trout (*Salmo trutta* L.) and catadromous eel (*Anguilla anguilla* (L.)). The Arctic char had, in 1977, a maximum length of 24 cm and 21—31 gill rakers (mean 24.3, n = 48). In spite of this dense stock of Arctic char the population of *H. saliens* was considerable.

In the present paper the simultaneous occurrence of *H. saliens* and a large stock of Arctic char in Lake Selura has been described and notes are given on the regulation of the ecological distribution of *H. saliens* and other *Heterocope* spp. by fish predation.

STUDY SITE

Lake Selura is a medium-sized (surface area 5.1 km^2, maximum depth 65 m), oligotrophic lake in SW Norway (Fig. 1). Temperature conditions are shown in Fig. 2. Some physicochemical characteristics are given in Table 1. The lake is situated in an area which receives high concentrations of acid pollutants (Brække 1976), and its considerable acidity may be due to this. The acidity of the lake may exert considerable influence on fish survival and the presence of very large numbers of rather sensitive Arctic char is difficult to explain. However, since 1977 there has been a marked decline in density. The stock of Arctic char was in 1982 characterized by partial recruitment failure and both growth and condition had increased (Andersen et al. 1984).

MATERIAL AND METHODS

Hydrography was investigated using standard methods. Plankton was sampled using a net, mesh 45 µm, drawn from the bottom to the surface with constant velocity at the pelagic station and horizontally between macrophytes at the littoral station. The pelagic and littoral stations are indicated in Fig. 1. Fish were sampled with a

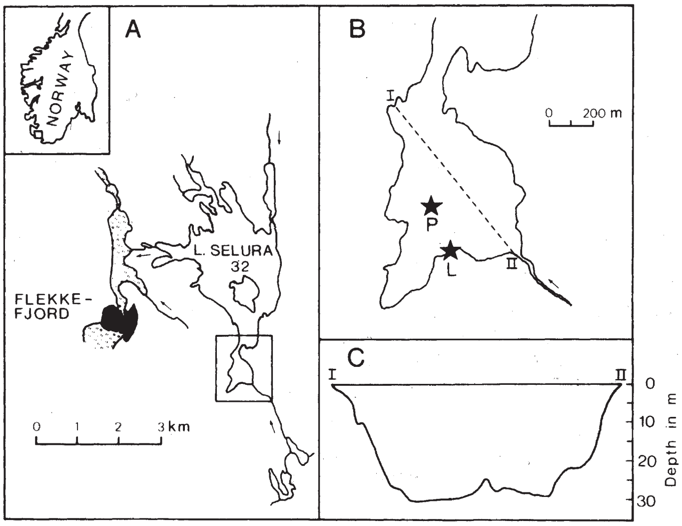

Fig. 1. Lake Selura 32 m a.s.l. A. the total area of the lake. B. the southern bight of the lake. P: pelagic station for physicochemical, zooplankton and fish samples. L: littoral station for zooplankton and fish samples. C: bottom profile of the southern bight along the I—II line.

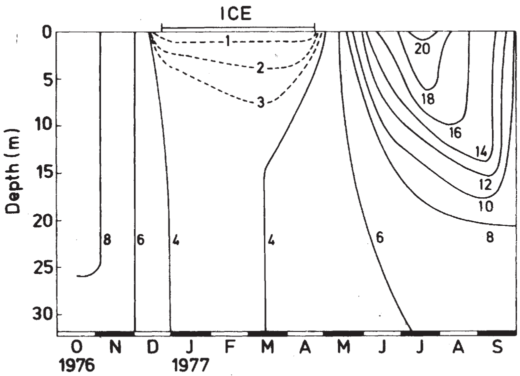

Fig. 2. Isotherms of Lake Selura at the pelagic station, southern bight.

Table 1. Physicochemical parameters of Lake Selura based on samples from 18.11.1974 (Wright & Snekvik 1977), and monthly samples 1976/77 (transparency, pH, conductivity (K_{20}) and Ca).

Parameter	Unit	Value (mean)	Range
Secchi depth	m	16.1	10—18
pH		5.0	4.7—5.2
K_{20}	S/cm	45.9	40.0—56.1
Ca	mg/l	1.3	1.1—1.4
Na	mg/l	5.3	
Mg	mg/l	0.8	
K	mg/l	0.5	
Al	mg/l	0.1	
Cl	mg/l	10.0	
SO_4	mg/l	5.1	
NO_3	mg/l	0.2	

floating net (25 x 6 m, mesh size: 19.5 mm) at the pelagic station, and with a beach seine (75 x 5 m, mesh size: 9 mm) at the littoral station.

All fish were measured, and the stomach contents of 120 randomly selected specimens were counted. Fishing and zooplankton sampling took place in a restricted area in the southern bight of Lake Selura, which has a fairly regular bottom with a maximum depth of about 30 m (see Fig. 1).

RESULTS AND DISCUSSION

Seasonal differences in pelagic and littoral zooplankton

Figure 3 shows the seasonal differences in pelagic and littoral zooplankton. The dominating Cladocera was *Bosmina longispina* morpha *lacustris* (Sars, 1862), which indicates considerable fish predation (cf. Nilssen et al. 1980). The nomenclature of this species has recently been revised (Nilssen and Larsson 1980). The presence of *Ceriodaphnia quadrangula* (O.F.M., 1785) also indicates strong fish predation (cf. Nilssen 1978). The most important copepods were *Eudiaptomus gracilis* (Sars, 1862) and *Cyclops scutifer* (Sars, 1862), but *Heterocope saliens* was also found in considerable numbers, especially in the littoral. *H. saliens* was established at the pelagic station about mid-June and disappeared at the end of October; the same temporal pattern was found at the littoral station (Fig. 3). The lake seems too acid to support *Daphnia*

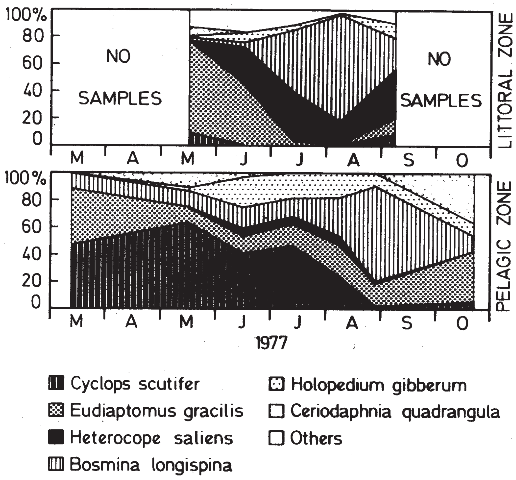

Fig. 3. Percentage abundance of Crustacea at the littoral and pelagic stations in the southern bight of Lake Selura, based on plankton net samples.

spp.; these often disappear in this region of Norway when acidity approaches pH = 5.0 (Nilssen 1980), but the absence here may also be due to predation from pelagic Arctic char (cf. Matzow et al. 1976).

Fish distribution and feeding

Horizontal and vertical distribution of Arctic char and brown trout varied seasonally (Fig. 4). Arctic char was caught in large numbers in the littoral zone during spring and early summer. Later in June, with surface temperatures rising above 16°C, it withdrew from the littoral and congregated deeper down. The same pattern was found at the pelagic station, where Arctic char during summer was mainly caught below the thermocline. Brown trout was generally restricted to the littoral zone, and only few fish were caught in the upper part of the pelagic zone. This habitat segregation of Arctic char and brown trout is known from earlier studies (Jonsson and Matzow 1979, Hindar and Jonsson 1982), but the Arctic char in Lake Selura seems to congregate deeper in the pelagic than earlier reported. The vertical distribution of Arctic char in the pelagic was probably not a result of interspecific competition with brown trout, because only a few brown trout were caught in this zone (Fig. 4).

To test if the avoidance of the epilimnion by Arctic char during summer was due to physico-chemical properties of the water, 20 Arctic char and 25 brown trout caught with a beach seine on the 14th of June were kept in separate enclosures in the littoral. In five days all Arctic char, but only one brown trout died. Already the first day after capture Arctic char started to die. Arctic char is considered a species adapted to cold water. It is also known that fish in acidic water show increased basic metabolism (Rosseland 1980). The avoidance by Arctic char of the epilimnion during summer may therefore be due to the combined effect of high temperature and acidic water.

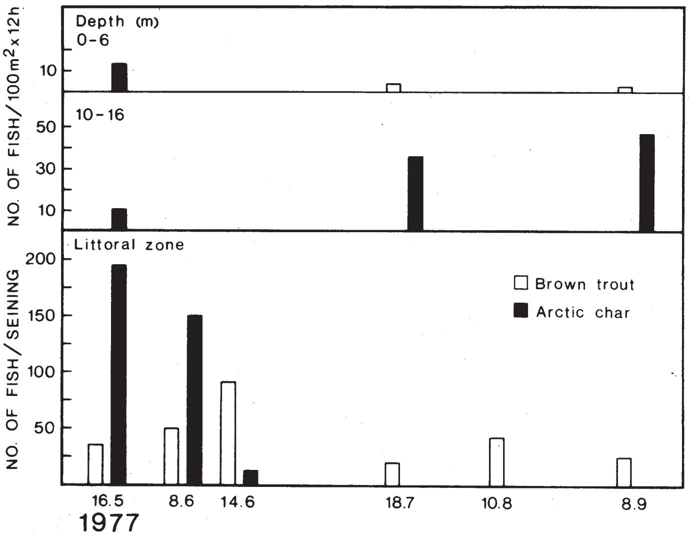

Fig. 4. Fish catches at the pelagic (0—6 m, 10—16 m) and the littoral stations of Lake Selura during different periods of 1977.

The food of Arctic char caught at the pelagic station is shown in Fig. 5. In May, *Bosmina longispina* was the dominant zooplankton food. In July, both *Bythotrephes longimanus* Leydig, 1860 and *Holopedium gibberum* Zaddach, 1855 were dominant food items, while *B. longimanus* was dominant in August. *B. longimanus* was not recorded in the zooplankton sampled. To a limited extent Arctic char fed on *Heterocope saliens* in July, while in August it was probably distributed below *H. saliens* in the pelagial zone. *H. saliens* is always distributed in the upper water masses of lakes (cf. Larsson 1978, Nilssen in prep.).

Mechanisms of co-existence of Arctic char and *Heterocope saliens*

During winter when Arctic char actively feed on both plankton and bottom animals (cf. Matzow et al. 1976), *Heterocope saliens* overwinters as resting eggs in the bottom sediments. During spring when *H. saliens* has not yet revived from diapause, the Arctic char eats both benthic and pelagic food, mainly *Bosmina longispina* (Fig. 5). When *H. saliens* appears from resting eggs it develops very rapidly into adults (cf. Larsson 1978), and during this period Arctic char feeds on both late copepodites and adults. Insolation in this area of Norway is strong and the surface water of the lake is rapidly warmed up. This results in a habitat displacement of the Arctic char which congregate below the thermocline both in the benthic and pelagic areas. *H. saliens* is distributed in the littoral as well as in the pelagial zone; the numerical abundance in the two habitats seems to be determined mainly by the predatory activity of fish. It is predated in the pelagial during summer (Fig. 5). However, this predation does not result in a lowering of the total lake population since *H. saliens* takes refuge in the littoral, an area not exploited by Arctic char when the water is warmed up above ca. 16°C.

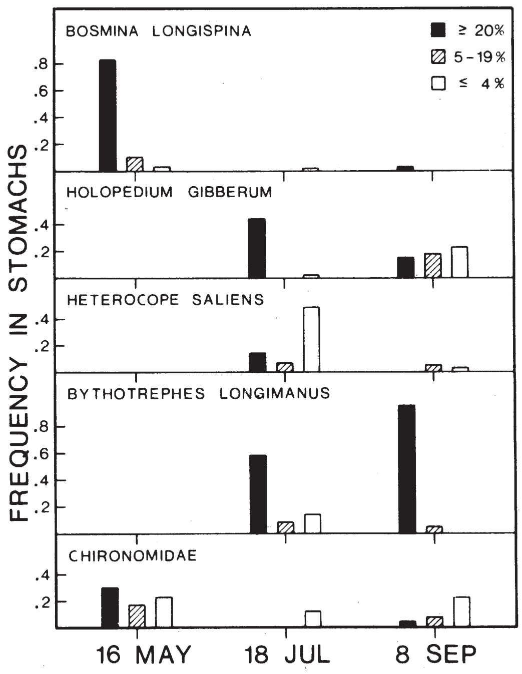

Fig. 5.Food items of Arctic char at the pelagic station of Lake Selura, based on frequency distribution.

Implications on the biogeography of *Heterocope* spp.

Heterocope saliens is probably an early immigrant to freshwater, with a considerable dispersal capacity, comparable to the other *Heterocope* species: *H. appendiculata* Sars, 1863 and *H. borealis* (Fischer, 1851) in the Palearctic, and *H. septentrionalis* (Juday & Muttkowski, 1915) in the Nearctic. *H. saliens* is spread over the whole of Norway, *H. borealis* has only been recorded in the northernmost county, Finnmark, while *H. appendiculata* seems to be a more recent immigrant, coming from the east of Northern Europe (Nilssen 1976). Fish predation seems to play an important role in the distribution of the three species. The largest species, *H. borealis,* is mostly recorded in habitats without fish or with reduced fish predation. *H. saliens* also seems to be strongly influenced by fish predation. In a comprehensive study from Northern Sweden (Nilsson & Pejler 1973) this species was found to be absent in lakes with predation from whitefish (*Coregonus* spp.). Only *H. appendiculata* was able to withstand considerable fish predation.

However, another mechanism may be in operation when considering the altitudinal distribution of the *Heterocope* species. Fish and zooplankton immigrated to Scandinavia after the last Weichselian glaciation. *H. saliens* may have been among the first to immigrate, judged from its present distribution in high mountain areas. It spreads rapidly to juvenile water bodies, created by recent ice withdrawal (cf. Halvorsen 1973). *H. appendiculata* is a species found in Eastern Norway and parts of Sweden, especially Northern Sweden.

Among freshwater fish, salmonids seem to have been the first immigrants, while coregonids came later (Huitfeldt-Kaas 1924). The observed co-occurrence of salmonids and *H. saliens* therefore may be due, wholly or in part, to the similar immigration history of salmonid fish and *H. saliens*. *H. appendiculata* is found lower in the watersheds where coregonids dominate; stronger fish predation may here have annihilated the largest and most pigmented of the two species: *H. saliens*. The distribution of the *Heterocope* species may also be influenced by intrageneric competition between *Heterocope* species — since they very seldom co-occur (Nilssen 1976).

Laboratory studies of *H. saliens* and *H. appendiculata* have revealed a strikingly different physiological reaction to pH. Whereas *H. saliens* was able to tolerate most ambient pH values, except for the most alkaline, *H. appendiculata* was not able to tolerate even medium acidic or alkaline conditions (Nilssen et al. 1983).

The distribution of *Heterocope* species in lakes with different fish predation is shown in Table 2. It is apparent that *H. saliens* does not occur when there is considerable fish predation in the pelagial, and it also disappears from the littoral in lakes with large population of perch (*Perca fluviatilis* L.) or sticklebacks (*Gasterosteus aculeatus* L.).

With increasing acidification, major fish species disappear, and the first sign indicating a lowered fish predation is the occurrence of *H. saliens* in the plankton (Nilssen 1980). The implication of *H. saliens* predation on the pelagic community (cf. Burckhardt 1944) and its autecology are presently being investigated.

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Table 2. Distribution of *Heterocope* spp. in different lake types, n: number of lakes within each category. P: distribution in the plankton, L: distribution in the littoral, xxx: very common, xx: common, x: uncommon, r: rare, o: not yet recorded in Norway under such conditions, —: outside the biogeographical range. In lakes with sticklebacks *H. saliens* is not recorded from the littoral (Table based on data from Nilssen MS).

Heterocope species		Acid fishless; n = 30	Alkaline fishless; n = 3	Brown trout; n = 28	Brown trout + Arctic char; n = 25	Brown trout + Arctic char + whitefish n = 30	Perch; n = 55 (+ brown trout)	Perch + Cyprinidae; n = 15	Dominant Cyprinidae; n = 18
H. borealis	P + L	—	xxx	x	r	r	—	—	—
H. appendiculata	P	o	o	x	x	x	o	xx	xx
H. appendiculata	L	o	o	o	o	o	o	o	o
H. saliens	P	xxx	—	xx	r	o	o	o	o
H. saliens	L	x	—	xx	r	o	o	o	o

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