Seasonal variation in the interactions between piscivorous fish, planktivorous fish and zooplankton in a shallow eutrophic lake

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Abstract

The interactions between the higher trophic levels in a shallow eutrophic lake were studied during the course of a year. Three fish species determined the main pathways of organic matter flow within the system: the predominantly planktivorous bream (*Abramis brama*), the obligate planktivorous smelt (*Osmerus eperlanus*), and the piscivorous pikeperch (*Stizostedion lucioperca*). Of the thirteen common zooplankton taxa *Daphnia hyalina* and cyclopoid copepods were utilized most by the planktivorous fish, while the large production of small cladocerans is almost left unutilized.

The seasonal variations of production and consumption are large. This is mainly affected by seasonal variation of the water temperature. The production of O + smelt is efficiently utilized by the pikeperch. Being the most important zooplankton consumer, as well as the most important prey group, O + fish plays a key role in the Tjeukemeer food web.

Introduction

Food web theory has centered around the idea of connectance, i.e. the fraction of total number of possible trophic connections actually observed (Rejmánek & Starý, 1979). The interaction strength proposed by May (1973) also focusses on this idea. The quantities of connectance and interaction strength are easily extracted from published studies which describe food webs in natural systems (see e.g. Cohen, 1978; Pimm, 1982). In a recent evaluation Paine (1988) criticized this static approach. He has not challenged the food web theory itself, but the way natural communities have been analyzed using simple equations for connectance and interaction strength. According to Paine food web studies should focus on the dynamic, rather than on the static properties of the ecosystem, thus taking into account the spatial and temporal variations within age classes of species.

In this study we investigate the food web of lake Tjeukemeer, using Paine's approach. In previous studies on this lake Vijverberg & van Densen (1984), Lammens *et al.* (1985) reported on the year to year changes in the zooplankton species- and size composition, as well as on changes in the condition and growth of bream and pikeperch because of large variations in the stocks of O + fish. Production of O + fish may differ by two orders of a magnitude from year to year. In the years 1976–1983 it ranged from 0.12 dry

wt m^{-2} yr^{-1} (6 kg fresh wt ha^{-1} yr^{-1}) to 11.7 g dry wt m^{-2} yr^{-1} (585 kg fresh wt ha^{-1} yr^{-1}), with a geometric mean production of 2.6 g dry wt m^{-2} yr^{-1} (130 kg fresh wt ha^{-1} yr^{-1}).

We will focus on the seasonal changes of trophic interactions between piscivorous and planktivorous fish on the one hand and between planktivorous fish and zooplankton on the other. We select the year 1978 for the data analysis, because O + fish production in this year (3.0 g dry wt m^{-2}) is close to the geometric mean value.

Study area

Tjeukemeer, situated in the North of the Netherlands, is a shallow (mean depth = 1.5 m), eutrophic freshwater lake and has a surface area of 2150 ha. The lake is a part of an interconnected system of water bodies, which act as a reservoir for the surrounding polders. This system receives water from the near by IJsselmeer (120000 ha) from May to September and polderwater which is rich in humic compounds in winter.

Secchi-disk depth is usually 20–35 cm and the algal biomass is dominated by the blue-green *Oscillatoria agardhii*. The littoral zone of the lake is poorly developed, representing only 1% of the lake's surface area.

Methods

Zooplankton

Zooplankton was sampled with a Friedinger closing sampler at five fixed stations at fortnightly intervals in May–September and at monthly intervals during the rest of the year. Although rotifers are often very abundant during spring, only copepods and cladocerans are important as fish food, and hence only microcrustacean zooplankton are considered. For each zooplankton species the population density and the size distribution were assessed (see Vijverberg, 1977; Vijverberg & Richter, 1982a). Mean monthly biomass was calculated using the appropriate length-weight relationship (Table 1).

Table 1. Length-weight relations used in this study, using ln W = b ln L + ln a. W is dry weight in g, and L is length in mm.

Species / age group	b	ln a	Source
Zooplankton			
Daphnia hyalina	2.52	− 11.356	Bottrell *et al.*, 1976
Bosmina spp.	2.53	− 11.104	Bottrell *et al.*, 1976
Chydorus sphaericus	4.64	− 8.543	Vijverberg & Frank, 1976
Cyclopoid copepods	2.40	− 11.862	Bottrell *et al.*, 1976
O + fish			
smelt	3.2	− 14.251	Mooij own obs.
pikeperch	3.2	− 14.182	Mooij own obs.
perch	3.2	− 13.675	Mooij own obs.
≥ I + fish			
bream			
sub adult	3.0	− 12.687	Mooij own obs.
spring	3.06	− 13.043	Lammens, 1982
autumn	3.10	− 13.177	Lammens, 1982
pikeperch			
spring male	3.51	− 14.885	van Densen & Vijverberg, 1982
spring female	3.23	− 13.057	van Densen & Vijverberg, 1982
autumn male	3.10	− 12.140	van Densen & Vijverberg, 1982
autumn female	2.94	− 11.176	van Densen & Vijverberg, 1982

Monthly production was calculated using P/B ratios, which were assessed under experimental conditions in earlier studies (Vijverberg, 1980; Vijverberg & Richter, 1982a, 1982b).

Fish

Young of the year fish (O +) were sampled using hoop nets from May to the first half of June, a 3 m trawl in the second half of June and a 5 m beam trawl from July onwards (van Densen, 1985). Older fish were caught using gill nets and a 5 m beam trawl. The number and size distribution of each species in the catch were noted. Absolute densities were estimated from the catches with the 5 m beam trawl, using a catching efficiency of 50% (van Densen, own obs.). Since the net efficiency for larger pikeperch is not known, pikeperch densities were estimated using the numbers of O + pikeperch in the previous years, combined with an instantaneous mortality rate per day (M) of 0.00055 d^{-1}, which is a conservative estimate based on Pauly's emperical formula for the natural mortality rate in fish stocks as a function of growth parameters and water temperature (Pauly, 1980). Mean monthly biomass (B) was assessed using Ricker's (1946) formula:

$$B = \frac{N_O \cdot W_O \cdot (e^{(G - M) \cdot t} - 1)}{(G - M) \cdot t} \qquad (1)$$

where N_O is the density and W_O is the mean dry weight at the start of the month; the weight was computed from the size distribution using the appropriate length-weight relationship, thus taking into account seasonal changes in condition (Table 1), G is the instantaneous growth rate per day, $t = 30$ days, and M is the instantaneous mortality rate per day; M was estimated from a negative exponential curve relating numbers with time. Monthly production (P) was calculated using:

$$P = G \cdot B \cdot t \qquad (2)$$

Gut contents were analyzed microscopically. The number and size distribution of each species in

the gut were noted (Lammens *et al.*, 1985; van Densen, 1985). Fish consumption was estimated using conversion factors between fish production and consumption taken from literature. Although many factors may influence this conversion (Brett & Groves, 1979; Soofiania & Hawkins, 1985), we did not take into account the effects of these factors, because they are very difficult to estimate quantitatively under field conditions. For O + fish we used a conversion of 25%, which is the average of the conversion efficiency for herbivorous and carnivorous young fish reported in literature (Brett & Groves, 1979). Consumption rates for ≥ I + piscivorous fish were calculated using a conversion efficiency of 20% (Popova, 1978) and for ≥ I + planktivorous fish of 12.5% (O'Grady & Spillett, 1985).

Results

Zooplankton

About 98% of the zooplankton densities was represented by *Daphnia hyalina, Bosmina coregoni, Bosmina longirostris, Chydorus sphaericus,* and cyclopoid copepods. *Leptodora kindtii* was the largest cladoceran present, but because of its very low densities (< 1 ind. l^{-1}) its biomass was very low. The two *Bosmina* species (*B. longirostris* and *B. coregoni*) were lumped.

Zooplankton biomass showed a distinct seasonal pattern (Fig. 1a). During winter the zooplankton biomass was virtually zero. The cyclopoid copepod peak in May was followed by a peak of *Daphnia hyalina* in June. In July the small zooplankton species (*Bosmina* spp. and *Chydorus sphaericus*) exhibited their peak biomass. In autumn the large zooplankton, *D. hyalina* and cyclopoid copepods, increased again, but their biomass maxima were lower than in the preceding spring and early summer. Zooplankton production (Fig. 1b) increased steadily to reach a peak in July and thereafter decreased again. The relative importance of the species changed during the year. Production of the small species was more important in July, but
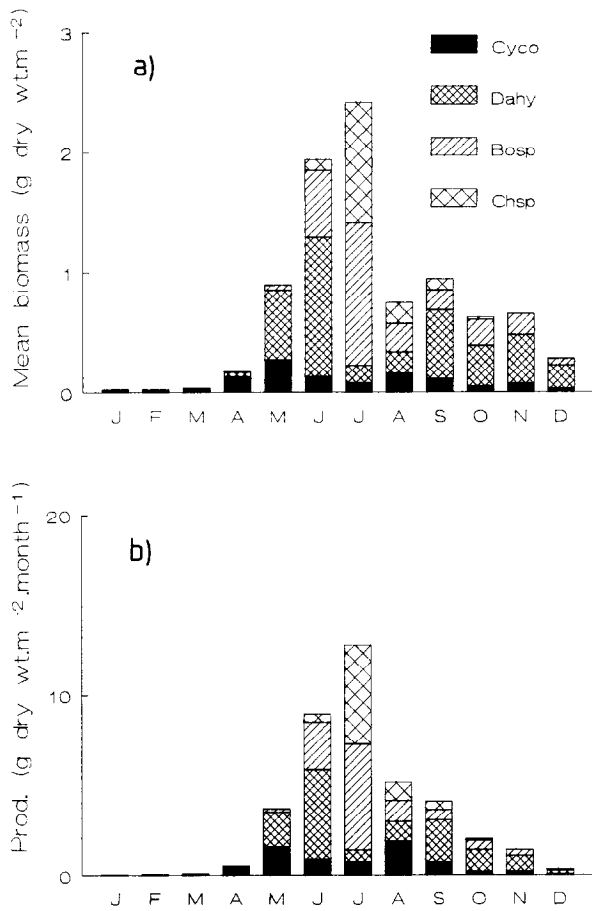
Fig. 1. Seasonal variation in zooplankton biomass and production. a. Mean monthly biomass (g dry wt m^{-2}), b. Monthly production (g dry wt m^{-2} month^{-1}). Dahy = *Daphnia hyalina*, Cyco = Cyclopoid copepods, Bosp = *Bosmina* spp., and Chsp = *Chydorus sphaericus*.

Fish

The open-water fish community of the lake consists of eight species: bream (*Abramis brama*), white bream (*Blicca björkna*), roach (*Rutilus rutilus*), smelt (*Osmerus eperlanus*), pikeperch (*Stizostedion lucioperca*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), and eel (*Anguilla anguilla*). The main pathways of organic matter flow within the community are determined by
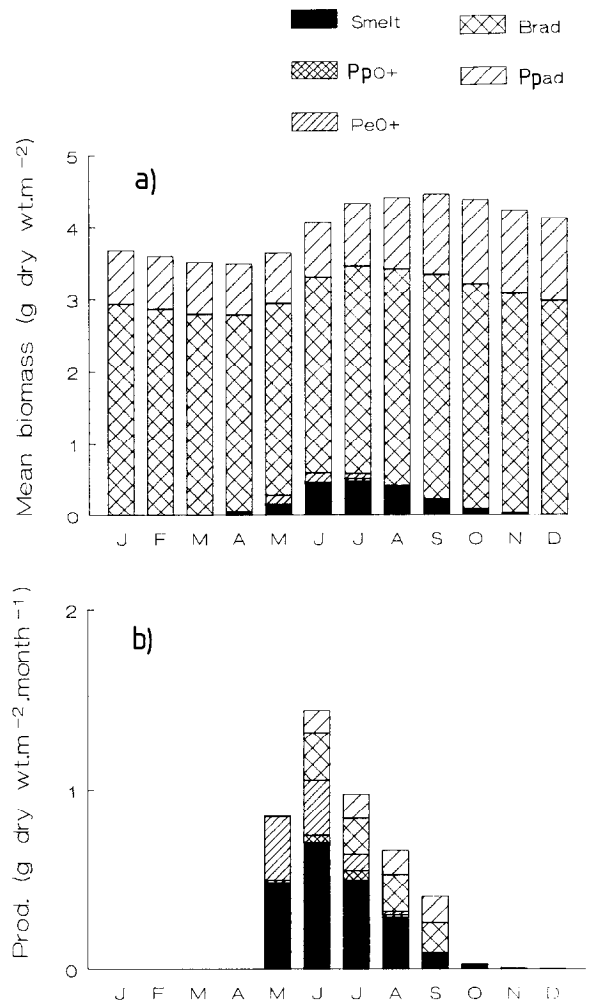
in spring, early summer and in autumn the large species contributed the most to the production.

Fig. 2. Seasonal variation in fish biomass and production. a. Mean monthly biomass (g dry wt m^{-2}), b. Monthly production (g dry wt m^{-2} month^{-1}). SmO + = O + smelt, PpO + = O + pikeperch, PeO + = O + perch, Brad = $\geq$ I + bream, and Ppad = $\geq$ I + pikeperch.

three groups; $\geq$ I + bream, $\geq$ I + pikeperch, and O + fish.

The bream population is the largest and the most stable component in the community (Fig. 2a). Its stability is based on a large number (15) of year classes. In 1978 approximately one quarter of the standing stock biomass was composed of III + (year class 1975) individuals, with individual lengths ranging from ca. 17 cm in spring to 22 cm in autumn. Production started in June and was relatively constant during the growing season (Fig. 2b).

Pikeperch is the main predator in Tjeukemeer and ≥ I + pikeperch is strictly piscivorous. In 1978 the standing stock biomass was composed mainly of two year classes: II + (1976), and III + (1975), with mean lengths of ca. 30 and 40 cm at the start of the season. Both the standing stock biomass and the production of pikeperch were relatively low compared with the biomass and production of bream (Fig. 2a, b).

The O + fish are the most unstable component in the system. Their first appearance in April–May, as a result of spawning, depend on the ambient temperature (Mooij & Van Tongeren, 1990). The rate of decrease in O + fish biomass during August–December depends largely on the predation pressure exerted by the pikeperch (Fig. 2a). Smelt dominates the O + fish group, comprising 80–90% of the biomass. Total recruitment of smelt can be influenced considerably by migration of larvae from IJsselmeer (van Densen & Vijverberg, 1982). In 1978 O + perch and O + pikeperch also contributed substantially to the total O + fish biomass. The biomass of O + fish is low as compared with the biomass of the ≥ I + bream. However, the production of O + fish is much higher than the production of bream (Fig. 2a, b). For instance the O + fish production in June was 70% of the total fish production, but its biomass was only 10% of the total fish biomass. This is caused by the much higher growth rates of the O + fish compared with the growth rates of the ≥ I + bream, and ≥ I + pikeperch. O + fish production was highest in June, decreasing thereafter until the end of the year.

Zooplankton production and consumption by planktivorous fish

From the gut content analysis of the planktivorous fish species it was observed that O + fish, the main tertiary producer, predates mainly on the large zooplankton species (see also van Densen, 1985). Usually the large prey species make up more than 95% of the fish diet. Only when the biomass of the large species in the environment is very low (July) are the small species also eaten

considerably (ca. 40%). ≥ I + bream also feeds size selectively on the large zooplankton species, but its feeding behaviour differs. Bream larger than 15 cm are filter feeders, whereas smaller bream are generally particulate feeders (Lammens, 1984). The size selection of the filter feeding bream depends primarily on the mesh size of the branchiospinal system of the fish, which increases with increasing fish size (Lammens & Hoogenboezem, in press). Moreover the mean proportion of benthic cladocerans and larval chironomids on biomass basis in the bream's diet is ca. 50%, because large bream regularly switch to benthic feeding. This different feeding behaviour resulted in a different consumption pattern of the zooplankton of the O + fish and ≥ I + bream.
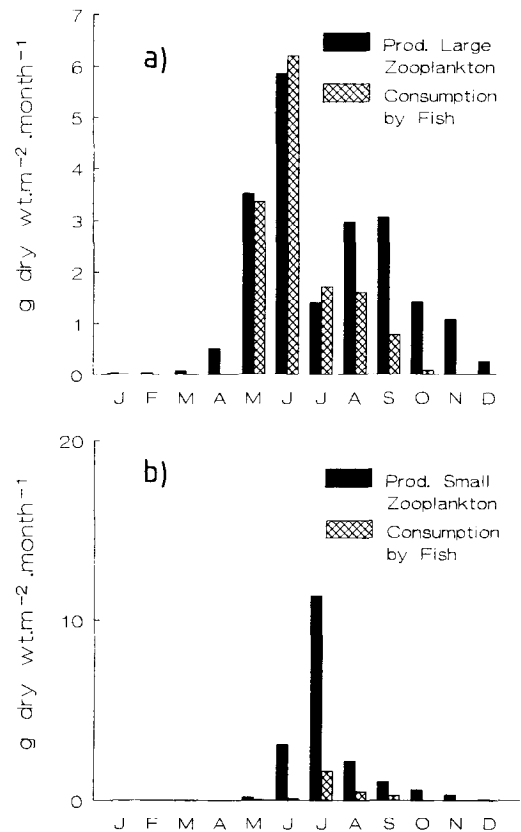

Fig. 3. Seasonal variation in the production of the zooplankton (g dry wt m^{-2} month^{-1}), and the total fish consumption (g dry wt m^{-2} month^{-1}). a. Production and consumption by fish of large zooplankton (*D. hyalina* and cyclopoid copepods), b. Production and consumption by fish of small zooplankton (*Bosmina* spp. and *Chydorus sphaericus*).
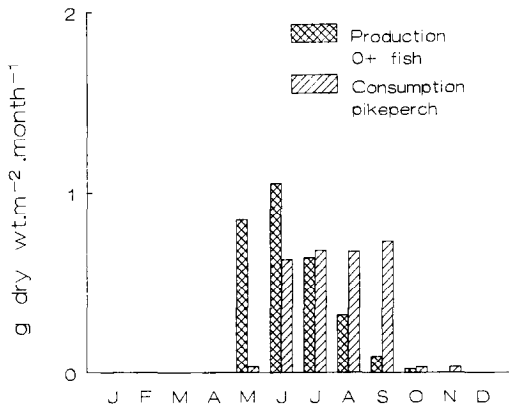
Fig. 4. Seasonal variation in the total production of O + fish (g dry wt m^{-2} month^{-1}) and the consumption by pikeperch (g dry wt m^{-2} month^{-1}).

In June O + fish only rarely fed on *D. hyalina*, whereas ≥ I + bream fed almost exclusively on *D. hyalina* at that time.

During the growth season almost the entire production of the large zooplankton was eaten by the planktivorous fish (Fig. 3a), in contrast with a very small proportion of the small zooplankton production that was consumed (Fig. 3b).

Planktivorous fish production and consumption by piscivorous fish

During winter and spring, ≥ I + pikeperch fed predominantly on I + fish, and occasionally also on II + fish. Larger prey cannot be handled by the 30–40 cm long predators. From June onwards pikeperch fed on the freshly recruited O + fish. Gut contents analysis does not indicate selection for certain fish species, and hence smelt which was most abundant was also eaten most often. In the first part of the growing season (May–June) pikeperch consumed only a small part of the O + fish production, later in the year, however, the consumption of pikeperch exceeded the production of O + fish (Fig. 4).

Discussion

On an annual basis planktivorous fish consumed 40% of the total zooplankton production. This may seem low, but the food chain efficiency is much higher if only the large zooplankton is taken into account; 70% of the large zooplankton production is consumed by planktivorous fish. Since ≥ I + bream is not eaten by II + and III + pikeperch the food chain efficiency of pikeperch consumption is only moderate. But the efficiency is very high if only O + fish are taken into account, since the O + production eaten by pikeperch is ca. 95% (Fig. 5).

Smelt only rarely fed on *D. hyalina* in June, although the biomass of this prey is considerable at that time, and from mid June onwards no morphological limitations exist to prevent consumption of even the largest *D. hyalina* present. We cannot explain this, but it could well be related to the earlier feeding history, namely feeding on copepods (Furnass, 1979). This not feeding on *D. hyalina* by O + smelt in June is offset by the high predation pressure of ≥ I + bream on *D. hyalina*; almost 100% of the bream diet consists of *D. hyalina*, which results in a consumption of almost the entire production of large zooplank-
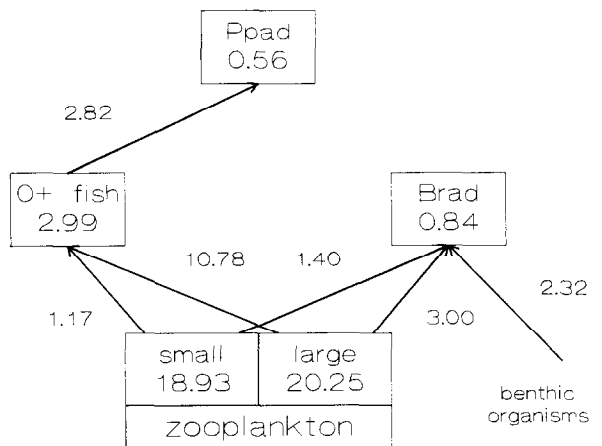

Fig. 5. The Tjeukemeer foodweb in 1978. Production (within squares), and consumption (next to arrows) of the most important groups (g dry wt m^{-2} year^{-1}). Ppad = ≥ I + pikeperch, Brad = ≥ I + bream, O + fish = Total of O + smelt, O + pikeperch, and O + perch.

ton in June. In July the O + fish exerts a very high predation pressure upon the large zooplankton, which wipes out almost all large zooplankton. The low biomass of large zooplankton in July causes both the O + fish and ≥ I + bream to switch to feeding on small zooplankton which is consumed in substantial amounts at that time. From August onwards the production of the large zooplankton is higher than the consumption of the planktivorous fish, and this production is thought to be lost for the next trophic level. During 1978 the size of the O + fish stock was moderate, and consequently the predation pressure on the zooplankton was moderate too. In years when the O + fish stock is larger, the large zooplankton will be reduced to low levels during July–September, and a greater part of the small species will be utilized by the O + fish (van Densen, 1985). Hence, a low utilization of the small zooplankton species by fish is characteristic of years with low or moderate O + fish stocks. Most of this small zooplankton production is probably consumed by invertebrate predators (i.e. cyclopoid copepods, *Leptodora kindtii*, water mites). When high O + fish stocks reduce the biomass of large zooplankton, large bream is forced to switch to a benthic feeding behaviour, because of its filter feeding habit and hence its relatively low ability to feed on small zooplankton (Lammens, 1984). Since the biomass of benthic invertebrates is generally low in Tjeukemeer the condition of ≥ I + bream will deteriorate (Lammens, 1982).

At first glance there is a poor agreement between the production of O + fish and its consumption by pikeperch. Pikeperch consumption is too low in the beginning of the year and too high at the end. However, this does not mean that the O + biomass produced in the beginning of the year is lost for consumption by pikeperch, since most of the production is accumulated in O + fish biomass. This O + fish biomass is still available for the pikeperch in the autumn when O + fish production is lower than the consumption by pikeperch. This conclusion is corroborated by the observation that O + fish biomass starts to decrease at the same time (July–August) that pike-

perch consumption exceeds O + fish production.

It can be concluded that the seasonal variations in production and consumption are large, caused mainly by differences in the water temperature (range 1–23 °C). Both zooplankton (Vijverberg, 1980) and fish growth (Mooij & van Tongeren, 1990) are very much temperature related. Temperature also affects the spawning and recruitment cycle of the fish, and hence the time O + fish enters the system. Being the most important zooplankton consumer, as well as the most important prey group, O + fish plays a key role in the Tjeukemeer food web.

Acknowledgements

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