

Impact of coelenterate predation on larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* stock in the western Wadden Sea

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ABSTRACT: During the seasonal immigration of plaice and flounder larvae into the Dutch Wadden Sea in spring, the coelenterates *Pleurobrachia pileus* L. and *Aurelia aurita* L. have been positively identified as predators of both flatfish species. Evidence for a causal relation between outbursts of the predatory coelenterates and the observed abrupt termination of larval flatfish immigration is found in (1) the coincidence of increases in coelenterate numbers and decreases in larval densities, (2) positive observations of larval flatfish in coelenterate stomach contents, (3) a comparison between food demand of the coelenterate population and standing stock of the pelagic food resource at that time. Impact of this predation on plaice recruitment is expected to be small, since most larvae have already completed their immigration into the Wadden Sea when the coelenterate outburst starts. Although the coelenterate outburst occurs at about the same time every year, their predation may have a density-dependent component, since the timing of plaice immigration seems to be related to abundance, with larger year-classes arriving later than smaller ones. For flounder larvae the impact will be greater, because of the shorter period of immigration and the coincidence between coelenterate outburst and maximum flounder abundance.

INTRODUCTION

Spawning of both plaice *Pleuronectes platessa* L. and flounder *Platichthys flesus* L. takes place from about December until March in the deeper and more saline parts of the southern North Sea (Harding et al. 1978). The developing eggs and larvae are transported by residual currents towards the coastal zone (Houghton & Harding 1976, Talbot 1976, 1978), from where the larvae migrate into the nursery areas (Creutzberg et al. 1978). Inside the nursery areas, of which the Wadden Sea is probably the most important one (Creutzberg & Fonds 1971, Zijlstra 1972), the larvae settle, mainly on the tidal flats (Bergman et al. 1980).

During transport from the spawning grounds towards the nurseries, the eggs and larvae suffer a heavy mortality, and their numbers are severely reduced (Harding et al. 1978). This mortality may be caused by either predation on the drifting eggs and larvae, or starvation of the larvae. Herring has been shown to prey selectively on plaice eggs, although it seems unlikely that this species represents the main cause of mortality (Daan 1976, Daan et al. 1984).

Coelenterates are also numerous, and known as potential predators. However, Tungate (1975) found that in the open sea their development starts too late to consider them significant predators on flatfish larvae, and plaice in particular.

In coastal waters the situation may be different since the larvae reach these areas 1 or 2 mo later. According to previous studies, larval immigration ends abruptly every year at the beginning of May (Creutzberg et al. 1978), while at the same time an outburst of coelenterates occurs near the Wadden Sea inlets (van der Baan 1980a, b, c). Among these coelenterates several species (e.g. the ctenophore *Pleurobrachia pileus*, the scyphomedusa *Aurelia aurita* and the hydromedusae *Sarsia tubulosa* and *Eutonina indicans*) are known as potential predators of fish larvae, under laboratory (Fraser 1969, Greve 1972, Arai & Hay 1982, Bailey & Batty 1983, Bailey 1984) or natural conditions (Möller 1980b, 1984, Arai & Hay 1982).

In this study attention is paid to the possible impact of coelenterate predation on the late pelagic larval stages of plaice and flounder entering the Wadden Sea nursery area. The following 3 questions are discussed:

(1) Is there any proof of significant predation by coelenterates on flatfish larvae in the area? (2) Can the sudden break-down in the immigration of flatfish larvae be due to predation by coelenterates? (3) How large can the impact be of coelenterate predation on larval stocks of these 2 flatfish species?

MATERIAL AND METHODS

From February to June in 1980, 1981, and 1982, samples were taken in a number of tidal gullies (5 to 10 m depth) surrounding a major settling area for flatfish larvae, the Balgzand, at the main entrance of the western part of the Dutch Wadden Sea (Fig. 1).

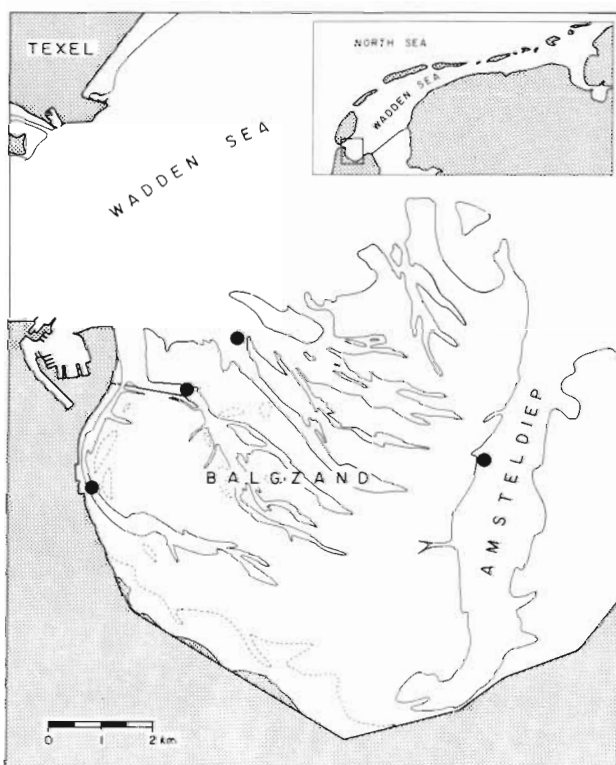


Fig. 1. Map of western part of Dutch Wadden Sea. Sampling stations (●) are indicated

Depending on weather conditions, from 1 to 4 tidal cycles were sampled per week, mostly during daytime but also partly during night-time. During each flood and ebb tide at least 5 double-oblique hauls were made at current velocities of over 20 cm s^{-1} . The nets were made of polyamid plankton gauze (Monodur no. 2000, 2 mm aperture) with an opening of 0.7 m^2 and a length of 5 m. The amount of water passing through the net was measured with a flow-meter mounted in the mouth of the net. The porosity (0.59) and the mesh area (12 m^2) of the net (definitions according to Smith et al.

1968) were large enough to prevent any serious clogging and overflow even during the spring bloom of the algae *Phaeocystis pouchetii*. The general reduction of water flow through the net was about 10% and independent of current velocity. However, during and after the bloom of *P. pouchetii*, this reduction increased to about 30% (van der Veer & Sadée 1984). Depending on current velocity, haul duration varied from 10 to 45 min and sample size between 300 and 2000 m^3 water filtered.

After the net washdown, all material was preserved in a 4% formalin seawater solution and afterwards sorted in the laboratory. Flatfish larvae were classified according to mm total length classes. No correction was made for shrinkage, since both Lockwood (1973) and Dapper (1978) found that, at least for plaice, shrinkage in 4% formaldehyde was negligible. Either the total catch or a subsample of the coelenterates, with the exception of *Aurelia aurita* specimens larger than 4 cm diameter, was put into a flat basin and photographed on slides. From these slides, numbers of the various species were counted on a projection screen. From each catch approximately 100 individual *Pleurobrachia pileus* were measured in mm classes, allowing a correction for shrinkage of 20% for all size classes (van der Veer & Sadée 1984). *A. aurita* specimens smaller than 4 cm were treated in the same way, allowing 10% shrinkage for all size classes (van der Veer & Oorthuysen 1985), whereas the larger specimens were measured alive to the nearest 0.5 cm below. Sizes of the umbrellas of *Sarsia tubulosa* and *Eutonina indicans* were not recorded. Subsamples were fixed for stomach content analysis.

No correction was made for net efficiency. The relatively small swimming speed of the larvae (Bailey 1984) and of the coelenterates compared to the high current velocities during fishing – up to 120 cm s^{-1} (van der Veer & Sadée 1984) – and the low reduction of water flow through the net both suggest that net avoidance does not seem likely. Moreover, plaice and flounder larvae caught during daytime showed an almost equal size distribution to those caught during the subsequent night (Table 1). In the case of an increasing net avoidance with length, a larger mean length during night-time would be expected. All flatfish and coelenterate data were expressed in numbers of individuals per 1000 m^3 ($\text{ind } 1000\text{m}^{-3}$) and arithmetic mean densities were calculated for each week.

The variance consistently surpassed the arithmetic mean by a large margin for all species, which pointed to uneven distributions in the water mass. For such distributions, confidence limits can be computed by using the factors derived from a $\log(x+1)$ transformation and applying them to the arithmetic mean of the samples (Elliot 1977). For 95% confidence limits, these

Table 1. Mean size distribution of plaice and flounder larvae caught during day- and subsequent night-time in 1981

Size (mm)	No. of plaice		No. of flounder	
	Day	Night	Day	Night
6	-	-	37	24
7	1	1	145	115
8	1	2	131	52
9	9	15	11	1
10	20	24	-	-
11	5	7	-	-
12	2	2	-	-
Mean	10.3	9.9	7.8	7.7

factors of the Student's t distribution ranged between 2.09 and 2.02, depending on the number of hauls made (20 to 40). Therefore, the 95% confidence limits would lie between 47 and 209% of the mean.

Part of the results concerning *Pleurobrachia pileus* and *Aurelia aurita* have already been published (van

der Veer & Sadée 1984, van der Veer & Oorthuysen 1985).

Stomach contents of coelenterates were examined in preserved material weekly in 1981 and 1982.

RESULTS

Flatfish larvae

Fig. 2 shows the abundances of flatfish larvae in the plankton as a weekly average over all sampling stations in 1980, 1981 and 1982. Plaice larvae were present from the beginning of March in these years. Densities increased in March and April to peak numbers of about 8 to 18 ind 1000m⁻³. In all years a sharp decrease in numbers occurred at the end of April, resulting in a nearly complete absence after the beginning of May. The total duration of plaice larval immigration was restricted to March and April. Weekly mean length of the larvae fluctuated slightly in all 3 yr,

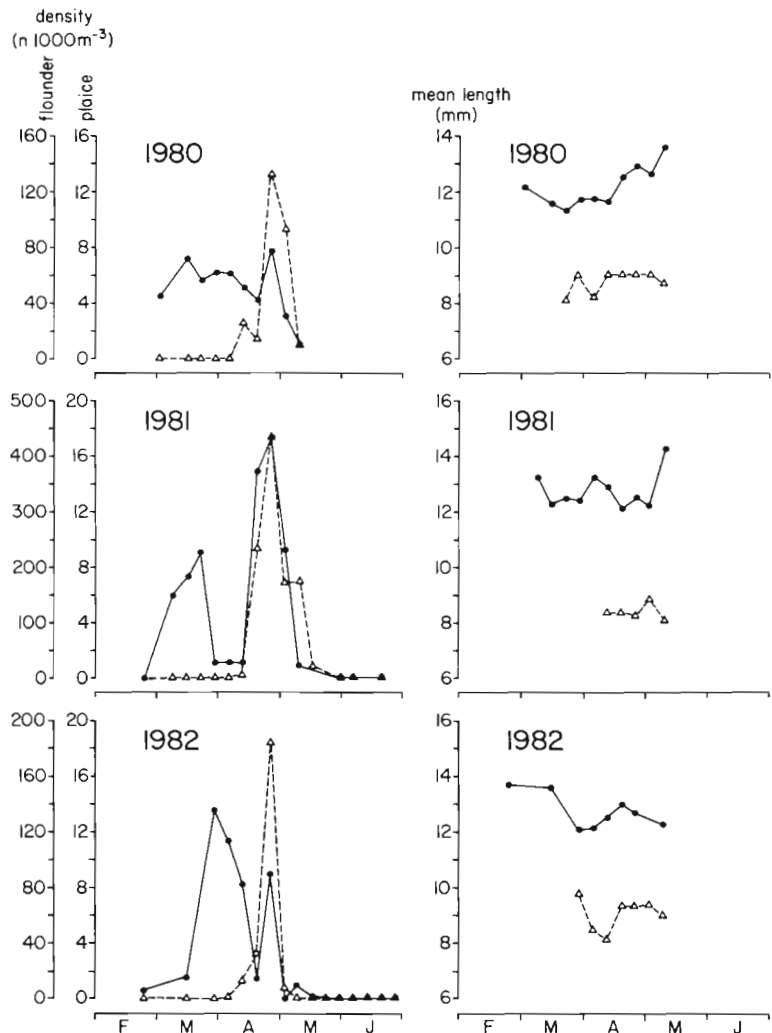


Fig. 2. *Pleuronectes platessa* and *Platichthys flesus*. Mean tidal abundance (ind 1000m⁻³) and mean length (mm) of pelagic plaice (—) and flounder (---) larvae near the entrance of the Wadden Sea in 1980, 1981 and 1982, based on 20 to 40 hauls per week

between 12 and 14 mm, without consistent trends between years.

The first flounder larvae arrived about 1 mo later than plaice; in none of the 3 yr was this before the beginning of April. Maximum numbers of flounder larvae were considerably higher than those of plaice: 135 to 450 ind 1000 m^{-3} . As for plaice, densities of flounder larvae showed a sharp decrease at the end of April leading to complete absence from the beginning of May. In contrast to plaice, the immigration of flounder was restricted to about 1 mo. The mean length of the larvae was on average about 8 to 9 mm, and always significantly smaller than the mean length of the plaice larvae.

Coelenterate species

The ctenophore *Pleurobrachia pileus* showed low abundances until mid-April in all 3 yr (Fig. 3). In the second half of April numbers started to increase

slowly, but it was not until the end of April that an outburst was observed up to maximum numbers of between 14 000 and 17 000 ind 1000 m^{-3} . After this peak, densities dropped sharply to less than 1000 ind 1000 m^{-3} at the end of June. Mean diameter increased over the period of observation from about 4 mm in March up to 12 mm in June.

The abundance of the scyphomedusa *Aurelia aurita* showed a similar development in 1981 and 1982 (Fig. 4). After being absent up to the end of April, its numbers increased sharply to maxima of 200 to 500 ind 1000 m^{-3} . Thereafter densities declined to a low level. Average bell size increased in both years from 2 cm in April to 16 to 24 cm in June.

The hydromedusae found in 1981 and 1982 were *Sarsia tubulosa* and *Eutonina indicans*, both appearing at the end of April (Fig. 5). Their patterns of abundance closely resembled those of *Pleurobrachia pileus* and *Aurelia aurita*, with peak densities of 2500 to 5500 ind 1000 m^{-3} for *S. tubulosa* and 22 ind 1000 m^{-3} for *E.*

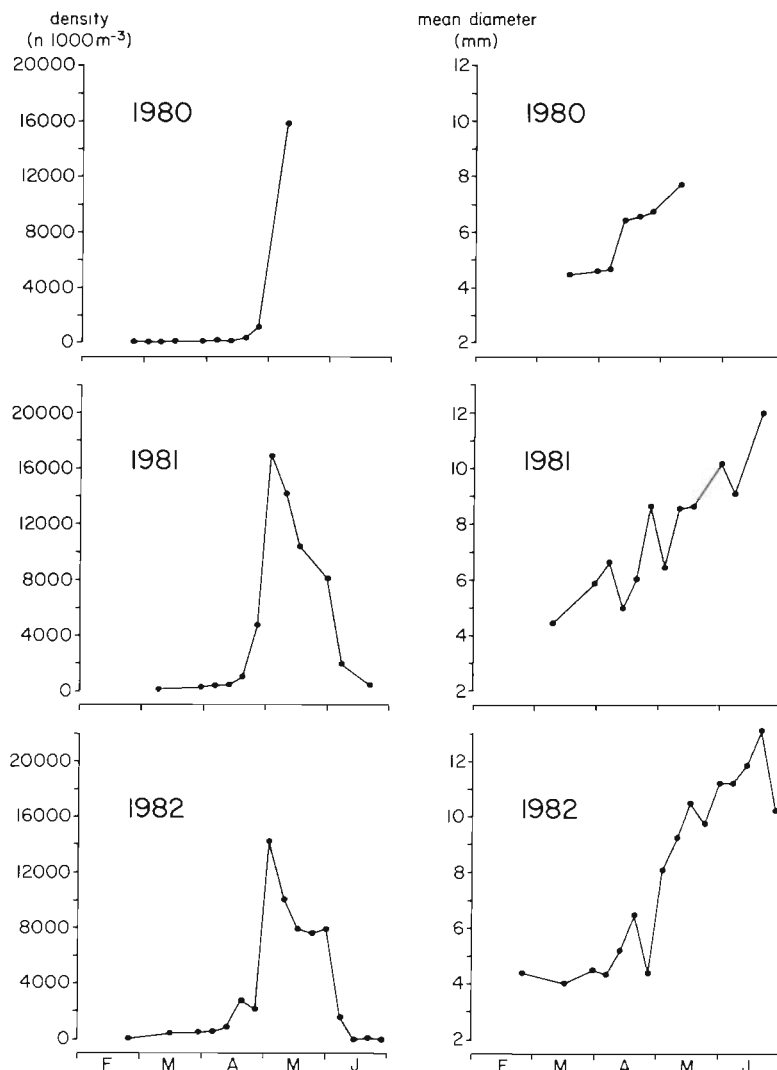


Fig. 3. *Pleurobrachia pileus*. Mean tidal abundance (ind 1000 m^{-3}) and mean diameter (mm) near the entrance of the Wadden Sea during larval flatfish immigration in 1980, 1981 and 1982, based on 20 to 40 hauls per week

Fig. 4. *Aurelia aurita*. Mean tidal abundance (ind 1000m⁻³) and mean bell size (cm) near the entrance of the Wadden Sea during larval flatfish immigration in 1981 and 1982, based on 20 to 40 hauls per week

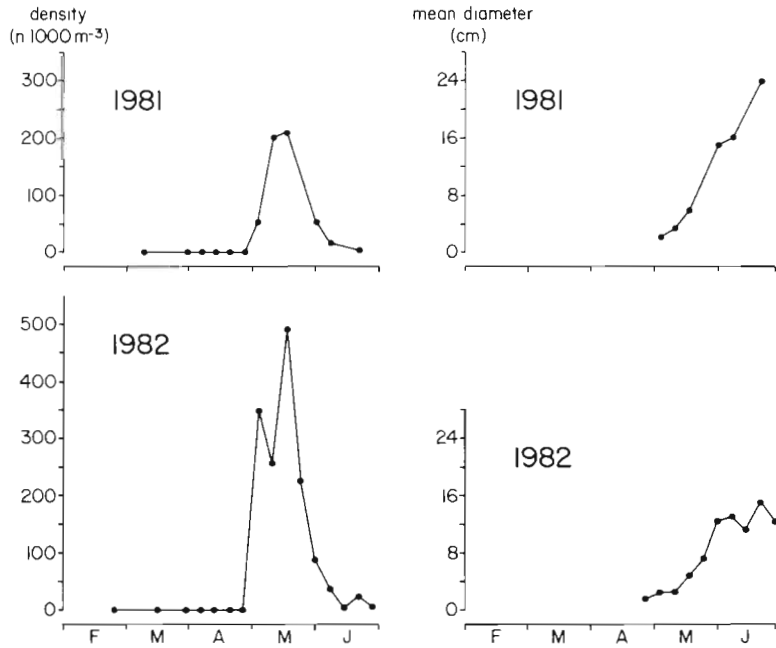
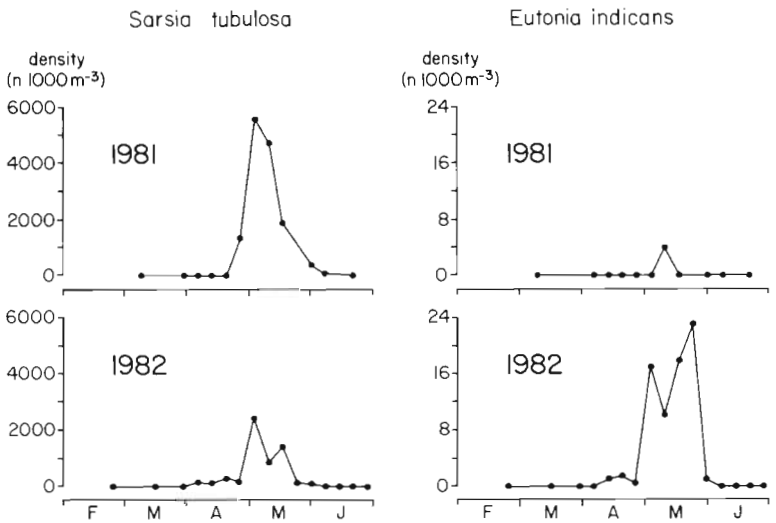


Fig. 5. *Sarsia tubulosa* and *Eutonina indicans*. Mean tidal abundance (ind 1000m⁻³) near the entrance of the Wadden Sea during larval flatfish immigration in 1981 and 1982 based on 20 to 40 hauls per week



indicans. In 1981 hardly any *E. indicans* were found up to the end of June.

Stomach content analysis

Table 2 summarizes all data obtained on the stomach contents of preserved coelenterates in 1981 and 1982. Predation on flatfish larvae was positively identified in both *Pleurobrachia pileus* and *Aurelia aurita*. With 1 exception, only flounder larvae were found. Possible regurgitation of stomach content during preservation was investigated for *Pleurobrachia pileus*. 200 individuals were checked before and after fixation on a 4%

formalin solution. The percentage of animals with a full stomach decreased from 66 to 4% after fixation, which means that 95% of the *P. pileus* had lost their stomach content.

DISCUSSION

The role of both ctenophores and medusae as carnivores among the macroplankton is well established. Their rapid population growth and mass occurrence can only be understood by the exertion of a heavy predation on the zooplankton community (Kremer 1976, Möller 1980a). Their diet spectrum is wide and

Table 2. Numbers of flatfish larvae detected in the stomachs of preserved coelenterates in 1981 and 1982. N: number of stomachs observed (roughly estimated); n: number of flatfish larvae observed; f: flounder; p: plaice

Date	<i>Pleurobrachia pileus</i>		<i>Aurelia aurita</i>		<i>Sarsia tubulosa</i>		<i>Eutonina indicans</i>	
	N	n	N	n	N	n	N	n
1981								
20–24 Apr	2000	1 (f)	–	–	300	0	–	–
27 Apr–1 May	3000	2 (f)	50	0	400	0	–	–
4–8 May	3000	2 (f)	50	1 (f)	400	0	–	–
11–15 May	3000	2 (f)	200	0	600	0	–	–
1982								
26 Apr–1 May	2000	1 (f)	150	1 (p)	200	0	40	0
3–8 May	2000	1 (f)	150	0	200	0	40	0

varies considerably between species. Some, e.g. the ctenophores *Beroë gracilis* and *B. cucumis*, feed exclusively on other coelenterates (Greve 1970), while other species seem to prefer copepods, barnacle larvae or fish larvae (Lebour 1922, 1923).

Evidence for fish predation by coelenterates is provided by a number of authors (Table 3). Most of the experimental work has been carried out with *Aurelia aurita*, and indicates that a number of fish larvae may fall prey to these species. Under natural conditions fish predation by coelenterates has also been observed, however mostly from preserved samples. Predation on plaice or flounder larvae has only been reported for *Pleurobrachia pileus* by Lebour (1923) and for *A. aurita* by Lebour (1923), Fraser (1969), Bailey & Batty (1983) and Bailey (1984).

Coelenterate predation on flatfish larvae in the open sea during drifting from the spawning grounds to the coastal nursery does not seem very likely. Tungate (1975) found, that at the time of the spring outburst of coelenterates, the patch of plaice larvae had already drifted towards the coastal zone. A comparison of the abundances of flatfish larvae and of coelenterates near the entrance to the Wadden Sea shows a different picture for the coastal area. At the end of April and the beginning of May plaice and flounder larvae immigrate in large numbers until the explosive increase of the various coelenterate species occurs, both in numbers and – since the increase in numbers is associated with increases in mean size – even more in biomass. Here, coelenterate predation on flatfish larvae seems a realistic possibility.

Table 3. Literature review of coelenterates known as potential fish predators and present in the coastal zone of the southern North Sea (van der Baan 1980a, b, c, this study) under laboratory and natural conditions

Species	Prey	Condition	Source
Ctenophores			
<i>Pleurobrachia pileus</i>	Sole	Laboratory	Greve 1972
	Plaice, herring	Natural	Lebour 1923
Scyphomedusae			
<i>Aurelia aurita</i>	Fish eggs and larvae	Laboratory	Lebour 1922
	Cod, flounder	Laboratory	Fraser 1969
	Herring	Laboratory	Arai & Hay 1982
	Herring	Laboratory	Bailey & Batty 1983
	Plaice, herring, flounder, turbot	Laboratory	Bailey & Batty 1983
	Plaice, flounder, cod, herring, turbot	Laboratory	Bailey 1984
	Flatfishes	Natural	Lebour 1923
	Herring	Natural	Müller 1980b
Hydromedusae			
<i>Sarsia tubulosa</i>	Herring	Laboratory	Arai & Hay 1982
	Herring	Natural	Arai & Hay 1982
<i>Eutonina indicans</i>	Herring	Laboratory	Arai & Hay 1982
<i>Phialidium hemisphericum</i>	Sole, other species	Laboratory	Lebour 1922
	Herring, sprat	Natural	Lebour 1923
<i>Rathkea octopunctata</i>	Herring, sprat	Natural	Lebour 1923

Coelenterate predation on flatfish larvae

Direct observations of attack and subsequent consumption of flatfish larvae under field conditions yield the best proof of predation. However, in estuarine areas such as the Wadden Sea, characterized by strong tidal currents and high turbidity (Postma 1954), such observations are practically unobtainable. Therefore, this study attempts to demonstrate predation by means of stomach content analysis of various potential predators, i.e. the coelenterate species. Such a stomach content analysis can be hampered by a number of factors which may bias the results, e.g. (1) feeding on flatfish larvae within the net during fishing and net handling; (2) regurgitation of stomach contents during net handling or fixation; (3) digestion of food remains before coelenterates were killed; (4) identification problems in the case of partly digested stomach contents.

Feeding of coelenterates during plankton hauls does not seem likely, because most of the fish larvae ingested were already partly digested. Regurgitation did occur in this study during fixation of *Pleurobrachia pileus*, although other investigators (Seip & Seip-Ottema 1981) did not find such an effect. In this study, regurgitation may be considered an important factor, which results in an underestimation of the predation rate by a factor of 20. For *Aurelia aurita* and the 2 hydromedusae no such data are available. Digestion time of fish larvae in *P. pileus* seems to be of the order of a few hours (Reeve & Walter 1978). Since net handling took about 15 min digestion can be considered an insignificant factor as compared to regurgitation. A further bias in the results may be related to identification problems of partly digested fish larvae. This will also lead to underestimation of actual predation pressure.

The problem of regurgitation together with the low ratio of fish larva to potential predator abundance at the time of the coelenterate outburst (approximately 1 flatfish larva to 100 coelenterates) make the chances of observing larvae in coelenterate stomachs very small. Nevertheless, in 1981 and 1982 respectively, 7 and 2 flatfish larvae were identified in stomachs of *Pleurobrachia pileus* and *Aurelia aurita*. No larvae were found in the stomachs of the hydromedusae species.

Table 4. Number of flatfish larvae detected in stomachs of living *Pleurobrachia pileus* in 1984. p: plaice; f: flounder

Date	No. of <i>P. pileus</i> examined	No. of larvae detected
23 Apr	270	1 (p)
7 May	445	12 (f)

These scarce results show, be it qualitatively, that coelenterate predation on flatfish larvae does occur in the coastal zone near the Wadden Sea at the end of April and the beginning of May. The species consuming plaice and flounder larvae in this study correspond with those mentioned by Lebour (1923).

Effects of coelenterate predation on flatfish immigration

Actual predation by coelenterates may be much higher than is suggested from stomach content analysis. Due to underestimations caused by regurgitation and identification problems, at least $20 \times 9 = 180$ flatfishes will in fact have been consumed by the 15 000 *Pleurobrachia pileus* investigated (Table 2), which means predation by about 1% of the ctenophores within the digestion time i.e. a few hours (Reeve & Walter 1978). Analysis of freshly caught, not preserved, material in early May 1984 showed as expected even more larvae in *P. pileus* stomachs: 12 flatfish larvae in 445 living ctenophores at an abundance of 18 plaice and 215 flounder larvae 1000m^{-3} . This means that 2.5% of the *P. pileus* population had consumed a flatfish larva shortly before collection (Table 4). Converted to the total population of about 14 000 ind 1000m^{-3} at the beginning of May, this would mean a predation of at least 140 flatfish larvae 1000m^{-3} per few hours, based on stomach content analysis of preserved samples (corrected for regurgitation only), and of 350 larvae 1000m^{-3} based on analysis of freshly caught animals. In both cases it implies a total removal of all flatfish larvae by *P. pileus* within the time needed for digestion. Moreover other coelenterates, at least *Aurelia aurita*, would also contribute to the consumption of flatfish larvae.

The effect of coelenterate predation is also indicated by the coincidence between the coelenterate outburst and larval depletion. During all 3 yr of this study, the sharp increase in numbers of coelenterates coincided with a dramatic drop in flatfish numbers. Creutzberg et al. (1978) reported that in earlier years (1974, 1975 and 1977), larval plaice immigration stopped at the same time of year. Although coelenterates were not quantified at that time, qualitative observations pointed to coincident outbursts of *Pleurobrachia pileus* (Creutzberg pers. comm.).

A comparison of consumption rates of predatorial coelenterates with biomasses of flatfish larvae and other food items may be another indirect way to assess whether coelenterate predation might be responsible for the abrupt break-down in larval abundance. Consumption figures of *Pleurobrachia pileus* and *Aurelia aurita* were obtained from van der Veer & Sadée (1984)

and van der Veer & Oorthuysen (1985). These rates are based on biomass data, which were estimated from abundance figures combined with diameter-weight relations. For these relations, published data were used, which showed good correspondence with a number of determinations by the author. For a detailed description see van der Veer & Sadée (1984) and van der Veer & Oorthuysen (1985). The resulting total consumption of the 2 species, in g of carbon per 1000 m³ per day (g C 1000m⁻³ d⁻¹), is shown in Fig. 6. This

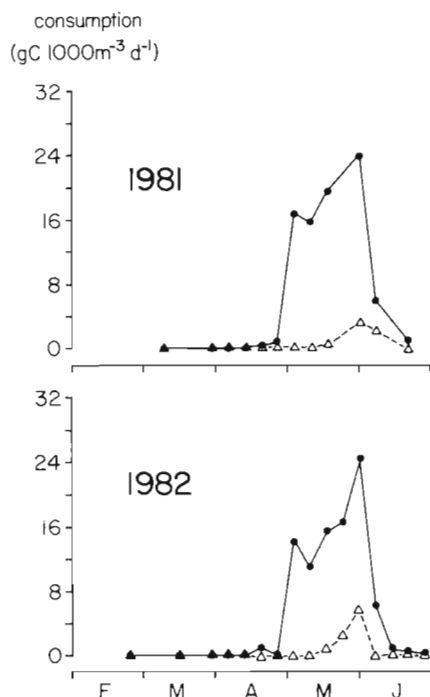


Fig. 6. Estimated total daily consumption (g C 1000m⁻³ d⁻¹) by the predatory coelenterates *Pleurobrachia pileus* (—) and *Aurelia aurita* (---) near the entrance of the Wadden Sea in 1981 and 1982

figure is probably an overestimation, because previous work revealed that *P. pileus* does not seem to encounter optimal feeding conditions in the coastal zone (van der Veer & Sadée 1984). By assuming a mean carbon content of 0.7 mg C per flatfish larva (Kuipers pers. comm.), the total biomass of flatfish larvae (mg C 1000m⁻³), can be computed for the 3 yr (Fig. 7). At the end of April peak values of between 100 and 320 mg C 1000m⁻³ are reached, mainly consisting of flounder larvae. Other larval fish species present in the same period, mainly herring and sprat, represent a smaller biomass of about 50 mg C 1000m⁻³ (Corten & van de Kamp 1979, Kuipers pers. comm.). Together with the main food source of the coelenterates, the zooplankton, with a biomass of about 40 to 60 g C 1000m⁻³ and a production of about 0.10 d⁻¹ in this area in the begin-

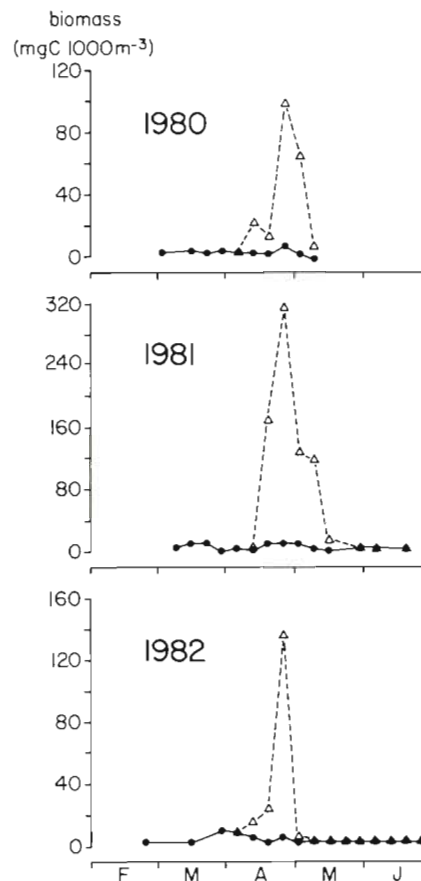


Fig. 7. *Pleuronectes platessa* and *Platichthys flesus*. Mean tidal biomass (mg C 1000m⁻³) of plaice (—) and flounder (---) larvae near the entrance of the Wadden Sea in 1980, 1981 and 1982

ning of May (Fransz 1981), it is clear that consumption by coelenterates appears to be very large compared with the standing stock of the food resources. According to this approach a virtual extinction of the flatfish larvae after the end of April through coelenterate predation might well be possible.

This predation process will not be limited to the Wadden Sea entrance. Flatfish larvae, entering the Wadden Sea on the tidal currents, will already have met the screen of predatory coelenterates somewhere offshore in the coastal area. Therefore, the actual predation process can be expected to last much longer than the period between larval immigration and subsequent settling on the tidal flats as measured within the boundary of the nursery.

Impact of coelenterate predation on larval flatfish populations

Coelenterate predation can affect the recruitment of a fish species. In Kiel Bight the scyphomedusal jelly-

fish *Aurelia aurita* consumes large amounts of yolk-sac herring larvae and reduces the population size considerably (Möller 1984). For flatfish larvae, predation by coelenterates seems to be dependent on larval size, at least as far as *A. aurita* is concerned (Bailey 1984). Because of their smaller size, flounder larvae will be more susceptible to predation than plaice larvae. Plaice and flounder also differ as to their behaviour after an encounter with a predator. Plaice larvae are more reactive than flounder (Bailey 1984), which may decrease the risk of predation.

A major impact of coelenterate predation on the recruitment of plaice seems unlikely, because in all 3 yr immigration of the larvae started in late February and had thus already lasted for 2 mo when the outburst of coelenterates occurred. Therefore, most of the larvae would have passed largely unaffected and have settled on the tidal flats of the Wadden Sea before serious coelenterate predation started. The onset of the coelenterate outburst occurs at approximately the same time every year. A significant moderating effect on between-year fluctuations of the larval stock can only be expected if the timing of larval immigration is related to the abundance of the year-class. This has indeed been suggested by Zijlstra et al. (1982) and by this study; larger year-classes show a somewhat delayed arrival, from March to April. Therefore, the coelenterate-induced mortality might have a density-dependent component, reducing the between year-class fluctuations.

For flounder the processes determining year-class strength are less known. Neither for the pelagic nor for the demersal phase have detailed studies been carried out. Larval immigration of flounder shows a regular pattern similar to that of plaice in all 3 yr. However, since it starts 1 mo later, the explosive outburst of predatory coelenterates coincides with maximum flounder immigration. Moreover, flounder larvae may be more exposed to predation because of their smaller size. A much greater impact on flounder is suggested by the larger numbers of larvae found in coelenterates stomachs. However, more insight into the fate of flounder after settlement is required before the precise effect can be evaluated.

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LITERATURE CITED

- Arai, M. N., Hay, E. (1982). Predation by medusae on Pacific herring (*Clupea harengus pallasii*) larvae. *Can. J. Fish. Aquat. Sci.* 39: 1537–1540
- Baan, S. M. van der (1980a). Hydromedusae in the surface water around the 'Texel' lightvessel. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel, 1980–1, p. 1–33
- Baan, S. M. van der (1980b). Overzicht macro-plankton onderzoek bij het lichtschip 'Texel', 1961–1966. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel, 1980–7, p. 1–20.
- Baan, S. M. van der (1980c). The seasonal occurrence of scyphomedusae in surface waters near the 'Texel' lightvessel. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel, 1980–9, p. 1–18
- Bailey, K. M. (1984). Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. *Mar. Biol.* 79: 303–309
- Bailey, K. M., Batty, R. S. (1983). A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. *Mar. Biol.* 72: 295–301
- Bergman, M. J. N., Spliethoff, P. J., Veer, H. W. van der (1980). De ecologie van 0-groep schol (*Pleuronectes platessa* L.) op het Balgzand. Deel I: Aantalsverloop, verspreiding en getijdenmigratie. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel, 1980–9, p. 1–40
- Corten, A., Kamp, G. van de (1979). Abundance of herring larvae in the Dutch Wadden Sea as a possible indication of recruitment strength. *Coun. Meet. int. Coun. Explor. Sea*, C. M.-ICES/H: 26, p. 1–5
- Creutzberg, F., Fonds, M. (1971). The seasonal variation in the distribution of some demersal fish species in the Dutch Wadden Sea. *Thassia jugosl.* 7: 13–23
- Creutzberg, F., Eltink, A. T. G. W., Noort, G. J. van (1978). The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. In: McLusky, D. S., Berry, A. J. (ed.), *Physiology and behaviour of marine organisms*, Proc. 12th Europ. mar. biol. Symp. Pergamon Press, Oxford, New York, p. 243–251
- Daan, N. (1976). Some preliminary investigations into predation on fish eggs and larvae in the Southern North Sea. *Coun. Meet. int. Coun. Explor. Sea* C. M.-ICES/L: 15, p. 1–5
- Daan, N., Rijnsdorp, A. D., Overbeeke, G. R. (1984). Predation of plaice and cod eggs by North Sea herring. *Coun. Meet. int. Coun. Explor. Sea* C. M.-ICES/L: 13, p. 1–16
- Dapper, R. (1978). De Balgzand scholgegevens 1975, 1976, 1977. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel 1978–12, p. 1–53
- Elliot, J. M. (1977). Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwat. biol. Ass.*, *Scient. Publ. No.* 25, p. 1–160
- Franz, H. G. (1981). Quantitative data on the plankton of the Wadden Sea proper. In: Dankers, N., Kühl, H., Wolff, W. J. (ed.) *Invertebrates of the Wadden Sea*. Balkema, Rotterdam, p. 125–133
- Fraser, J. H. (1969). Experimental feeding of some medusae and chaetognaths. *J. Fish. Res. Bd Can.* 26: 1743–1762
- Greve, W. (1970). Cultivation experiments on North Sea ctenophores. *Helgoländer Meeresunters.* 20: 304–317
- Greve, W. (1972). Ökologische Untersuchungen an *Pleuro-*

- rachia pileus* 2. Laboratoriumuntersuchungen. Helgoländer Meeresunters. 23: 141–164
- Harding, D., Nichols, J. H., Tungate, D. S. (1978). The spawning of plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. Rapp. P.-v. Réun. Cons. int. Explor. Mer 172: 102–113
- Houghton, R. G., Harding, D. (1976). The plaice of the English Channel: spawning and migration. J. Cons. int. Explor. Mer 36: 229–239
- Kremer, P. (1976). Population dynamics and ecological energetics of a pulsed predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley, M. (ed.) Estuarine processes, Vol I, Uses, stress and adaptation to the estuary. Academic Press, New York, p. 197–215
- Lebour, M. (1922). The food of plankton organisms. J. mar. biol. Ass. U.K. 12: 644–677
- Lebour, M. (1923). The food of plankton organisms II. J. mar. biol. Ass. U.K. 13: 70–92
- Lockwood, S. J. (1973). Weight and length changes of 0-group plaice (*Pleuronectes platessa* L.) after preservation in 4 % neutral formalin. J. Cons. int. Explor. Mer 35: 100–101
- Möller, H. (1980a). Scyphomedusae as predators and food competitors of larval fish. Ber. dt. wiss. Kommn. Meeresforsch. 28: 90–100
- Möller, H. (1980b). Population dynamics of *Aurelia aurita* in Kiel Bight, Germany (FRG). Mar. Biol. 60: 123–128
- Möller, H. (1984). Reduction of a larval herring population by jellyfish predator. Science 224: 621–622
- Postma, H. (1954). Hydrography of the Dutch Wadden Sea. Archs néerl. Zool. 10: 405–511
- Reeve, M. R., Walter, M. A. (1978). Nutritional ecology of ctenophores. A review of recent research. In: Russell, F. S., Young, M. (ed.) Advances in marine biology, Vol 15. Academic Press, London, p. 249–289
- Seip, P., Seip-Ottema, M. (1981). De betekenis van predatie voor de dichtheidsafname van de calanoïde copepoden in juni/juli in de zuidelijke bocht van de Noordzee. Interne Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel, 1981–3, p. 1–66
- Smith, P. E., Counts, R. C., Clutter, R. I. (1968). Changes in filtering efficiency of plankton nets due to clogging under tow. J. Cons. perm. int. Explor. Mer 32: 232–248
- Talbot, J. W. (1976). The dispersal of plaice eggs and larvae in the Southern Bight of the North Sea. J. Cons. int. Explor. Mer 37: 221–248
- Talbot, J. W. (1978). Changes in plaice larval dispersal in the last fifteen years. Rapp. P.-v. Réun. Cons. int. Explor. Mer 172: 114–123
- Tungate, D. S. (1975). The distribution and abundance of chaetognaths and the ctenophore *Pleurobrachia pileus* in the southern North Sea in 1968 and their importance as predators on plaice larvae and eggs. Fish. Lab. Tech. Rep. Ser. 18. Fish. Lab. Lowestoft, Suffolk, p. 1–31
- Veer, H. W. van der, Sadée, C. F. M. (1984). The seasonal occurrence of the ctenophore *Pleurobrachia pileus* in the western Dutch Wadden Sea. Mar. Biol. 79: 219–227
- Veer, H. W. van der, Oorhuysen, W. (1985). Abundance, growth and food demand of the scyphomedusa *Aurelia aurita* in the western Dutch Wadden Sea. Neth. J. Sea Res. 19: 38–44
- Zijlstra, J. J. (1972). On the importance of the Wadden Sea as a nursery area in relation to the conservation of the southern North Sea fishery resources. Symp. zool. Soc. Lond. 29: 233–258
- Zijlstra, J. J., Dapper, R., Witte, J. Y. (1982). Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea. Res. 15: 250–272

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