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The biology of the greater weever (*Trachinus draco*) in the commercial fishery of the Kattegat

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The scarce published literature on greater weever in western and northwestern European waters is reviewed and synthesized, along with a summary of a Danish investigation in the Kattegat for the years 1961–1973. Distribution, growth, mortality, migration, fecundity, abundance, and stock abundance in relation to the directed local commercial fishery are described. The greater weever has not been and still is not in any way protected by legislation or management, although it moves little, grows slowly, has high catchability, and has been exposed to high total mortality. Since the mid-1980s, directed fishing effort has declined, likely as a consequence of the decreasing catches, and because the effort applied through poundnets, which earlier produced about 40% of the total yield, has for other reasons almost halted. Total landings concomitantly decreased, and the current yield is now only by-catch from trawlers and from two or three 40-ft vessels occasionally directly targeting the species.

Keywords: abundance, distribution, fecundity, food and feeding, growth, migration, mortality, stock abundance.

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Introduction

The greater weever (*Trachinus draco*) ranges from the Black Sea, through the Mediterranean, to Atlantic coastal waters from Northwest Africa to Bergen (Norway), and the northern part of the Danish Straits (Whitehead *et al.*, 1989). In Denmark, it has been landed as a by-catch of a poundnet fishery along the western coast of the Kattegat (Figure 1) since at least 1834, for use as bait on longlines and locally also for human consumption (Krøyer, 1838). After the turn of the 20th century, the species was also sold as fodder for trout farming. After the second World War, the rapid development of mink and trout farming created increasing demand for fodder, which led to an overall increase in effort in the Danish industrial fishery deploying small-meshed gear. This development alarmed fishers in the area who fished protected demersal species. Among various proposals to restrict the industrial fishery, the need for protection of the greater weever was questioned, because specimens >25 cm constituted a valuable export for human consumption. Because little was known about its biology and stock status, investigations on the fishery in the central and southern Kattegat, and on the life history of the species, were initiated in 1961 (Bagge, 1966), including port and research vessel sampling, and tagging. Sampling continued until 1973, although more samples have been taken recently. My main aim here is to describe the results as a reference for future studies.

Material and methods

The area

The waters of the Kattegat are strongly stratified, with a distinct halocline at 12–15 m during the whole year, and a thermocline present in summer and early autumn. Temperature varies between 1 and 17 °C in surface water, and between 5 and 13 °C on the seabed. Salinity increases with depth from 18 at the surface to 33 at the bottom. The western portion, where most of the samples were taken, is mostly <20 m deep, but in part also 20–30 m deep. Generally, beyond the 20-m isobath, depth increases steeply to 35 m.

Landings and sampling

Danish landings from the Kattegat peaked at more than 1000 t in 1957, then declined gradually to around 100 t in

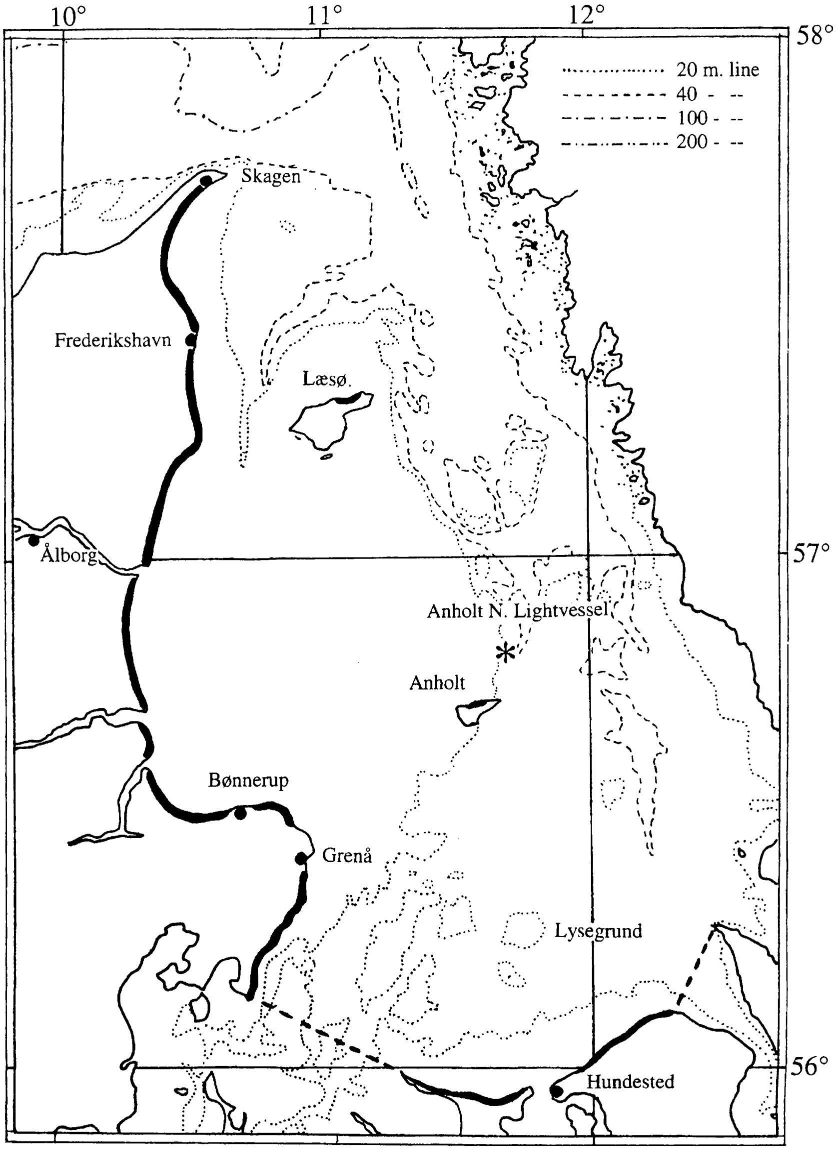

Figure 1. The Kattegat, showing some of the more prominent geographical localities mentioned in text and the main depth contours. The bold lines along the coast indicate areas where the fishery with poundnets is or was performed. The star indicates the position of a Danish light vessel from which daily observations on temperature and salinity at 5-m intervals were made.

the early 1970s (Table 1). After a subsequent peak of close to 500 t, recent landings have been about 40 t. The catch record for Sweden is incomplete, but it does indicate a peak in 1988 of 106 t, and in recent years, a virtually zero catch. The Danish and Swedish series (1975–1996) correlate significantly ($r = 0.77$, $n = 22$, $p = 0.001$). Of other nations' catch, some 1.5 t annually were landed at Kiel (0.4% of the Danish landings in the same period) between 1954 and 1959, but information on Norwegian catches is lacking.

Over the period 1952–1976, the summer poundnet fishery (May–September) accounted for 41% of the landings, but this fishery has been gradually abandoned since then (Table 2). The balance of the landings was taken by trawl (mainly October–April). Currently, only 2–3 fishing vessels from Grenå occasionally direct their effort on the species, the balance being by-catch only.

A Johansen's young fish trawl (Nielsen and Bagge, 1985), and a Sonderborg standard trawl (Bagge and Nielsen, 1986) were used to sample fish between May and September, off and along the coasts of Anholt at depths of 1.6–7.5 m; Figure 1). Larvae were sampled with a 2-m ring trawl or a neuston net (mesh 300 μm). The ring trawl fished the discontinuity layer (12–15 m), except at depths

Table 1. Landings (t) of greater weever from the Kattegat by Denmark and Sweden, 1952−2001.

Year	Denmark	Sweden	Total
1952	169		169
1953	241		241
1954	183		183
1955	337		337
1956	560		560
1957	1 006		1 006
1958	733		733
1959	192		192
1960	445		445
1961	284		284
1962	555		555
1963	340		340
1964	355		355
1965	208		208
1966	191		191
1967	190		190
1968	158		158
1969	158		158
1970	119		119
1971	123		123
1972	99		99
1973	63		63
1974	134		134
1975	170	23	193
1976	193	18	211
1977	160	10	170
1978	111	12	123
1979	202	6	228
1980	170	31	201
1981	245	36	281
1982	140	35	175
1983	112	15	127
1984	160	18	178
1985	255	14	269
1986	238	34	272
1987	163	46	209
1988	468	106	574
1989	215	13	228
1990	158	24	182
1991	154	17	171
1992	200	25	225
1993	130	27	157
1994	94	21	115
1995	77	17	94
1996	45	6	51
1997	50	1	51
1998	37		37
1999	52		52
2000	39		39
2001	48		48

<10 m, when it was fished 1 m above the bottom. Eggs could not be sampled quantitatively because of the large quantities of algae and ctenophores in the area, but larvae were sorted and preserved in 4% buffered formalin for later measurement ashore (length measured to the mm below). A neuston net was set during darkness (22:00−04:00 GMT) in late July 1970 (19 stations), but no larvae were caught.

Table 2. Yield of greater weever in poundnets by month (May−September), 1952−1976.

	Yield (t)					
Year	May	Jun	Jul	Aug	Sep	Total (t)
1952	14	79	28	16	13	150
1953	50	83	63	32	5	233
1954	36	69	19	6	8	138
1955	13	94	98	50	19	274
1956	82	183	57	31	4	357
1957	6	51	100	23	5	185
1958	2	64	37	13	9	125
1959	7	72	23	2	14	118
1960	28	98	16	4	10	156
1961	24	108	20	14	2	168
1962	15	44	14	9	7	89
1963	65	86	14	5	3	173
1964	15	55	16	1	1	88
1965	5	63	10	0	1	79
1966	9	20	19	1	1	50
1967	3	26	10	0	0	39
1968	2	15	32	0	0	49
1969	22	14	0	0	1	37
1970	12	3	1	0	0	16
1971	5	2	0	0	0	7
1972	5	16	4	1	1	27
1973	3	9	1	0	7	20
1974	4	14	1	1	7	27
1975	19	21	0	0	1	41
1976	3	26	9	4	2	44
Mean	18.0	52.6	23.7	8.5	4.8	107.6
s.d.	20.6	42.7	28.0	12.9	5.1	89.1

Monthly random samples of 20 kg were taken from the unsorted catch of commercial trawlers and from poundnets, and analysed in the laboratory following standard procedures, including total length (mm), weight (g), sex, maturity (according to a modified version − Tomkiewicz *et al.*, 2002 − of the scale of Maier, 1908), and other biological parameters. In all, 113 samples were taken, a total of 23 363 fish. Samples from commercial vessels were obtained at depths of 20−28 m.

Tagging experiments were carried out in the area around Anholt in spring and autumn, 1962−1966. The fish were caught in hauls of 10−15-min duration at 5−10 m, then transferred to a 1000-l tank with constant water supply. After 1 h, fish swimming at the surface were removed and the balance measured to the mm below, tagged with a hydrostatic Lea tag attached in front of the dorsal fin by a 0.5-mm steel wire coated with soft polyethylene, and released. In all, 3779 fish were tagged and released.

Biology

To estimate absolute fecundity, 56 fish were collected on 3 July 1971 at a station 23 m deep and 12 miles north of Anholt. They were selected on the criteria that they would spawn that year, contained no transparent oocytes, and that they covered the largest possible length range. Each fish was measured (mm below) and weighed (g), otoliths were taken, and the ovaries were removed, weighed, and preserved in Gilson's fluid. Subsamples of eggs were counted by eye under a binocular microscope.

Total fecundity (number of oocytes; F) was estimated by volumetric subsampling in two steps of thoroughly mixed total egg masses in 1000 ml (four estimates per fish). For comparison, fecundity was also estimated for ten fish by raising the wet weight of counted subsamples to the total wet weight of the ovary. The wet-weight method yielded on average a 16% higher fecundity than the volumetric method, but because it takes longer and is sensitive to variations in water content between sample and total weight, the volumetric method was preferred.

Studies of food and feeding were carried out by examining the stomach contents of fish sampled monthly from commercial catches and research surveys. Samples from poundnets were disregarded because the fish may stay in the gear for up to 24 h before the net is lifted, likely preying on species also caught that may not normally be obtainable. To investigate diel variations in food composition and time of feeding, hauls with the Johansen's young fish trawl were made round the clock in June/July 1963 off the northwest coast of Anholt, with two hauls each of 10-min duration every second hour. In May 1995 and June 1996, the same depths as before were trawled with the same gear, and in 1996 also, depths of about 7.3 m.

Between 1962 and 1965, a small feeding experiment was carried out under almost constant environmental conditions in the Danish Aquarium at Charlottenlund, to investigate whether greater weever had a circadian rhythm in food intake. In September 1962, 36 fish caught south of Anholt were transferred to 200-l tanks, each with 8 cm of sand on the bottom and with circulating aerated water (14 and 16°C; salinity 20; 12:12-h light:dark regime). On 9 January 1963, the experiment started with 12 live fish in healthy condition (mean length 15.5 cm; mean weight 25.3 g). The fish were offered boiled *Mytilus edulis* as food every second day. The experiment lasted until 8 August 1965, by when four fish had survived (mean length 21.2 cm; mean weight 74.0 g).

Length-at-age was estimated by applying the Petersen method, and from otolith reading (Creutzberg and Witte, 1989). In addition, increments obtained from tagging experiments were available. Because greater weever spawn in July and August, 1 August was taken as the birthdate. Fish grow both before and after spawning, and the rings do not coincide with the anniversaries. The total number of fish sampled was 23 323 in 113 samples, and otoliths from 20 481 were collected (one otolith per fish) for determination of age. Otoliths were cleaned, dried, and viewed in 90% alcohol under a binocular microscope at 8× magnification, using reflected light and a black background.

Mean length-at-age and s.d. for males and females (1961–1971) were used to estimate the von Bertalanffy parameters k, L_∞, and t_0, using the method of Gulland and Holt (1959). Mean weight-at-age was derived from mean length-at-age using a mean condition factor ($q = 100w/L^3$; Fulton, 1891) over all quarters and years, and assuming isometric growth ($q = 0.00646$ and 0.00659 for males and females, respectively).

Total mortality (Z) was estimated from tagging experiments, and from catch per unit effort (cpue) data. Recaptures were registered up to seven years after tagging, making the experiments well suited for estimating average Z, assuming that the intervening fishing effort had been constant. To minimize the bias caused by non-random mixing of tagged fish in the population, recaptures during the first year after tagging were omitted from the analysis.

For the Anholt fleet, data on catch per day per vessel in the directed fishery on greater weever, and in the mixed fishery, were collected in the period 1956–1970, together with otoliths, for age distribution of the catch. The 1958 year class was abundant, and recruited fully to the gear in use at that time in August 1962, at age 4. This year class was easy to recognize in subsequent years. The mean fraction of the 1958 year class by number and year was estimated for each of the years 1962–1970, and the natural logarithm of the values obtained regressed on years to obtain a value of Z.

For estimating natural mortality (M), the von Bertalanffy growth parameters for sexes separately, and a mean monthly water temperature of 8.9°C (1961–1970), were used as input for the regression method of Pauly (1980).

Results

Distribution

During winter, samples were drawn, on average, from deeper water (23–27 m) and from commercial catches exclusively, whereas summer samples were also taken from poundnets in shallow water (9–18 m). In winter, especially in March, the month of lowest seabed water temperature, some trawl hauls of very short duration (12–15 min) yielded very large catches (up to 7 t), indicating that greater weever may be distributed in high-density patches. Such a trend in depth distribution is corroborated by the recapture data (Table 3). In the areas from which the trawl samples were derived, the seabed is described as fine- to medium-grain sand and/or muddy fine sand, with 1.5–10% fines (silt and clay particles <50 μm) and 1.2–2.3% organic matter (Figure 2; after Pearson *et al.*, 1985). This

Table 3. Mean depth and s.d. at the positions where the monthly samples of fish for tagging were taken, and the positions where monthly recaptures were reported.

	Samples			Tagged fish recaptured		
Month	Number of samples	Depth (m)	s.d.	Number of fish	Depth (m)	s.d.
January	13	23.4	2.5	31	21.5	3.1
February	7	25.1	2.7	47	25.2	4.8
March	16	22.8	2.6	97	24.7	4.5
April	8	24.7	1.4	55	23.1	7.1
May	4	16.5	5.9	15	16.9	4.9
June	8	9.9	3.5	10	9.1	6.1
July	4	17.8	5.1	13	18.9	5.5
August	6	13.2	3.1	6	17.2	6.6
September	6	15.7	8.8			
October	3	27.1	4.1	32	24.2	7.1
November	21	24.1	2.9	73	23.1	5.6
December	9	22.4	2.8	58	23.1	4.1
Total	105			437		

suggests that greater weever prefer habitats with bottom sediments displaying these characteristics.

To collect information on the distribution of the trawl fishery over the year, fishing positions of demersal trawlers (excluding those fishing for Norway lobster, *Nephrops norvegicus*) landing greater weever on Anholt were sampled one week per month, from 1962 to 1968 (Figure 3). Only 9.7% of the annual effort was in summer.

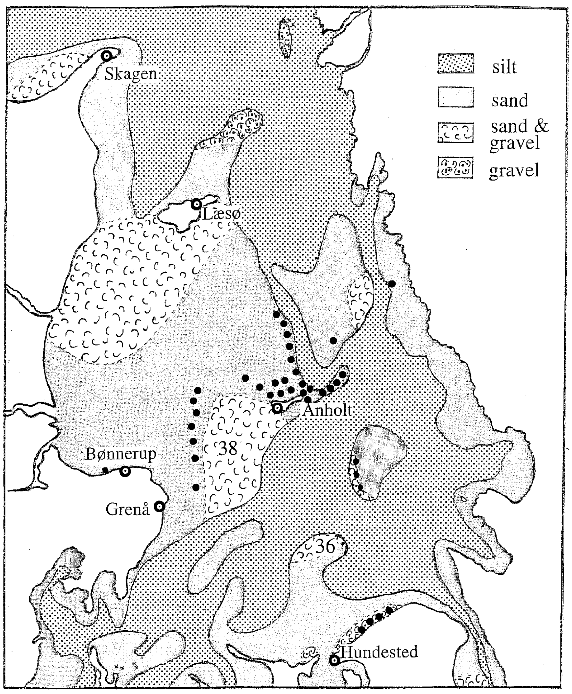

Figure 2. Catch positions (dots) of the directed bottom-trawl fishery performed from Anholt, Hundested, and Grenå, from which samples were taken, and the types of sediments.

The results of the tagging experiments indicated no recaptures north of Skagen or south of latitude 56°N, suggesting that greater weever in the Kattegat constitute a local stock. As recaptures were made in all types of gear, they should better mirror changes in distribution than the data from the trawl fishery that targeted the species (Figure 4). This suggests that the species is most abundant in the central part of the Kattegat, where the bottom is covered with sand and gravel.

Reproduction

Table 4 shows the distribution of maturity stages among 2223 fish sampled between May and September from commercial landings or research vessels, at depths of 10–18 m. Both males and females reach spawning condition (stage 6), and >50% of both sexes were spent (post-spawning condition) in July. By September, no greater weever in spawning condition was observed. The data clearly indicate that spawning is restricted to the period June–August, peaking in July.

Larvae were caught in significant numbers only in 1963, 1967, and 1969, when mean temperatures were relatively high, and mean salinities relatively low (Table 5). Mean length varied between 4.8 and 6.2 mm.

Fecundity estimates were variable (Figure 5). Nevertheless, the correlations between fecundity, and length and weight were significant ($n = 57$; $10^{-3} \times F = 0.0031 \times L^{3.1093}$; $r^2 = 0.543$; $10^{-3} \times F = 0.06243 \times W - 2.2581$; $r^2 = 0.5524$; $p < 0.001$). Relative fecundity (mean 593; s.d. 177; range 291–1040), defined as the number of oocytes per g total body weight (Nikolski, 1963; Bagenal, 1973), was not significantly correlated ($r^2 = 0.02$) with condition factor q.

Condition factor, growth, and mortality

Female condition factor (q) was highest in June, just before spawning, lowest during and just after spawning, in July and August, then increased during autumn, decreased in winter, and finally increased again in May. Values of male q were lower in June than for females, and highest in late autumn (Table 6).

Because of difficulties in separating males and females at age 1, sexes were combined for this age group. Estimated mean length and weight-at-age, and estimated growth parameters (Table 7), indicated a small but consistent sexual dimorphism, females being slightly larger than males of similar age. Also, among the larger and older age groups, females were more numerous.

Estimates of Z from the autumn and spring tagging experiments were almost identical ($Z = 0.67$ and 0.69, respectively), though slightly higher than estimates based on cpue ($Z = 0.62$). Applying Pauly's (1980) regression,

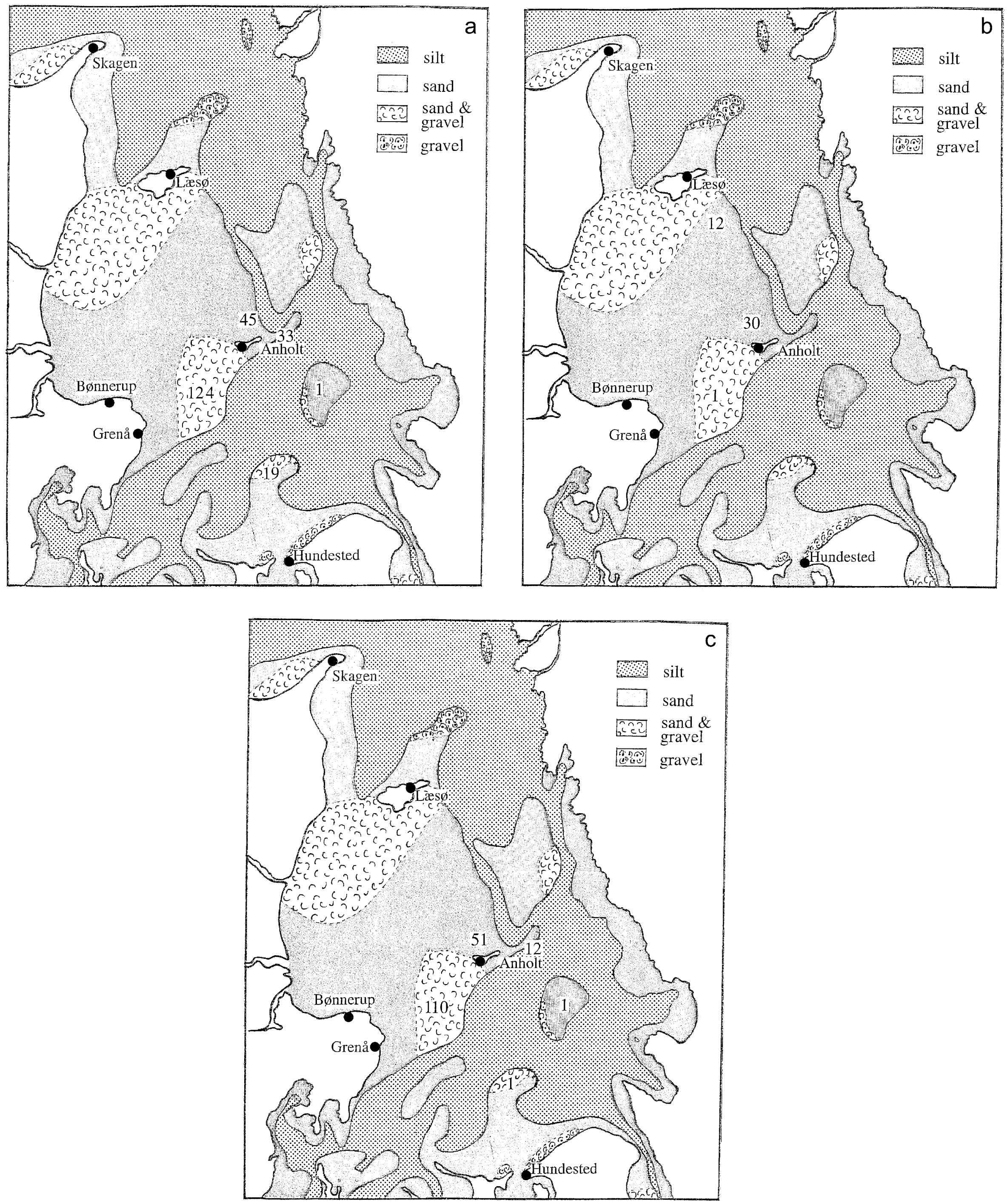

Figure 3. Catch positions of all demersal trawlers (except those fishing Norwegian lobster) landing greater weever on Anholt (1962–1968). (a) January–April, (b) May–August, (c) September–December (numbers refer to the number of days fishing).

values of natural mortality were M = 0.30 and 0.29 for males and females, respectively. Subtracting M from Z suggests fishing mortality coefficients (F) are in the range 0.3–0.4.

Food and feeding

The percentage of empty stomachs in the period January–April was very high, close to 100% in some months (Table 8). In May, the percentage empty dropped abruptly, then

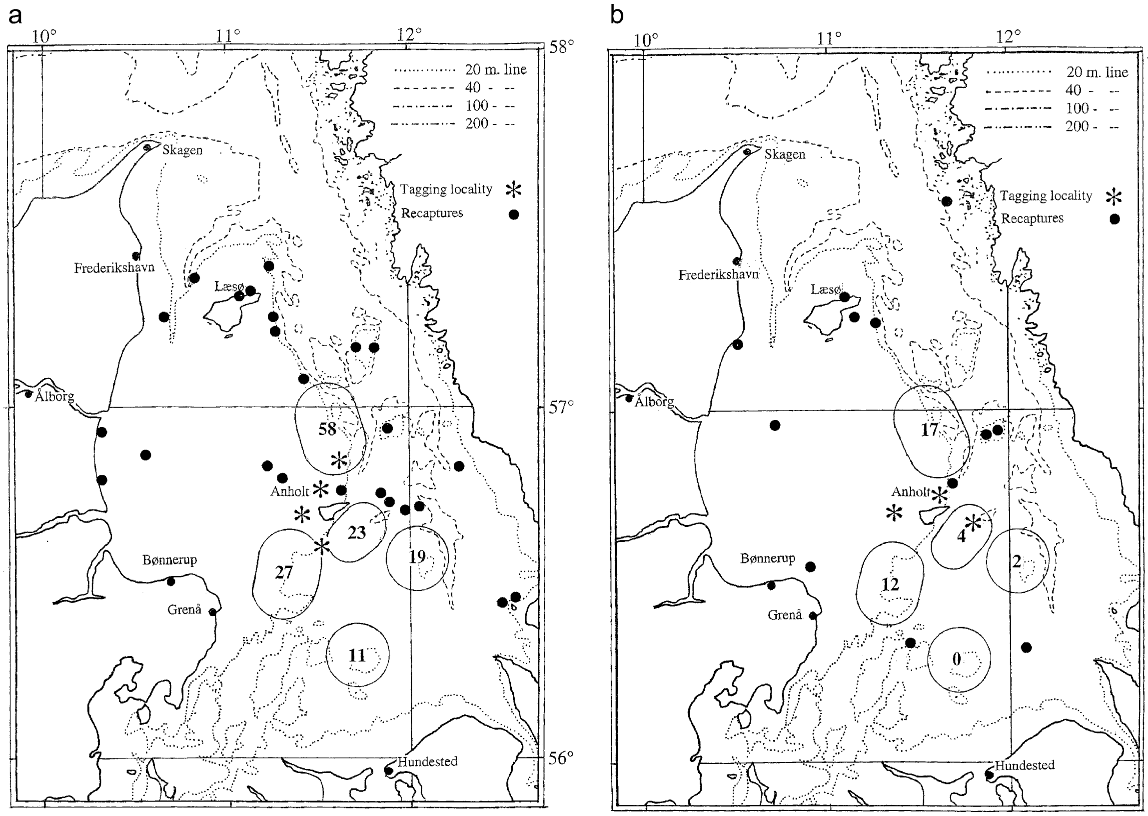

Figure 4. Positions of recaptures from tagging experiments (> 1−7 years after tag and release): (a) tagged in spring; (b) tagged in autumn.

remained <50% through to September. In October and November, more than 60% of the stomachs were again empty.

The results of the analysis of stomach contents are summarized as percentage wet-weight composition per four-month period (here referred to as summer, autumn, and winter) in Table 9. In summer, crustaceans dominated the food, and among these *Crangon crangon* was the most prevalent. Fish only represented 22% of the food, sandeels being the most common fish prey. In contrast, fish, specifically small whiting (*Merlangius merlangus*) and to a lesser extent clupeoids, represented the bulk of the prey during autumn. Finally, prey found in winter were small quantities of largely unidentifiable remains.

Table 4. Monthly distribution of maturity stages by sex, May−September.

Year(s) and month	Sampling depth (m)	Sex	Number of fish	Maturity stage					
				1−2	3	4	5	6	7−8
1989 May	18	Male	237	0.13	0.34	0.35	0.18		
		Female	187	0.03	0.21	0.44	0.32		
1961/1968 Jun	2−15	Male	505	0.08	0.06	0.13	0.35	0.37	0.01
		Female	542	0.04	0.13	0.15	0.07	0.59	0.02
1963/1968 Jul	2−15	Male	545	0.03			0.08	0.32	0.57
		Female	245	0.01			0.01	0.42	0.56
1967/1968 Aug	2−17	Male	190					0.12	0.88
		Female	108					0.06	0.94
1961/1963 Sep	6−24	Male	237	0.05	0.03				0.92
		Female	267	0.07	0.08				0.85

Table 5. Mean temperature and mean salinity at the depths at which larvae of greater weever were captured in the central Kattegat with a 2-m ring trawl, 1963–1969, and with a neuston net in 1970.

Year	Date	Mean temperature (°C) at 12 and 15 m	Mean salinity at 12 and 15 m	Number of stations	Total number of larvae	Number of larvae per 20 min	Mean length (and s.d.) of larvae		Gear
1963	26 Jul to 1 Aug	16.3–16.1	25.3–27.5	11	85	7.7	6.00	(1.44)	Ring trawl
1964	24–27 Jul	14.6*	30.8*	11	1	0.1			Ring trawl
1965	3–7 Aug	14.7*	29.7*	20	1	0.05			Ring trawl
1967	7–9 Aug	16.2–14.5	20.3–23.0	16	242	15.1	4.79	(1.02)	Ring trawl
1968	29 Jul to 8 Aug	15.0–13.0	25.0–30.0	12	4	0.3			Ring trawl
1969	31 Jul to 5 Aug	18.3–17.4	22.5–25.5	16	74	4.6	6.19	(1.42)	Ring trawl
1970	30–31 Jul	16.0–16.0	20.3–20.3	19	0	–			Neuston net

*Mean at 12, 13, 14, and 15 m – only one larva captured.

Figure 6 shows variations in the total weight of stomach contents with time of day in summer 1963. Values between midnight and noon were much higher than those in the afternoon and evening on both occasions that sampling was undertaken.

The percentage of empty stomachs by month was significantly related to the monthly mean temperature at the depths of sampling (Table 8; $r = 0.77$; $n = 12$; $p < 0.01$), suggesting that temperature affects feeding activity. The temperature at the seabed representing the border between feeding and non-feeding in the Kattegat was at approximately 6°C. However, the results of the aquarium experiment under constant temperature, light, and salinity suggest otherwise. Although the experiment started in January, the fish did not react to food until early April. At that time only eight fish were still alive, and they fed throughout summer. Then from October 1963 to the end of March 1964, all food offered was again refused, whereafter the surviving fish fed readily again until the beginning of November. Feeding then ceased again until 5 March 1965, whereafter normal feeding was observed until the experiment ended on 8 August. The pattern observed is indicative of an endogenous feeding rhythm.

Discussion

The available literature provides very little information about the biology of the greater weever, and most of it is anecdotal. For Irish waters, Quigley *et al.* (1990) refer to

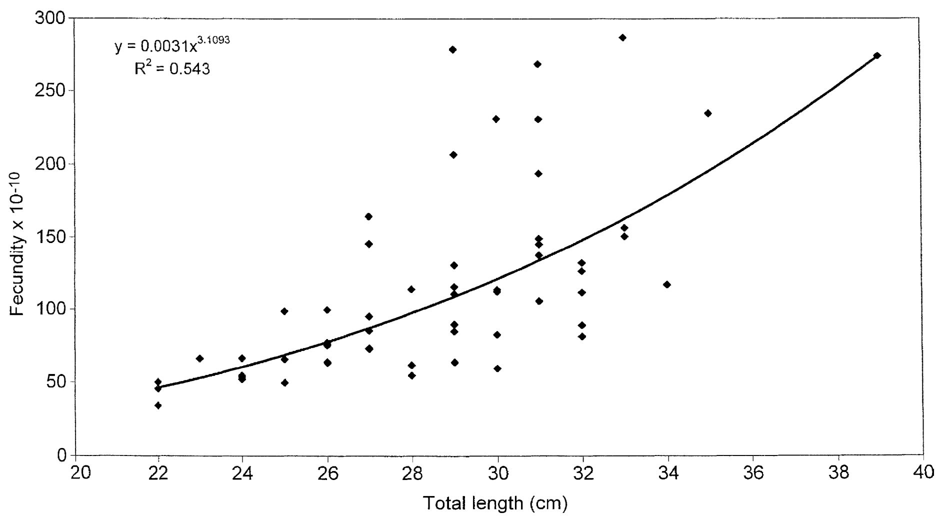

Figure 5. Estimates of fecundity plotted on total length of greater weever.

Table 6. Mean monthly condition factor of greater weever in the Kattegat.

	Males			Females		
Month	$q \times 10^3$	CV	Number	$q \times 10^3$	CV	Number
January	6.61	8.63	310	6.73	9.39	273
February	6.45	9.16	382	6.49	8.49	266
March	6.34	8.02	321	6.41	8.31	248
April	6.28	8.42	233	6.34	8.63	165
May	6.38	8.20	287	6.42	8.36	380
June	6.67	8.43	414	7.13	12.62	247
July	6.01	8.47	271	5.15	9.92	165
August	5.97	8.39	318	6.24	11.92	157
September	6.56	9.89	214	6.68	9.93	257
October	6.63	9.07	448	6.72	8.48	381
November	6.74	8.03	197	6.66	7.94	197
December	6.65	8.08	394	6.79	8.69	254
Weighted mean	6.45	Total	3 789	6.59	Total	2 990

catches of three (almost) spawning females, one in August and two in September. Ehrenbaum (1905–1909) gives June–August as the spawning season in the southern North Sea, based on the presence of eggs and larvae. Krøyer (1838) mentions the end of July and the beginning of August for the Kattegat, and Otterstrøm (1912) specifies July and August for the same area. The current results largely confirm these earlier data, but suggest that spawning starts as early as June.

Larvae were only caught in the ring trawl, not in the neuston net. Although sampling was restricted to a single year, there was no indication that larvae of greater weever congregate near the surface, as has been shown for its smaller counterpart, the lesser weever (*Trachinus vipera*), in the North Sea by Nellen and Hempel (1970).

The picture emerging about the seasonal distribution of greater weever is that they inhabit the muddy fine sand of the deeper (16–25 m) waters of the Kattegat during winter, where temperatures are <6°C, when they are caught effectively by otter trawls. They almost completely cease feeding, relying on energy reserves – the change in condition factor suggests a 5% weight loss. In May, they start moving inshore (<15 m) to their preferred habitat of fine sand, where they start feeding, mainly on brown shrimp. At the same time, their gonads develop, at least when they are reaching the end of their second year of life. In June, spawning starts, and it continues into August, in water temperatures ranging from 6 to 16°C. At that time, they are available to the traditional, but now largely abandoned, inshore poundnet fishery. In September, they start moving towards deeper water (15–24 m), but while the temperatures are still relatively high (6–12°C), they feed mainly on fish, particularly young of the year whiting and clupeoids. The surface water above the halocline (12–14 m) cools more rapidly than the water below this, where temperatures remain more stable, because the salinity difference prevents turbulence and mixing with the surface layer. The species may try to compensate for the decreasing temperature by moving to warmer, deeper water. Although temperature seems to be the dominant regulating factor, it remains intriguing that greater weever in the aquarium under constant environmental conditions maintained their seasonal cycle of feeding and fasting over a three-year period.

Table 7. Mean length- (L) and weight-at-age (W), maximum length recorded (L_{max}), and von Bertalanffy growth parameters (L_∞, k, t_0, W_∞).

	Males			Females		
Age	Number	L (cm)	W (g)	Number	L (cm)	W (g)
1	87	9.2	5.1	87	9.2	5.1
2	244	14.7	20.5	170	14.8	21.4
3	1 136	17.1	32.3	1 057	17.3	34.1
4	1 900	19.7	49.3	1 757	20.2	54.3
5	2 063	22.2	70.6	1 634	23.0	80.2
6	2 297	23.7	85.9	2 282	24.4	95.7
7	1 167	24.8	98.4	1 426	26.2	118.5
8	873	25.8	110.8	827	27.7	140.1
9	483	26.4	118.7	570	28.8	157.4
10	79	28.1	154.1	175	30.9	194.4
11	35	30.5	183.0	95	32.8	232.5
12	16	31.7	205.5	45	33.0	236.8
13	8	32.5	221.4	24	34.1	261.3
14				7	37.6	350.3
L_{max}	37.0			40.0		
L_∞	35.1			38.3		
k	0.16			0.15		
t_0	−0.51			−1.08		
W_∞	278.9			370.2		

Table 8. Number of samples (n), number of stomachs sampled (N), mean percentage empty (%E), mean depth (D, m), mean temperature (T, °C), and standard deviations (s.d.; in parenthesis) by month.

Month	n	N	%E (s.d.)	D (s.d.)	T (s.d.)
January	7	1 870	87.8 (14.6)	24.7 (4.3)	6.5 (1.1)
February	8	1 816	94.3 (7.3)	24.9 (2.5)	4.6 (0.8)
March	6	1 353	98.2 (3.2)	23.7 (3.9)	4.8 (1.7)
April	5	938	98.0 (3.2)	24.3 (1.8)	4.9 (0.6)
May	7	766	38.0 (36.1)	16.3 (5.9)	5.9 (0.9)
June	17	1 548	19.3 (12.0)	7.0 (3.6)	13.1 (1.8)
July	6	452	18.6 (23.1)	17.3 (11.3)	12.3 (2.6)
August	5	219	47.6 (23.1)	11.3 (0.9)	12.3 (2.6)
September	4	313	28.9 (27.1)	17.6 (8.4)	14.1 (1.5)
October	4	475	60.3 (19.7)	24.3 (8.3)	12.4 (0.7)
November	19	3 116	60.0 (29.5)	24.6 (4.3)	10.9 (1.0)
December	6	962	43.9 (23.4)	22.9 (2.9)	7.8 (1.4)

Table 9. Food of greater weever in relation to season.

Parameter/taxon	Summer (May–July)	Autumn (September–December)	Winter (January–April)
Number of stomachs	721	946	5 977
% Empty stomachs	22.7	55.3	94.6
Depth (m)	1.6–7.3	17.9–24.6	23.7–24.9
Gear	Trawl 1	Commercial samples	Commercial samples
Mean wet weight (g)	0.527	0.345	0.014
	Percentage of total wet weight	Percentage of total wet weight	Percentage of total wet weight
Total fish	22.3%	93.8%	Insignificant quantities of unidentifiable fish remains
Clupeoid juveniles		14.4	
Merlangius merlangus		68.6	
Agonus cataphractus		0.1	
Limanda limanda		0.5	
Ammodytes tobianus	68.5		
Gobiidae	12.6	0.8	
Other fish	3.3		
Unidentified fish	15.6	15.6	
Total crustaceans	72.6%	4.7%	Insignificant quantities of crustacean remains, possibly *Idotea* sp. and *Crangon crangon*
Crangon crangon	90.5		
Bathyporeia sp.	7.5		
Other crustaceans	2.0	0.2	
Mytilus edulis	2.0	0.6	
Polychaetes	3.1	0.7	

For lesser weever in the North Sea, a similar cessation of feeding has been reported from November to May, associated with a loss of weight of 16–23% (Creutzberg and Duineveld, 1986). Also, the diel rhythm in food intake, with high ingestion from midnight until noon, and low ingestion in the afternoon and evening, appears to be similar among the two species (Creutzberg and Witte, 1989).

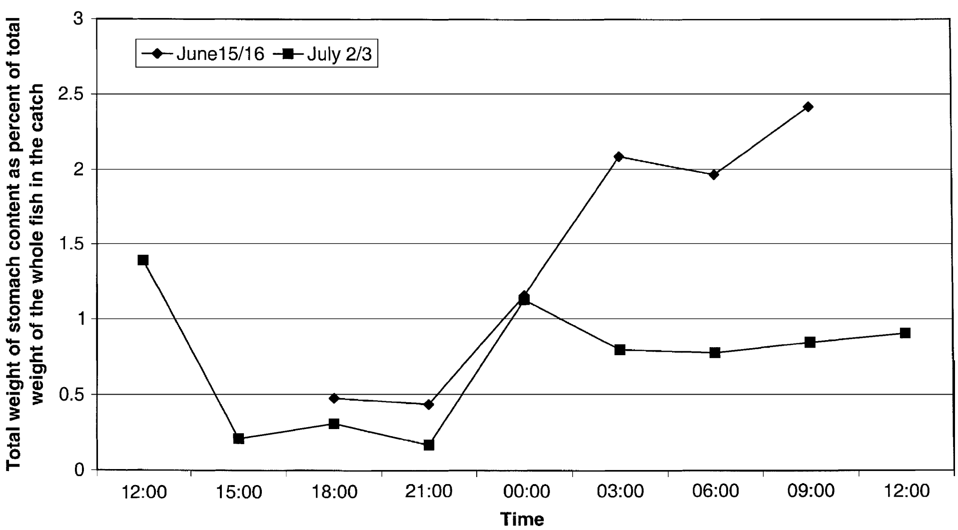

Figure 6. Diel variations in greater weever stomach content weight during June and July 1963, in shallow water (1.5–4.0 m).

Available knowledge of potential predators in the Kattegat suggests that predation on greater weever is relatively low. Blegvad (1916) and Bagge (1981) never found greater weever in cod (*Gadus morhua*) stomachs, nor did Flintegaard (1981) in whiting stomachs. Fishers in the area also never see them in cod stomachs, although they are very occasionally observed in turbot (*Scophthalmus maximus*) stomachs. According to Creutzberg and Witte (1989), the lesser weever has also not been reported from cod or whiting collected in the southern North Sea, although they are found frequently in stomachs of turbot and brill (*Scophthalmus rhombus*). Thus, turbot and brill remain the only candidate predators of greater weever in the Kattegat. The landings of these species during the period 1961–1970 were 71 and 134 t, respectively, suggesting that their stocks are relatively small and that associated predation mortality would likely be low. Because greater weever appear to spend most of their time buried in the sand, except for the eyes, armed with the venomous spine of the first dorsal fin, they are probably effective at defending themselves against predators, so predation mortality should be low, perhaps lower than the value of 0.3 suggested by Pauly's (1980) regression.

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