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Dynamic self-thinning lines indicate that flatfish nursery ground carrying capacity is not reached in the productive Dutch Wadden Sea

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ABSTRACT: We tested the hypothesis that flatfish nursery ground carrying capacity is not being reached for juvenile flatfish populations in the productive Balgzand intertidal (Dutch Wadden Sea). Dynamic self-thinning lines (the logarithmic relationship between the annual development of population density and mean individual weight) were estimated over the period 1975–2019, whereby a slope of −4/3 would indicate that carrying capacity was reached. In 0-group plaice *Pleuronectes platessa* L., a decrease in slope occurred from −2.69 on average in the 1980s to −0.81 in the 2010s. In 0-group flounder *Platichthys flesus* (L.), slopes increased from −0.98 in the 1980s to −1.77 in the 2010s. These slopes indicated that flatfish nursery ground carrying capacity was not reached at the Balgzand intertidal. This finding is in contrast to British bays, likely because of lower benthic food biomass in British bays (few g dry mass m^{-2}) compared to Balgzand (tens of g dry mass m^{-2}). Interannual differences in the slope of the dynamic self-thinning lines at Balgzand reflected changes in density during the season. From 1975–2019, the average daily instantaneous rate of change in 0-group flounder reflected mortality and was about 0.042 d^{-1} but with large interannual variations. In 0-group plaice, the rate of change in density was 0.020 d^{-1} in the 1970s, also reflecting mortality, but increased over time due to increased emigration. Dynamic self-thinning lines can be used to analyse flatfish nursery ground carrying capacity; however, in many flatfish nursery grounds, carrying capacity will presently not be reached.

KEY WORDS: Dynamic self-thinning · Carrying capacity · Mortality · Nursery area · Juvenile flatfish · Plaice · Flounder · Wadden Sea

1. INTRODUCTION

Coastal ecosystems are among the most productive marine systems due to their often-high nutrient concentrations, together with a fast nutrient release and recycling (see e.g. Teal 1962, Nixon et al. 1986). This productivity also directly transfers to the next trophic level, such as estuarine macrobenthos (Herman et al. 1999), which in turn is a direct food source for a variety of predatory fish, birds and mammals, hence affecting and also determining their productivity. Therefore, the carrying capacity of coastal systems is an important issue, even more so since these areas are under strong anthropogenic pressure from eutrophication, pollution and, more recently, climate warming (e.g. Jackson et al. 2001, Bijma et al. 2013).

The concept of carrying capacity was introduced in relation to ecosystem productivity by Leopold (1933) and Errington (1934). Ecosystem productivity has been considered through the maximum number of

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species that a habitat can support (Errington 1934), the size of species or population relative to the asymptote of the ideal logistic growth curve (Odum 1953) and the population size at which the per capita population growth rate is zero (McCall 1990). All of these approaches are reviewed by Kashiwai (1995). In essence, the focus is on carrying capacity as an intrinsic characteristic of the species (the logistic growth equation), or as a measure of the ecosystem productivity.

Carrying capacity implicitly assumes that density-dependent mechanisms (growth, reproduction, mortality [predation]) are operating to regulate individual or population size. Density-dependence has been found in many studies in marine ecosystems (e.g. Cushing 1974, Lockwood 1980); however, instead of a situation of semi-equilibrium, large interannual and seasonal fluctuations in environmental conditions and an influx of new individuals often occur. Therefore, carrying capacity is likely to vary over time, and estimating it in any form will be a challenge.

The most promising systems for estimating carrying capacity are those that are relatively stable in space and time. Temperate coastal north European flatfish nursery grounds are such systems. Over a relatively large geographical range, a small group of flatfish species (especially plaice *Pleuronectes platessa*, flounder *Platichthys flesus*, sole *Solea solea*, and dab *Limanda limanda*) use coastal areas in high numbers as nursery grounds during their first years of life (Zijlstra 1972, Gibson 1994 and references therein). Interannual variability in abundances can occur as a consequence of interannual variations in larval supply (Bannister et al. 1974, Creutzberg et al. 1978, Rijnsdorp et al. 1985, van der Veer 1985). Normally, seasonal fluctuations in abiotic conditions are within the physiological tolerance limits of the species (Fonds 1979, van der Veer & Bergman 1986, Fonds et al. 1992, Freitas et al. 2010); however, in exceptional cases, temperature conditions can become too high, causing a mass exodus (Berghahn 1983, 1984). Furthermore, for these demersal juvenile flatfishes preying on (epi)benthos (Macer 1967, Edwards & Steele 1968, Kuipers 1977, de Vlas 1979, Pihl 1982, van der Veer & Witte 1993), food conditions are relatively stable (see for instance Jung et al. 2017). Finally, density-dependent predation has been found to operate during the first year of life (Lockwood 1980, van der Veer 1986, van der Veer et al. 2000a).

The question remains how to approach the analysis of the carrying capacity of these temperate coastal north European flatfish nursery grounds. At first, the focus was on growth conditions as an indicator of habitat quality on the Balgzand intertidal in the Dutch Wadden Sea (Zijlstra et al. 1982, van der Veer 1986, Freitas et al. 2012, Cardoso et al. 2016). Subsequently, the per capita population growth was also considered in other European nurseries (van der Veer et al. 2000a). Analyses of individual and population growth suggest enough food during most of the growing season (the maximum growth–optimal food condition hypothesis; van der Veer & Witte 1993) up until late summer (van der Veer et al. 2016). The linear relationship between the energy requirements of an individual and its metabolic biomass ($W^{0.8}$) (Winberg 1956, Fonds et al. 1992) allowed an analysis of per capita population growth in terms of population metabolic biomass of flatfish populations. For the Balgzand intertidal, such a calculation suggested that the carrying capacity was never reached (van der Veer et al. 2000a).

Carrying capacity implies a relationship between density and individual growth or biomass: as the animals grow, their energy requirements increase, and as soon as they become limiting, individual growth is reduced and becomes density-dependent. At the population level, this results in an inverse linear relationship between population density and mean individual biomass on a log–log plot (see the Appendix Text A1 and Fig. A1). These species-specific lines, so-called dynamic self-thinning lines, can be defined as boundaries beyond which combinations of density and mean individual weight are not possible, and they reflect, in essence, the carrying capacity of the environment. This concept of dynamic self-thinning originates from plant ecology (Tadaki & Shidei 1959, Yoda et al. 1963) and has also been applied to animal populations, e.g. sessile organisms living in a single layer (Hughes & Griffiths 1988) and in multi-layered distributions (Fuentes-Santos et al. 2014) as well as mobile fishes (Rincón & Lobón-Serviá 2002).

Nash et al. (2007) applied dynamic self-thinning for British flatfish nursery grounds and found that in these open bays, flatfish density was only occasionally high enough to reach the site-specific self-thinning line, suggesting that these populations — although rarely — sometimes approached the carrying capacity of the bays. These observations are in contrast to the flatfish growth studies for the Balgzand intertidal, reviewed by van der Veer et al. (2000a). One of the explanations might be the relatively low benthic food biomass in British bays, a few g dry mass (McIntyre & Eleftheriou 1968), compared to a much higher food availability at the Balgzand intertidal, on the order of tens of g ash-free dry mass (Jung et al. 2017). If true, this means that at Balgzand intertidal, growth patterns will be more or less the same with some interannual variability.

Here, we test the hypothesis that in areas with high benthic food conditions such as the Balgzand intertidal, dynamic self-thinning is not apparent in the population's development over time and carrying capacity is never reached. The analyses are based on juvenile flatfish data of 0-group plaice and 0-group flounder from a long-term sampling programme at the Balgzand intertidal between 1975 and 2019 (Jung et al. 2017). The data was used to examine the relationship between population density and mean individual weight in the context of dynamic self-thinning lines.

2. MATERIALS AND METHODS

2.1. Sampling

Published and unpublished data from the Royal Netherlands Institute for Sea Research (NIOZ) Balgzand High Water sampling programme were used. The programme started in 1975 (Zijlstra et al. 1982) and covers the period 1975–2019 (1975–1976, 1979–1983, 1986, 1991, 1993–2002, 2007, 2009, 2014, 2019). The programme consisted of a grid of 36 stations distributed over the Balgzand, an isolated tidal flat system of 50 km^2 in the western part of the Dutch Wadden Sea (Fig. 1). Over the years, sampling methodology and sampling stations remained the same.

Fish samples were collected over a period of 3 h, centred around high water during daytime, when the flatfish population is randomly distributed over the area (Kuipers 1977). Fishing was done with a rubber dinghy and a standard 2 m beam trawl with one tickler chain between February and September at frequent intervals (in principle, every 2–4 wk). Hauls of about 100 m were made at a speed of about 35 m min^{-1}, following the protocols of Riley & Corlett (1966). The location of the hauls was established by wooden poles inserted into the sediment at the start of the tow, and in later years, by GPS. The length of the trawls was assessed with a calibrated metre wheel fitted outside the trawl. During each cruise, bottom water temperature was measured.

Each sample was stored individually in plastic bags on board, transported to the laboratory on the same day and preserved in 4% formalin–seawater (until 1990) or deep-frozen (after 1990) within a few hours.

2.2. Data analysis

All samples were sorted and the fish were identified to species. The 0-group flatfish were separated from other juvenile flatfish (I- and II group) based on their length. During most of the growing season, 0-group flatfish could simply be selected by their small size

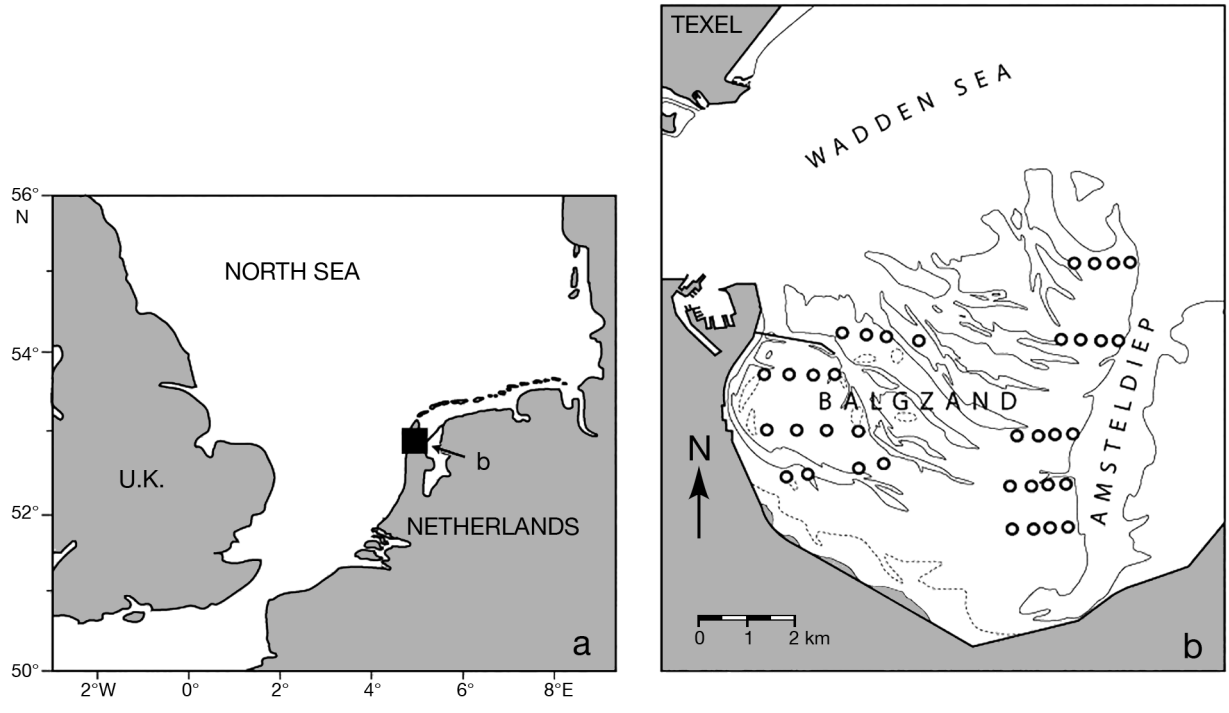

Fig. 1. The Balgzand intertidal area in the western Dutch Wadden Sea (52.53.14° –52.59.38° N, 4.47.08–4.57.05° E) with 9 transects each consisting of 4 sampling hauls, indicated by an open circle. Solid lines: mean low-water mark; dashed lines: mean high-water mark

(see de Vlas 1979). By the end of the growing season, sometimes there was doubt as to the age group (0- or I-group), and in that case, sagittal otoliths were removed and checked by eye for annual rings.

Each individual 0-group flatfish was measured within a few weeks of collection to the nearest mm total length. No correction for shrinkage was applied. For each haul, numbers caught were corrected for size-selective mesh and catch efficiency. The number of plaice *Pleuronectes platessa* caught was corrected after Dapper (1978) for size-selective mesh efficiency and after Kuipers (1975) for catch efficiency. Flounder *Platichthys flesus* were assumed to be similar to plaice, so the same procedures for size selection and catch efficiency were used. Subsequently, for 0-group plaice and flounder, all corrected numbers of individuals caught were expressed as individuals per 1000 m^2 (ind. $[10^3\ m^2]^{-1}$). The arithmetic mean density and mean size were calculated based on all stations sampled during a given cruise (cf. Kuipers 1977, Zijlstra et al. 1982). For a detailed description and overview of the sampling effort, see Jung et al. (2017).

Rates of change in density during the demersal stage were estimated according to the protocol of Iles & Beverton (1991). From the cruise with maximum observed density (peak settlement), the natural logarithm of the average population density was plotted against the date of sampling for each of the cruises for each year separately. Daily instantaneous rate of change (M; d^{-1}) was estimated from the slope of the linear regression. For more details and information about precision in the estimation, see Iles & Beverton (1991) and van der Veer et al. (2000a).

Dynamic thinning lines were estimated according to Nash et al. (2007). Mean population length was converted into mean weight according to known species-specific length–mass relationships:

$$W = (\delta_m L)^3 \quad (1)$$

where wet mass (W) is in g; δ_m is a species-specific shape coefficient (0.219 and 0.224 for plaice and flounder, respectively; see van der Veer et al. 2001) and L is total length in cm. Next, the logarithm of the average population density was plotted against mean population weight for each species and each year separately. The trajectories of these relationships were examined for the period after peak settlement, when population density decreased due to nursery-ground mortality and mean population weight increased due to individual growth.

All calculations and analyses were done in the R statistical computing programme (R Core Team 2023). Correlations between variables were estimated with Spearman's rank correlation. The graphics were made using the 'ggplot' package (Wickham 2016).

3. RESULTS

3.1. Abundance and size

Over the period 1975–2019, 0-group plaice *Pleuronectes platessa* and 0-group flounder *Platichthys flesus* were found regularly in the Balgzand intertidal (Figs. 2A & 3A). For individual years, see Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m763p081_supp.pdf. Individuals of 0-group plaice and flounder were present in all years, with large interannual variability in abundance. Peak abun-

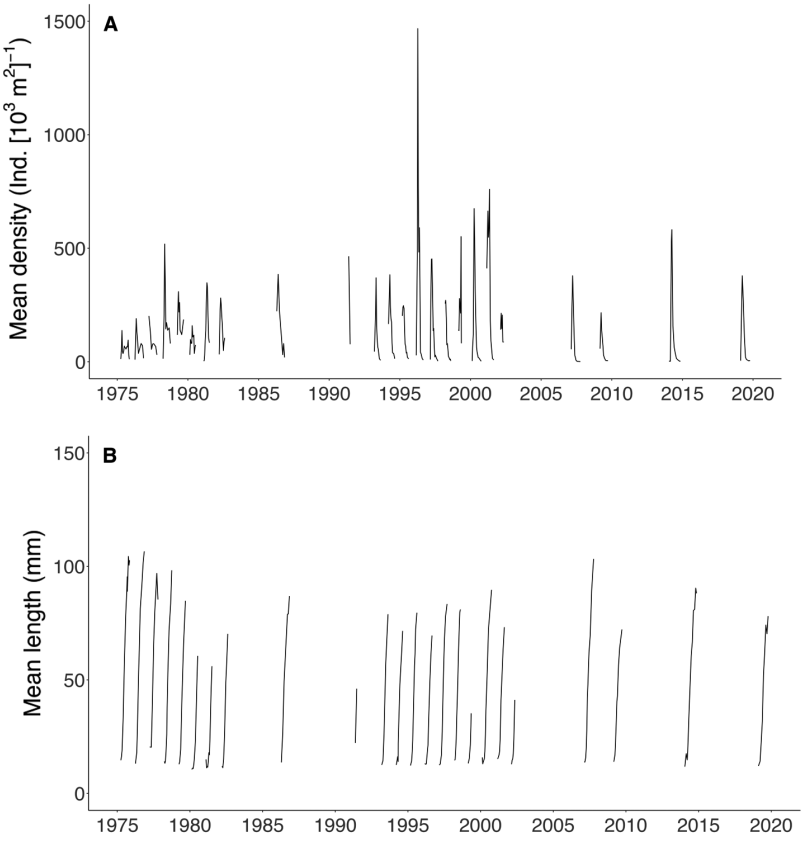

Fig. 2. (A) Mean density and (B) mean population length of 0-group plaice at the Balgzand intertidal between 1975 and 2019

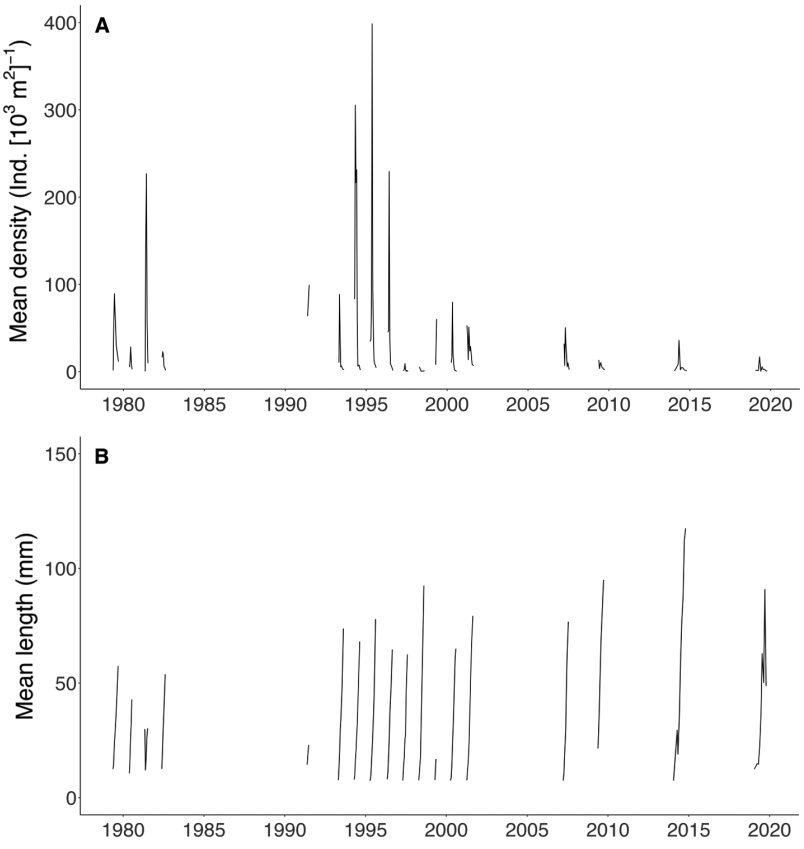

Fig. 3. (A) Mean density and (B) mean population length of 0-group flounder at the Balgzand intertidal between 1979 and 2019

dance of 0-group plaice varied among the years by a factor of 10: between 137 ind. $(10^3\ m^2)^{-1}$ in 1975 and 1282 ind. $(10^3\ m^2)^{-1}$ in 1996 (Table 1). No pattern or trend was found over the years. In 0-group flounder, peak abundance was lower in most years and showed a larger variability among years: between 9 ind. $(10^3\ m^2)^{-1}$ in 1997 and 399 ind. $(10^3\ m^2)^{-1}$ in 1995 (Table 1). Peak abundance from 2000 onwards was lower than in the previous periods (Fig. 3A, Table 1).

Growth patterns of 0-group plaice remained the same with some variability over the years (Fig. 2B, Fig. S1). Individual 0-group flounder reached a higher mean length over time at the end of the growing season in recent years (Fig. 3B, Fig. S2).

In both 0-group plaice and flounder, large interannual variations in the rate of change in density were found. In 0-group plaice, the rate of change increased over time, from 0.011 d^{-1} on average in the 1980s, 0.027 d^{-1} in the 1990s and 0.037 d^{-1} from 2000. In 0-group flounder, no such trend was observed. In contrast, the lowest values were found in recent years (on average, 0.020 d^{-1} from 2000, compared with 0.050 d^{-1}) (Fig. 4, Table 1). On average, *M* in 0-group flounder was about 0.040 d^{-1} and twice as high as that for 0-group plaice (0.020 d^{-1}). In the 1980s, *M* was highest in 0-group flounder. From 2000 onwards, *M* was highest in 0-group plaice (Fig. 4).

3.2. Dynamic self-thinning slopes

The data of average weight against average density for 0-group plaice and 0-group flounder for the various years are presented in Fig. 5. For individual years, see Figs. S3 & S4. In all years, the general trend was similar, with an initial phase with increasing densities only (reflecting immigration and settlement of individuals) followed by a phase with increasing mean weight and simultaneously decreasing densities. This general trend was more variable in 0-group flounder. Dynamic self-thinning lines with estimates of slope and intercept could be estimated for most of the years (Fig. 6, Table 2).

The dynamic thinning slopes were variable in 0-group plaice: between −1.48 and −4.23 during the 1980s, between −0.85 and −1.75 during the 1990s and between −0.66 and −0.96 from 2000 onwards. The slope decreased significantly from −2.69 on average in the 1980s to −1.26 in the 1990s and −0.84 from 2010 onwards (Spearman rank correlation: $R_S = -0.96$, $n = 19$, $p < 0.001$) (Fig. 6). The intercept was highest in the 1980s (average: 5.23) but decreased over time to 2.32 on average in the 1990s and 1.28 from 2000 onwards (Fig. 6, Table 2).

The slopes in 0-group flounder were less variable than those in 0-group plaice and did not show a significant trend over time (Spearman rank correlation: $R_S = 0.41$, $n = 13$, $p > 0.05$) (Fig. 6). The slopes in 0-group flounder were −0.98 on average in the 1980s, −1.01 in the 1990s and −1.77 in the 2010s (Fig. 6). The intercept did not show a clear trend over time (Table 2, Fig. 6).

3.3. Relationships

During the respectively decreasing and increasing trend in the slopes of the dynamic (self)-thinning lines over time, they were in the range predicted for dynamic self-thinning (−4/3) for both 0-group plaice and flounder only in the 1990s. However, in both species,

Table 1. Rates of change in density of 0-group plaice and 0-group flounder at the Balgzand intertidal for various years between 1973 and 2019. Maximum observed density (D_{max}) and data of maximum observed density (T_{max} in days from 1 January) are listed together with the number of cruises for which data are included in the regression calculations (*v*), the constant of regression calculation (*a*), the mean daily instantaneous rate of change in density based on the slope of the regression equation (*M*), estimated standard error of *M* (SE *M*), the proportion of variation accounted for by regression equation (R^2), significant level associated with test of $M = 0$ (p) and total stage decrease: $M \times$ difference between T_{max} and days until 30 September (Mt). DoY: day of the year

Year	T_{max} (DoY)	D_{max} (ind. $[10^3\,m^{-2}]^{-1}$)	*v*	*a*	*M* (d^{-1})	SE *M*	R^2 (%)	p	Days until 30 Sept	Mt (-)	Reference
0-group plaice											
1973	129	500	23	6.700	0.010	0.003	31	0.005	141	1.410	Kuipers (1977) in Iles & Beverton (1991)
1975	122	137	15						148		Zijlstra et al. (1982) in Iles & Beverton (1991)
1976	126	191	9	6.000	0.009	0.003	58	0.018	144	1.296	Zijlstra et al. (1982) in Iles & Beverton (1991)
1977	88	202	7	5.700	0.007	0.002	71	0.017	182	1.274	Zijlstra et al. (1982) in Iles & Beverton (1991)
1978	129	519	7	6.900	0.009	0.003	68	0.022	141	1.269	Zijlstra et al. (1982) in Iles & Beverton (1991)
1979	121	320	6	6.400	0.008	0.003	67	0.048	149	1.192	Zijlstra et al. (1982) in Iles & Beverton (1991)
1980	113	164	7	6.100	0.011	0.005	45	0.099	157	1.727	van der Veer (1986) in Iles & Beverton (1991)
1981	126	360	5	9.100	0.025	0.002	98	0.002	144	3.600	van der Veer (1986) in Iles & Beverton (1991)
1982	118	297	8	7.300	0.014	0.004	67	0.004	152	2.098	van der Veer (1986) in Iles & Beverton (1991)
1986	142	385	5	8.272	0.016	0.004	84	0.023	128	2.048	van der Veer & Witte (unpubl. data)
1993	117	370	5	8.800	0.034	0.005	92	0.006	153	5.202	van der Veer et al. (2000b)
1994	108	375	6	9.252	0.030	0.005	89	0.003	162	4.860	van der Veer et al. (2000b)
1995	94	244	6	8.338	0.029	0.002	97	0.001	176	5.104	van der Veer et al. (2000b)
1996	98	1282	5	9.065	0.021	0.003	90	0.010	172	3.612	van der Veer et al. (2000b)
1997	100	453	5	9.231	0.031	0.004	92	0.006	170	5.270	van der Veer et al. (2000b)
1998	91	262	5	7.721	0.026	0.007	72	0.043	179	4.654	van der Veer et al. (2000b)
1999	83	312	3	7.690	0.022	0.007	83	0.190	187	4.114	van der Veer et al. (2000b)
2000	94	674	8	9.821	0.034	0.002	96	0.001	176	5.984	van der Veer & Witte (unpubl. data)
2001	125	760	3	12.893	0.057	0.007	97	0.005	145	8.265	van der Veer & Witte (unpubl. data)
2002	63	324	4	7.214	0.024	0.011	72	0.150	207	4.968	van der Veer & Witte (unpubl. data)
2007	85	379	5	9.997	0.044	0.007	90	0.010	185	8.140	van der Veer & Witte (unpubl. data)
2009	90	216	4	8.057	0.029	0.005	94	0.024	180	5.220	van der Veer & Witte (unpubl. data)
2014	93	582	6	9.064	0.031	0.002	96	0.001	177	5.487	van der Veer & Witte (unpubl. data)
2019	87	379	5	9.362	0.036	0.005	94	0.004	183	6.588	van der Veer & Witte (unpubl. data)
0-group flounder											
1979	162	89	3	8.156	0.023	0.002	98	0.042	108	2.484	van der Veer et al. (1991)
1980	163	28	3	15.928	0.071	0.003	98	0.028	107	7.597	van der Veer et al. (1991)
1981	153	227	3	19.264	0.089	0.001	97	0.040	117	10.413	van der Veer et al. (1991)
1982	158	23	5	10.266	0.043	0.005	94	0.003	112	4.816	van der Veer et al. (1991)
1986											
1993	130	88	6	8.120	0.034	0.009	76	0.021	140	4.760	van der Veer & Witte (unpubl. data)
1994	122	305	7	12.088	0.050	0.008	88	0.001	148	7.400	van der Veer & Witte (unpubl. data)
1995	136	399	6	12.088	0.050	0.008	90	0.004	134	6.700	van der Veer & Witte (unpubl. data)
1996	153	229	5	13.005	0.054	0.010	90	0.012	117	6.318	van der Veer & Witte (unpubl. data)
1997	146	9	5	7.342	0.039	0.020	58	0.138	124	4.836	van der Veer & Witte (unpubl. data)
1998											
1999											
2000	122	80	6	10.617	0.055	0.006	94	0.001	148	8.140	van der Veer & Witte (unpubl. data)
2001	127	51	5	6.266	0.022	0.003	90	0.009	143	3.146	van der Veer & Witte (unpubl. data)
2002											
2007	113	51	6	7.778	0.035	0.005	90	0.004	157	5.495	van der Veer & Witte (unpubl. data)
2009	139	13	5	2.941	0.006	0.011	8	0.640	131	0.786	van der Veer & Witte (unpubl. data)
2014	121	36	6	3.964	0.016	0.006	52	0.105	149	2.384	van der Veer & Witte (unpubl. data)
2019	114	28	7	3.004	0.012	0.001	20	0.303	156	1.872	van der Veer & Witte (unpubl. data)

intercept and slope were significantly inversely related (Fig. 7) in contrast to the dynamic-self-thinning predictions (see the Appendix Figs A1 & A2).

In both 0-group plaice and flounder, the self-thinning slope showed a significant relationship with the rate of change in density, respectively ($r^2 = 0.66$, $p < 0.01$, $n = 19$ and $r^2 = 0.49$, $p < 0.01$, $n = 13$) (Fig. 8). The slope of the positive relationship was larger in 0-group plaice than in 0-group flounder (Fig. 8).

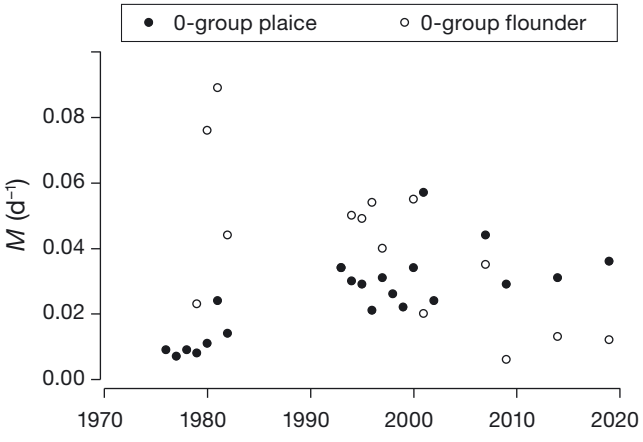

Fig. 4. Trend in mean daily instantaneous rate of change in density (M; d^{-1}) in 0-group plaice and 0-group flounder at the Balgzand intertidal between 1975 and 2019

4. DISCUSSION

In this study, we applied the concept of dynamic self-thinning to flatfish nursery grounds to test the hypothesis that in systems with high benthic food conditions, such as the Balgzand intertidal, carrying capacity is not reached. The analysis confirmed the hypothesis: dynamic self-thinning (lines with a slope of −4/3) were not apparent in the population's development at Balgzand over time in either in 0-group plaice or in 0-group flounder.

4.1. Dynamic (self-)thinning lines and flatfish nursery ground capacity

Carrying capacity will be reached in systems below a certain food availability per individual, caused by

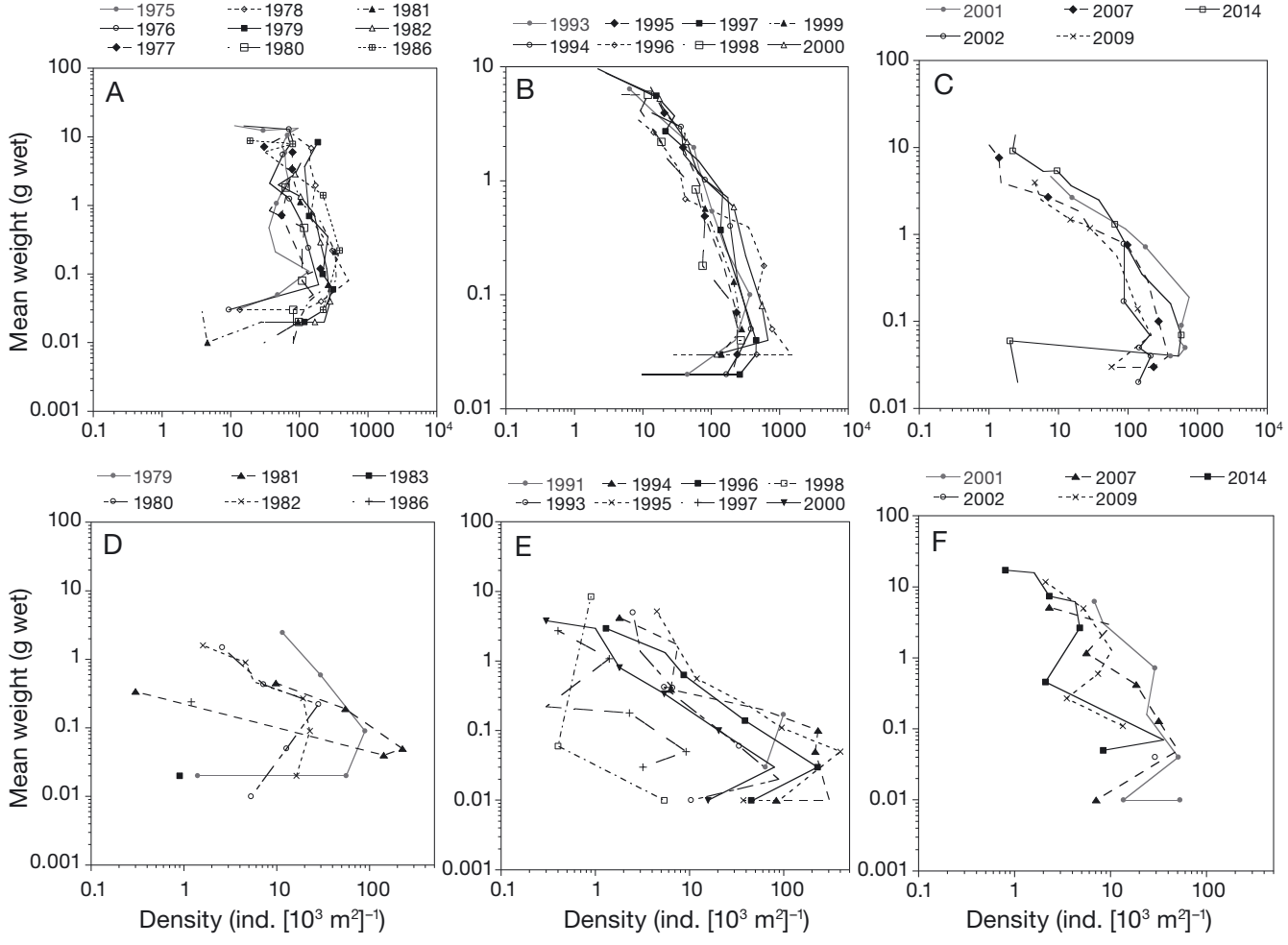

Fig. 5. Relationship between log density and log mean weight of (A,B,C) 0-group plaice and (D,E,F) 0-group flounder at the Balgzand intertidal between 1975 and 2019, split for convenience into three periods: 1975–1986 (A,D); 1991–2000 (B,E) and 2001–2019 (C,F). For slopes and intercepts of individual years, see Figs. S3 & S4 and Table 2

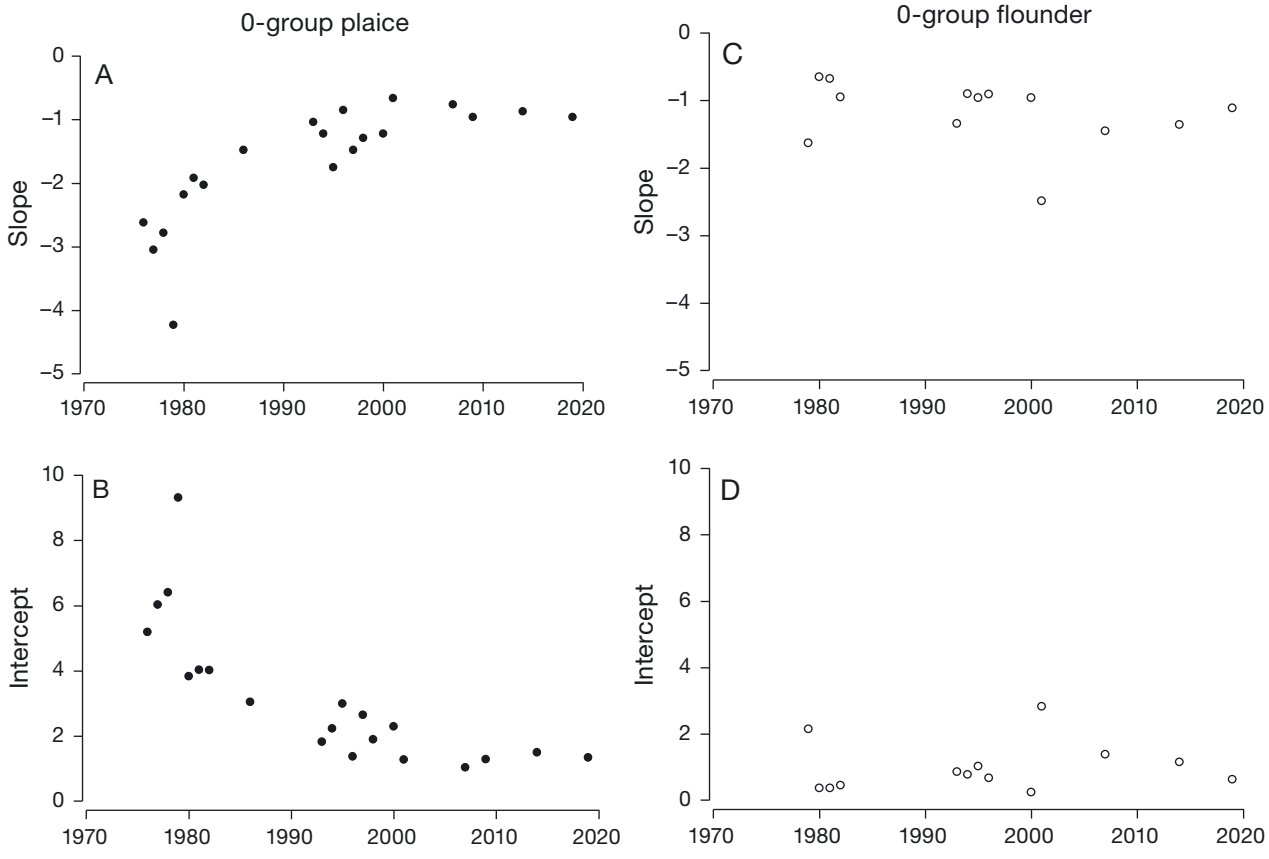

Fig. 6. Trends in relationships between (A,C) slope and (B,D) intercept of the relationship between log density and log mean weight of 0-group plaice and 0-group flounder at Balgzand intertidal between 1975 and 2019. Only slopes and intercepts of significant relationships are listed

either low food productivity or high densities, or a combination of both. The primary and secondary productivity of coastal areas such as the Wadden Sea, with an intermediate position between the marine and freshwater environment, is relatively high because it is supported by the input of nutrients and organic matter from both sides (Houde & Rutherford 1993, Nixon 1995, Cloern et al. 2014, Carstensen et al. 2015). Eutrophication in the late 1970s and 1980s even increased the productivity of coastal areas, especially in the southern North Sea (for an overview, see Desmit et al. 2020). The flatfish nursery grounds in the Wadden Sea system are characterized by a heterogeneous benthic landscape varying not only across multiple gradients but also interannually. Benthic biomass is substantial in a large part of the intertidal (Compton et al. 2013, Singer et al. 2023). Food availability at the Balgzand intertidal is in the order of 10s of g ash-free dry mass per m^2 (Jung et al. 2017), compared to benthic biomass values of a few g dry mass in Swedish and British open bays (McIntyre & Eleftheriou 1968, Evans 1984).

Most flatfish nurseries show high densities during and just after larval settling in spring because settling larvae tend to concentrate spatially into these areas. Peak densities of recently settled flatfish are in the range of 1 to even more than 10 per m^2 in open Swedish (Pihl 1989) and British bays (Nash & Geffen 2000) in spring. At the Balgzand intertidal, peak densities are normally lower, less than 1 ind. m^{-2} for the whole area (about 50 km^2). Sometimes extremely strong year-classes and subsequently extremely high juvenile flatfish densities can occur, such as in plaice after the cold winter in 1963 and 1996 (Harding et al. 1978, van der Veer et al. 2000b). It has been proposed that the carrying capacity of juvenile habitats might become 'saturated', typified by the concentration hypothesis (Beverton 1995); however, even during this extremely strong year-class of 1996 (Table 1), the carrying capacity at the Balgzand intertidal was not reached for 0-group plaice.

In the past, the situation might have been different, and due to lower food availability and higher fish densities, a situation of resource limitation might have oc-

Table 2. Dynamic thinning lines for 0-group plaice and flounder at the Balgzand. Start and end dates of regression are listed, together with number of observations (N), slope and intercept with standard error (SE) and significance (p). ns: not significant at $p < 0.10$. Missing years for 0-group flounder are due to densities and/or number of observations that were too low

Year	Date		N	Slope (SE)	Intercept (SE)	p	Date		N	Slope (SE)	Intercept (SE)	p
	Begin	End					Begin	End				
	0-group plaice						**0-group flounder**					
1975	2 May	8 Oct	13	ns		0.87						
1976	5 May	13 Oct	8	−2.62 (0.38)	5.19 (1.90)	0.04						
1977	29 Mar	20 Sept	6	−3.05 (1.41)	6.03 (2.79)	0.10						
1978	10 May	2 Oct	7	−2.78 (0.56)	6.40 (1.27)	<0.01						
1979	18 Apr	10 Sept	7	−4.23 (2.04)	9.31 (4.69)	0.09	12 Jun	10 Sep	3	−1.63 (0.07)	2.14 (0.11)	0.03
1980	10 Apr	14 Jul	8	−2.18 (0.95)	3.83 (1.86)	0.07	13 Jun	14 Jul	3	−0.65 (0.05)	0.36 (0.05)	0.04
1981	6 May	8 Jul	5	−1.92 (0.35)	4.03 (0.79)	0.01	3 Jun	8 Jul	5	−0.68 (0.11)	0.36 (0.20)	0.10
1982	28 Apr	6 Jul	6	−2.03 (0.54)	4.01 (1.18)	0.02	8 Jun	9 Aug	5	−0.95 (0.20)	0.45 (0.19)	0.02
1986	17 Apr	5 Nov	6	−1.48 (0.61)	3.04 (1.25)	0.07						
1993	27 Apr	18 Aug	7	−1.04 (0.13)	1.82 (0.24)	<0.01	10 May	18 Aug	6	−1.34 (0.18)	0.85 (0.20)	<0.01
1994	18 Apr	22 Aug	8	−1.22 (0.20)	2.22 (0.41)	<0.01	2 May	22 Aug	7	−0.90 (0.17)	0.77 (0.30)	<0.01
1995	3 Apr	14 Aug	9	−1.75 (0.16)	2.99 (0.29)	<0.01	16 May	14 Aug	6	−0.96 (0.14)	1.02 (0.22)	<0.01
1996	9 Apr	28 Aug	9	−0.85 (0.09)	1.37 (0.21)	<0.01	3 Jun	28 Aug	5	−0.91 (0.06)	0.66 (0.08)	<0.01
1997	26 Mar	4 Aug	9	−1.48 (0.15)	2.65 (0.31)	<0.01	26 May	4 Aug	5	ns		0.21
1998	17 Mar	11 Aug	11	−1.29 (0.11)	1.89 (0.20)	<0.01						
1999	8 Mar	10 May	4	ns		0.12						
2000	4 Apr	3 Oct	8	−1.22 (0.10)	2.29 (0.22)	<0.01	2 May	2 Aug	6	−0.96 (0.07)	0.24 (0.07)	<0.01
2001	7 May	21 Aug	5	−0.66 (0.06)	1.27 (0.11)	<0.01	7 May	21 Aug	6	−2.49 (0.60)	2.82 (0.80)	0.01
2002	2 Apr	9 May	3	ns		0.43						
2007	26 Mar	11 Oct	10	−0.76 (0.09)	1.03 (0.14)	<0.01	23 Apr	19 Jul	6	−1.45 (0.29)	1.38 (0.34)	0.01
2009	31 Mar	23 Sep	8	−0.96 (0.11)	1.29 (0.17)	<0.01	19 May	23 Sep	6	ns		0.18
2014	3 Apr	10 Nov	10	−0.87 (0.07)	1.49 (0.11)	<0.01	1 May	21 Oct	7	−1.36 (0.44)	1.15 (0.31)	0.03
2019	27 Mar	16 Sept	8	−0.96 (0.10)	1.34 (0.18)	<0.01	24 Apr	14 Oct	7	−0.11 (0.24)	0.63 (0.17)	<0.01

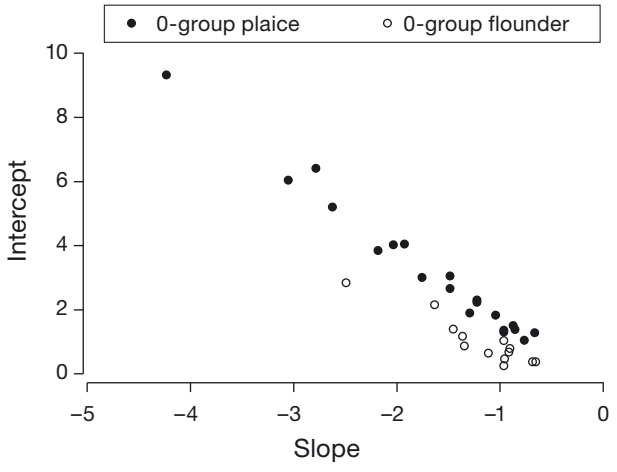

Fig. 7. Relationship between slope and intercept of dynamic self-thinning lines for 0-group plaice and 0-group flounder at Balgzand intertidal between 1975 and 2019. For 0-group plaice: Intercept = −0.68 × Slope − 2.31, $R^2 = 0.98$; for 0-group flounder: Intercept = −0.71 × Slope − 1.43, $R^2 = 0.86$. Only slopes and intercepts of significant relationships are listed

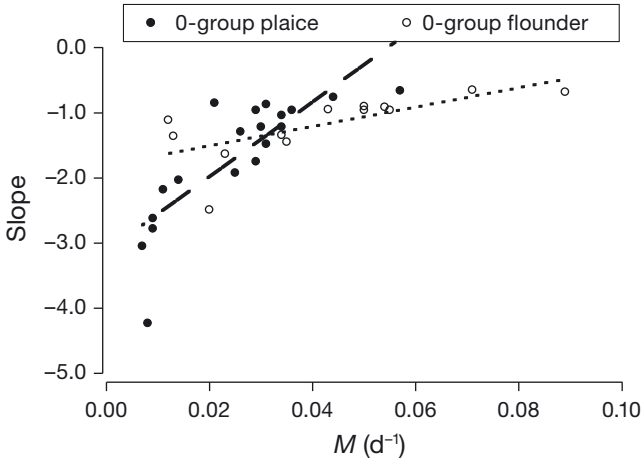

Fig. 8. Relationship between mean daily instantaneous rate of change in density (M) and self-thinning slope for 0-group plaice and 0-group flounder at Balgzand intertidal between 1975 and 2019. For 0-group plaice: Slope = 57.6 × M − 3.15, $R^2 = 0.66$, $p < 0.01$; for 0-group flounder: Slope = 15.0 × M − 1.82, $R^2 = 0.48$, $p < 0.01$

curred (Jones 1989). Nutrient discharges of total nitrogen and total phosphorus in the western Wadden Sea, fuelling primary production, were respectively much lower before the 1970s (van der Veer et al. 1989) up to more than a factor of 2 and 4 lower than in 1935 (van Raaphorst & de Jonge 2004). Furthermore, juvenile flatfish densities of I-, II- and even III-group plaice were much higher in the area before the 1980s (Fonds

1983, van der Veer et al. 2022). With an overlapping prey preference of the various age groups (de Vlas 1979), the 0-group flatfish might have experienced a situation of resource limitation by the combination of higher food competition and lower food availability.

This means that the flatfish nursery ground carrying capacity might have been reached more often in the past. Presently, systems with no nutrient input by river runoff such as open bays are most likely areas with a low primary and secondary productivity, and hence the only systems in which carrying capacity might be reached. In such systems, dynamic self-thinning still can be applied as a tool to analyse carrying capacity.

The relationship between the dynamic self-thinning slope and intercept might give a first impression of whether the system is at carrying capacity. In case carrying capacity is reached, there is no density-dependent growth and no relationship between slope and intercept is expected. In the absence of carrying capacity (and no density-dependent growth), self-thinning lines reflect changes in population density, and slope and intercept will be inversely related (see the Appendix Figs A1 & A2).

4.2. Interpretation of dynamic self-thinning slopes for the Balgzand flatfish nursery

In the 1990s, the dynamic self-thinning slopes of 0-group plaice and 0-group flounder were in the range of −4/3, which corresponds with theoretical predictions of limitation due to carrying capacity (Begon et al. 2006, Nash et al. 2007). However, it is unlikely that such a slope of −4/3 during the 1990s represented an indication that flatfish nursery ground carrying capacity was reached during that period. First of all, juvenile flatfish predation pressure and potential competition were highest and food availability was lowest in the 1970s and not in the 1990s (Jung et al. 2017, van der Veer et al. 2022). Secondly, stomach content composition illustrates that 0-group plaice and flounder show an overlap in prey preference (de Vlas 1979, Poiesz et al. 2020). In combination with a similar growth pattern over time at the Balgzand intertidal with maximum growth at the beginning of the growing season (van der Veer et al. 2010, Freitas et al. 2012), it would be expected that dynamic self-thinning lines would be similar for 0-group plaice and 0-group flounder with similar trends over time. Thirdly, in the case that during the growing season carrying capacity was reached, interannual variability in nursery ground carrying capacity due to differences in flatfish abundance and food availability would translate into interannual differences in intercept but not in the slope of −4/3 (Begon et al. 2006), and hence not in a relationship between slope and intercept as found at Balgzand for both 0-group plaice and 0-flounder (see the Appendix Figs A1 & A2). The fact that annual growth patterns for 0-group plaice and flounder at Balgzand are similar and mainly determined by prevailing water temperature (Zijlstra et al. 1982, van der Veer 1986, van der Veer et al. 2010, Freitas et al. 2012, this study) imply that differences between 0-group plaice and 0-group flounder in the relationship between log density and log mean size must represent differences in density patterns over time, caused by mortality and/or migration.

Applying the concept of dynamic self-thinning for 0-group plaice and flounder at the Balgzand intertidal nursery grounds resulted in a large variability in slopes that, in almost all years, differed from −4/3. In 0-group plaice, a significant decrease in slope from −2.69 on average in the 1980s to −0.81 in the 2010s was found, and in 0-group flounder, the slope showed variation but no significant trend from−0.98 in the 1980s to −1.77 in the 2010s. The question is why these trends differ between 0-group plaice and flounder.

With respect to differences between plaice and flounder, experimental studies reveal that the physiological performance of juvenile plaice and flounder is very similar. The optimal temperature and tolerance range are almost the same (Freitas et al. 2010), as is their maximum possible daily growth under optimal food conditions in relation to water temperature (Fonds et al. 1992, Freitas et al. 2012). The life cycles of 0-group plaice and 0-group flounder at the Balgzand intertidal also show a similar pattern: settling pelagic larvae in spring, a fast growth during the summer and a migration to deeper water in autumn. Differences between both species occur relative to the timing of larval immigration (March–April in plaice versus April–May in flounder) and larval size at settlement (10–15 mm in plaice versus 5–10 mm in flounder). Settlement of flounder at the Balgzand intertidal is also restricted to more silty habitats (van der Veer 1986, van der Veer et al. 1991).

This earlier settlement of plaice at a larger size results in a lower decrease in numbers during the growing season compared to 0-group flounder, as found in the 1980s. The decrease in density in the 1980s in both species was mainly caused by mortality (van der Veer 1986, van der Veer et al. 1991). In 0-group flounder, this pattern of decrease in density has not changed over time.

In contrast, spatiotemporal changes in distribution have occurred in 0-group plaice since the mid-1980s:

settlement of 0-group plaice still occurs at the Balgzand intertidal, but they start to move to deeper waters much earlier, in early summer (Freitas et al. 2016). This earlier migration to deeper waters results in an additional source of decrease in numbers and an increase in the rate of decrease in numbers of 0-group plaice over time.

These trends in the rate of decrease in density in both species are reflected in the dynamic self-thinning slopes over time. The slopes in 0-group flounder show interannual fluctuations but without any trend. In 0-group plaice, the slopes showed a significant decreasing trend, reflecting greater reductions in density at the Balgzand intertidal during the season.

4.3. Accuracy of dynamic self-thinning lines

To be able to interpret the dynamic self-thinning lines for the Balgzand flatfish populations correctly, the question arises of how accurate and robust the estimates of slope and intercept are. The procedures to estimate flatfish density and to estimate the rate of change in density followed respectively Zijlstra et al. (1982) and Iles & Beverton (1991) to be able to compare the results with previous studies. Density estimates at the Balgzand intertidal are based on surveys using a 2 m beam trawl, with a high number of hauls (up to 36) and detailed information about catch efficiency. For small 0-group flatfish, the catchability is 100%, decreasing to 75% at the end of the season at a fish size of 12 cm (Kuipers 1975). By repeating the survey within a few days and by comparing both estimates, an indication of the precision of the density estimate was obtained, suggesting confidence limits of the mean abundance estimates of about ~35% (Zijlstra et al. 1982, NIOZ unpubl. data).

The rate of change in density was estimated based on regression analysis of the natural logarithm of mean density against date of sampling of the various surveys from peak density onwards (Iles & Beverton 1991, van der Veer et al. 2000b). Due to the high frequency of sampling of the Balgzand intertidal (in principle, twice a month), each regression analysis could be based on at least 3–9 surveys. This resulted for both species in significant relationships with a standard error of on average 19% in both 0-group plaice (range: 6–33%) and in 0-group flounder (range: 1–26%) in almost all years (Table 1).

The calculated dynamic self-thinning lines at the Balgzand intertidal resulted in significant correlations between log mean density and log mean weight in 22 out of 23 years for 0-group plaice and in 14 out of 16 years for 0-group flounder (Table 2). Standard errors of the slope and intercept for slopes were 20% (range: 8–48%) and 14% (range: 4–32%), respectively, on average for 0-group plaice and 0-group flounder; for the intercept, 23% (range: 7–50%) and 27% (range: 5–56%). These standard errors of the slopes and intercepts were, except for the slope in 0-group flounder, larger than the standard errors in the change in mean density. Although statistical analyses that take into account the error in the estimate of the change in density might be more sophisticated, the results of the methods used in this study also appear reliable and robust.

There were a high number of significant relationships found in this study between the annual development of population density and mean individual weight (36 out of 39 cases) compared with only 2 (out of 12 cases) significant relationships in the analyses for Port Erin Bay (Isle of Man) and Ardmucknish Bay (Scotland) by Nash et al. (2007). The reasons for these differences are unclear; however, there are differences in the structure of the nurseries when comparing the Balgzand intertidal with the British bays. It illustrates that under these conditions, significant correlations between log mean density and log mean weight can be obtained for mobile as well as sessile animal populations. However, accurate estimates over a number of years are a pre-requirement.

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Appendix

Text A1. The concept of dynamic self-thinning

Self-thinning refers to the situation in which population biomass no longer increases exponentially due to a population-level growth cessation caused by resource limitation (competition for food) or structural or physiological constraints (competition for space). Under constant food or energy conditions, as the individuals grow, energy requirements increase, and self-thinning starts operating as soon as energy becomes limiting. The resulting slope of the dynamic thinning line between population density and mean biomass is species-specific and determined by the (temperature-dependent) relationship between energy requirements for maintenance and metabolic biomass (W^{β}). As soon as growth becomes zero, total biomass remains constant, resulting in a linear relationship between population density and mean individual biomass on a log–log plot. These species-specific boundary lines can be defined as lines beyond which combinations of density and mean individual weight are not possible, and they reflect, in essence, the carrying capacity of the environment.

If food remains constant throughout the growth of a plant population (for which light is the resource), the slope of the line between population density and mean biomass is −3/2 as a result of a squared decrease in density accompanying a cubic increase of weight (Yoda et al. 1963, Begon et al. 1986). In animal populations, the slope of self-thinning is more likely −4/3 compared to −3/2 self-thinning in plants, given that the metabolism of an individual and hence food requirement is proportional to weight$^{0.75–0.80}$, the so-called metabolic biomass (Winberg 1956, Duncan & Klekowski 1975, Peters 1986). Therefore, for an animal population, the average metabolism should be proportional to mean weigh$^{0.75–0.80}$. In addition, food available per individual is determined by total food available (F) and animal density (D), which results in:

$$F / D = \mathrm{c} \times W(3/4)$$

which is equal to

$$W = \mathrm{c} \times D(-4/3) \text{ and } \log W = c(-4/3) \times \log D$$

where c is a constant.

This relationship might differ depending on the species-specific exponent of metabolic biomass (between 0.75 and 0.80), animal mobility and fluctuating food conditions. For more detail, see Begon et al. (1986).

For juvenile flatfishes under constant food conditions, in the case of dynamic self-thinning, it would follow the line described in Fig. A1. First, an initial phase with an increase in numbers and a relatively slower increase in biomass due to still ongoing settlement of small individuals. Next, settlement density should decrease due to nursery ground mortalities, and mean weight should increase at a faster rate. If the density reaches the carrying capacity of the nursery ground, then self-thinning occurs and the relationship between density and mean weight during this phase follows a slope of ca. −4/3. At the end of the growing season, flatfish density declines rapidly due to the beginning of emigration. Mean weight may also decrease, and apparent growth rate slows because the larger individuals move off the nursery grounds first, leaving the smaller individuals behind. In the case of self-thinning, the intercept represents the maximum possible density whereby mean weight approaches zero.

Interannual variations in productivity can result in interannual variability in carrying capacity within and among nursery grounds. Differences in carrying capacity are reflected in dynamic self-thinning lines oriented parallel to each other, which means lines with similar slopes but different intercepts (Fig. A2 A). In this case, carrying capacity is not reached, growth is not density-dependent and interannual variability in dynamic self-thinning is caused by differences in changes in density over time (Fig. A2 B).

In the case where carrying capacity is reached, slope and intercept will not be related (Fig. A2 C); in the case where carrying capacity is not reached, slope and intercept will be inversely related (Fig. A2 D). Interannual variability in environmental conditions and sampling accuracy will cause some error in the estimates of slope and intercept. Therefore, preferable information covering a number of years should be collected.

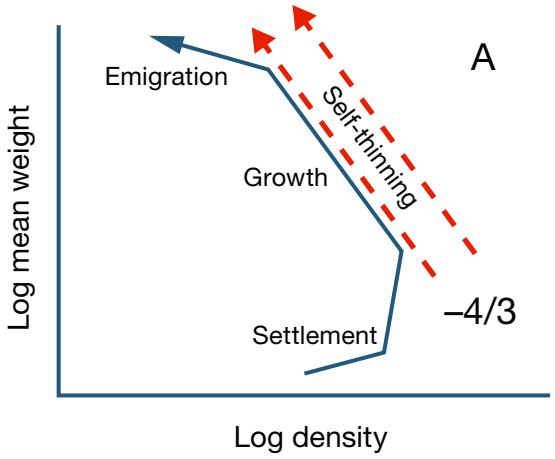

Fig. A1. Expected seasonal pattern of the relationship between log flatfish density and log mean weight in the case of dynamic self-thinning. Red lines: different levels of self-thinning (different levels of carrying capacity). Redrawn from Nash et al. (2007)

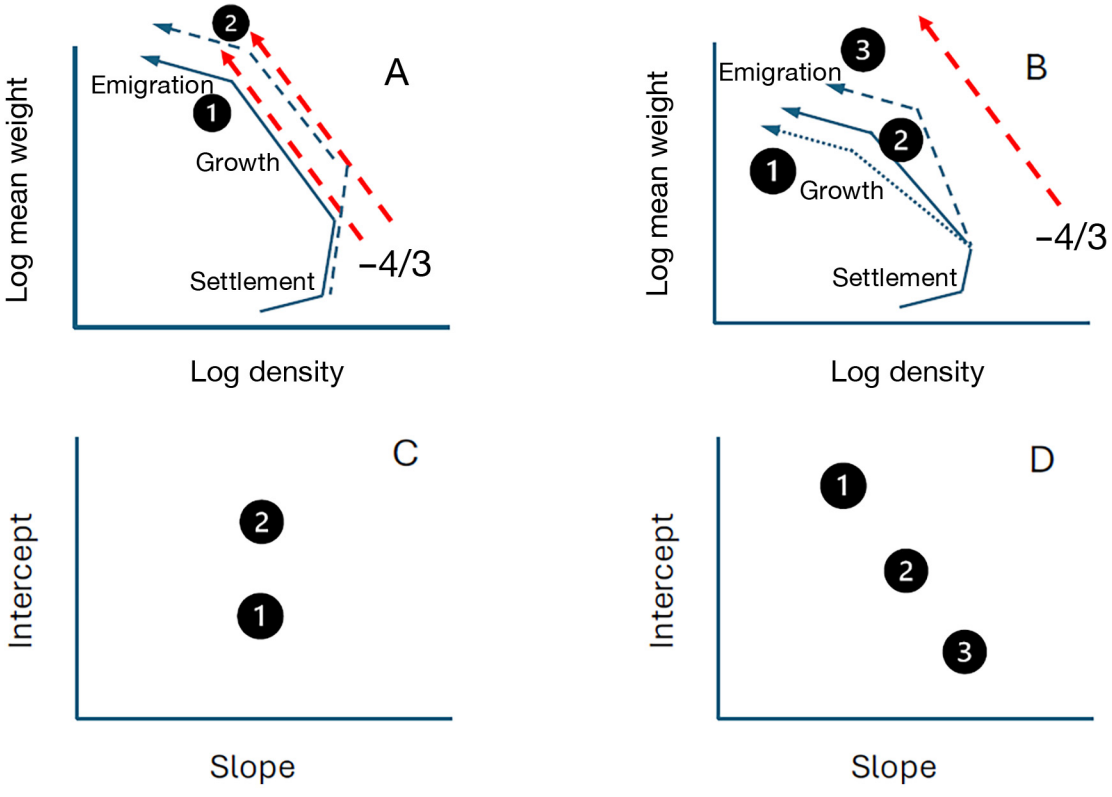

Fig. A2. Theoretical patterns between log density and log mean weight in which carrying capacity is (A) reached and (B) not reached. (C,D) Predicted resulting relationships between slope and intercept, respectively. Red dashed lines: different levels of carrying capacity; numbered dots: different years; blue solid, dashed and dotted lines: patterns in different years. For more information, see Text A1

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