Growth, Survival, and Mortality of Juvenile and Adult Alien Conrad's False Mussel *Mytilopsis leucophaeata* (Conrad, 1831) (Mollusca, Bivalvia, Dreissenidae) in a Brackish Canal

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GROWTH, SURVIVAL, AND MORTALITY OF JUVENILE AND ADULT ALIEN CONRAD'S FALSE MUSSEL *MYTILOPSIS LEUCOPHAEATA* (CONRAD, 1831) (MOLLUSCA, BIVALVIA, DREISSENIDAE) IN A BRACKISH CANAL

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ABSTRACT The false mussel, *Mytilopsis leucophaeata* originating from the Atlantic coast and Gulf of Mexico in North America invaded brackish water systems in Europe. Seasonal sessile population structure is determined by spat fall, growth, and mortality. Juvenile and adult *M. leucophaeata* were kept in cages in a brackish water canal to study their mortality and to estimate annual and seasonal shell growth rate in relation to shell size and water temperature. Mortality increased with increasing temperature with the strongest effect on the 4–6 mm and 8–10 mm size classes. The average mortality of all size classes of *M. leucophaeata* in cage experiments was lowest in winter, increased from April to July, and peaked in July and August. Between a water temperature of 18 and 23°C, a strong growth was observed for mussels of size classes 2–14 mm, whereas mussels of size class 14–16 mm showed only a slight growth ($<20\ \mu\text{m day}^{-1}$) and size classes 16–18 mm and 18–22 mm showed no growth at all. When water temperature was between 9 and 18°C, there was no or slight growth, and at lower than 9°C, hardly any growth. Especially for the small mussels, the influence of the water temperature on shell growth is strong. Polynomial regression showed a mean summer growth rate of $94\ \mu\text{m day}^{-1}$ for the 2–4 mm class, $37\ \mu\text{m day}^{-1}$ for the 10–12 mm class, and no growth for the 18–22 mm class. Analysis of all available (literature) data yielded mean summer and annual growth rates of *M. leucophaeata* collected in brackish western European harbors and canals ranging from 30 to $133\ \mu\text{m day}^{-1}$ and 8 to $49\ \mu\text{m day}^{-1}$, respectively. Increase of water temperature by climate change or thermal discharges will increase growth rates and mortality of this mussel.

KEY WORDS: *Mytilopsis leucophaeata*, brackish water, Conrad's false mussel, dark false mussel, Dreissenidae, population dynamics, growth, mortality, survival

INTRODUCTION

Dreissenid bivalves belong to world's most successful invaders (Nalepa & Schloesser 1993, 2013, Van der Velde et al. 2010). The Zebra mussel [*Dreissena polymorpha* (Pallas, 1771)] and Quagga mussel [*Dreissena rostriformis bugensis* Andrusov, 1897] are well-known invasive species. Both species originating from the Ponto-Caspian region invaded nearly all countries in Europe and many states in North America (Van der Velde et al. 2010, Benson 2014, Matthews et al. 2014). These bivalves can have severe ecological and economic impacts in freshwater areas (Jenner et al. 1998, Kelly et al. 2010, Mackie & Claudi 2010). A third dreissenid species, Conrad's false mussel or dark false mussel, *Mytilopsis leucophaeata* (Conrad, 1831) originating from the Atlantic coast and Gulf of Mexico in North America invaded brackish waters in Europe and Asia Minor (Zhulidov et al. 2015 and literature therein). Several biological aspects of this species have already been studied in Europe and North America; however, the current body of knowledge on the biology of Conrad's false mussel is far behind that of the well-studied Zebra mussel and Quagga mussel (Kennedy 2011).

In some areas with brackish water, *Mytilopsis leucophaeata* can reach very high densities. They attach themselves after settlement by means of byssus threads on hard substratum. Therefore, this species poses biofouling risks for industrial

(cooling) water facilities (Jenner et al. 1998, Mackie & Claudi 2010, Rajagopal & Van der Velde 2012). Their densities and seasonal population structure in relation to the environmental factors was studied earlier. Spat fall, growth, and mortality are important factors determining the size-frequency distribution and densities of the full-grown mussels (Van der Gaag et al. 2014, 2017).

Growth in mussels is mostly measured in terms of shell length. Several methods are used to assess growth, viz., the use of mean or modal size-frequency distributions (Van der Gaag et al. 2017), measurements of marked mussels, the use of annual disturbance and seasonal growth stop lines on the shell (Schütz 1969), and the use of experimental cages containing mussels of different initial sizes (Seed 1976). According to Seed (1976), all methods to estimate growth have their own intrinsic problems. Most reliable estimates could only be obtained by using a combination of methods.

In the present study, *Mytilopsis leucophaeata* was kept in cages to determine (1) the mortality of differently sized mussels in relation to water temperature, (2) the influence of water temperature on their growth, (3) the annual and seasonal shell growth rate, and (4) the relation between shell size and growth of this species.

MATERIALS AND METHODS

Study Area

This study was carried out in the North Sea Canal (Dutch name Noordzeekanaal) near Velsen (canal km 3),

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Figure 1. Map of the North Sea Canal. The study location is indicated by an arrow.

the Netherlands (Fig. 1). In this brackish water canal, a salinity gradient is present as it connects the North Sea with oligohaline ports of Amsterdam. *Mytilopsis leucophaeata* is present in this area since 1895 (Maitland 1897) and can reach high densities here (Van der Gaag et al. 2017 and literature therein).

Sampling of Water Quality Parameters

Water temperature (°C) and salinity of the North Sea Canal were monthly measured, using a mercury thermometer and YSI model 33 S-C-T meter, respectively. Chlorophyll *a* data were derived from Servicedesk Data Data-ICT-Dienst Rijkswaterstaat, Delft for the North Sea Canal near Velsen. All physico-chemical measurements were carried out in the surface water in the period 1989 to 1995. Salinity was only measured during 1989 to 1993.

Collection of Data from Mussels in Cages

Over the period 1990 to 1993, five experiments were performed to study growth and mortality of *Mytilopsis leucophaeata* in cages under further natural environmental conditions. Two stainless steel perforated cages (40 by 40 cm, height 15 cm, mesh size 2 mm, and all mesh 30% of the surface) with nine perforated compartments measuring 13 × 13 cm in size were used. In each compartment, 25 or 35 mussels of various size classes were put [shell lengths 2–4 mm (when present), 4–6 mm, 6–8 mm, 8–10 mm, 10–12 mm, 12–14 mm, 14–16 mm, 16–18 mm, and 18–22 mm] (Table 1). The cages were made heavier by attaching a tile (30 × 30 × 4.5 cm, weight 9.5 kg) to their underside. The cages were placed at the canal bottom at a water depth of 75 cm in the shallow littoral zone under a pier at the landing site of a ferry and attached by stainless steel cables to the pier pole. Refreshment of water in the cages via flow through the numerous pores was guaranteed

TABLE 1.
Experimental setup of the cage experiments with *Mytilopsis leucophaeata*.

Experiment	Mussels per compartment	Number of compartments	Date of start experiment	Termination of experiment
Cage 1	25	9	June 14, 1990	June 30, 1992
Cage 2	25	9	July 25, 1990	June 30, 1992
Cage 3	35	8	May 17, 1991	August 17, 1992
Cage 4	35	8	August 18, 1992	May 3, 1995
Cage 5	35	8	April 21, 1993	March 1, 1996

Figure 2. Water temperature and chlorophyll *a* in the North Sea Canal in Velsen in the period 1989 to 1994 (data chlorophyll *a* from Servicedesk Data Data-ICT-Dienst Rijkswaterstaat, Delft).

because of wind- and shipping-induced currents and by regular cleaning of the cages to keep the pores open.

The cages were extracted monthly from the water whereafter empty shells and dead mussels were removed from their compartments. At each monthly visit during the 1990 experiment, shell length of each mussel was measured with a Vernier caliper (accuracy 0.1 mm). Shell length is indicated in the paper as (shell) size and increments of (shell) size as shell growth. In the 1991 experiment, only the numbers of survived mussels were recorded monthly and the dead ones and empty valves were removed. In the 1992 and 1993 experiments, the monthly survival was recorded, and at several dates during the growing season, all shell lengths of the survivors in the cages were measured. During each visit, the cage was cleaned from fouling [mostly caused by barnacles *Amphibalanus improvisus* (Darwin, 1854) and the hydroid *Cordylophora caspia* (Pallas, 1771)]. When present, young mud crabs [*Rhithropanopeus harrisii* (Gould, 1841)] were removed as individuals in early life stages and were able to enter the cages through pores (2 mm) and small cracks between the cover and the cage. Living mussels were put back in their compartment after measurements. Visits continued every month and the mussels were followed by the previously mentioned procedure until 100% mortality of the mussels was recorded. Both cage experiments from 1990 (started June 14 and July 25) were used to generate combined data for analysis of growth (further mentioned combined experiments) or used as separate experiments named by their

start date. In both experiments, shell length was measured monthly. For the combined data, a correction was made for the mean growth between the two different starting days of the experiments. June 14 was used as the starting date for the combined data. A distinction was made between summer growth (June 14, 1990 up to August 23, 1990) and overall growth (June 14, 1990 up to January 16, 1991). Marking of small *Mytilopsis leucophaeata* shells is difficult. Therefore, individual mussels could not be distinguished and the increase in average size of mussels for each compartment was used to calculate growth rates ($\mu\text{m day}^{-1}$).

Statistical Analyses

The relation between growth rate and average initial size was analyzed by fitting a polynomial regression. Including cage did not significantly improve the model of the summer and the overall growth.

A linear model (LM) was used to analyze the effect of water temperature and the fixed effect of size class on growth using the LM function in R statistics (R Core Team 2015) and a binomial generalized LM (GLM) was used to analyze the effect of water temperature and the fixed effect of size class on the fraction of dead individuals. The analyses were performed using the GLM function in R statistics. Model selection was based on the lowest Akaike information criterion value in combination with testing for a significant model improvement. The latter was decisive. Significant model improvement was analyzed using the difference in deviance between the two models. The difference in deviance is Chi-square distributed. Subsequently, the *P* value was calculated using the difference in deviance and the corresponding degrees of freedom. Nesting effects of experimental year were not included as including random slopes did not significantly improve the model. Overall mortality across the four experimental runs was analyzed using a binomial GLM using R statistics.

SigmaPlot for Windows Version 11 (2008) was used for calculations of mean, standard deviation, and polynomial regression (i.e., the regression equation with the highest R^2) with parameters and plotting of data.

RESULTS

Environmental Conditions

The surface water temperature at the sampling site varied between 2.9 and 26.2°C (mean 15.2°C $\pm$ SD 6.3°C) (Fig. 2). Chlorophyll *a* concentrations reached a maximum peak in March and April when the water temperature rose followed by some lower peaks in summer until the end of September

TABLE 2.

Generalized linear model results of the size class-dependent mortality of *Mytilopsis leucophaeata*—dependent variables are water temperature, size class, and the interaction between water temperature and size class.

Source	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
Size class dependent mortality					
NULL	—	—	432	1,321	—
Water temperature	1	22	431	1,299	<0.001
Size class	7	19	424	1,280	<0.01
Water temperature: size class	7	29	417	1,251	<0.001

Figure 3. (A) Cumulative mortality of *Mytilopsis leucophaeata* (%) and water temperature in the North Sea Canal during the cage experiments of 1990, 1991, 1992, and 1993. (B) Relation between water temperature and dead individuals for the various size classes.

(Fig. 2). During wintertime, chlorophyll *a* showed very low concentrations. The salinity varied between 2.7 and 9.2 (mean $5.4 \pm \text{SD } 1.6$), rising in dry periods and lowering in rainy periods when more fresh water flows into the North Sea Canal from the surrounding area and the Amsterdam–Rhine Canal.

Mortality and Survival

In the combined experiments from 1990, the mortality increased with increasing temperature ($Df = 1$, deviance = 22.286, P value < 0.001) and with increasing size ($Df = 7$, deviance = 18.816, P value < 0.01) (Table 2). A significant

Figure 4. (A) Survival (%) of shell length classes of *Mytilopsis leucophaeata* in the cages during 13 mo after start (month 1) of the experiments [experiment 1990 (2×) + 1991 + 1992 + 1993]. (B) Overall survival of individuals (%) in relation to time for these experiments. 100% mortality was observed after 1,289 days.

interaction was found between temperature and size ($Df = 7$, deviance = 28.756, P value < 0.001), indicating that the effect of temperature varies across size classes. The highest effect of temperature on mortality was found for the 4–6 mm and 8–10 mm size class (Fig. 3B). Both chlorophyll *a* and salinity did not significantly improve the model and were excluded. Overall mortality in 1990 significantly increased with time (days) ($Df = 1$, deviance = 14.789, P value < 0.001) (Fig. 4B). After 726 days, 99% of the initial individuals were dead (100% mortality after 746 days). The overall mortality of all classes of *Mytilopsis leucophaeata* in the cages in four experiments (1990, 1991, 1992, and 1993) showed in all cases over 4 y the lowest mortality in winter, an increasing mortality from April to July, and high mortality peaks in July and August (Fig. 3A). Lumped data on survival for various size classes of all cage experiments (1990, 1991, 1992, and 1993) of *M. leucophaeata*, for 14 mo, are shown for each size class in Figure 4A. In the first 7 mo, the 4–6 mm class showed a lower survival than the other classes. In the second 7 mo, the 16–18 mm class and the 18–22 mm class showed a lower survival. After 14 mo, 2.0%–13.2% of the mussels had survived. A polynomial regression equation with respect to the survival percentage over time (days) was calculated ($103.87Y = 12.33X - 0.42X^2$, $R^2 = 0.973$, P value < 0.001, $n = 1176$) (Fig. 4B).

Growth

Between a water temperature of 18 and 23°C, a strong growth was observed for the size classes from 2 to 14 mm. The classes from 14 to 22 mm showed weak growth (<20 $\mu\text{m day}^{-1}$) or no growth at all (Fig. 5). In the cage experiment from June 14 to August 23, 1990, a fast shell growth period was observed, followed by a slow growth period from August 23 to December 13 (Table 3). For the first period (70 days), a polynomial regression line ($Y = 0.0165X^3 - 0.445X^2 - 3.09X + 105.87$; $n = 9$; $R^2 = 0.996$, F value: 428, P value < 0.001) was calculated giving the optimum fit between shell size (X) and shell growth (Y).

With increasing initial size of *Mytilopsis leucophaeata*, growth decreased significantly (F value: 6.23, Df : 7, P value < 0.001). Higher water temperatures significantly increased growth (F value: 41.15, Df : 1, P value < 0.001), although this

TABLE 3.

Growth of various size classes of *Mytilopsis leucophaeata* in a cage in the North Sea Canal at Velsen.

Size class (mm)	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–22
Mean shell length (mm) June 14 start	3.5	5.1	7.2	9.1	10.8	13.0	14.9	16.8	19.2
Mean shell length (mm) August 23	10.1	10.6	12.0	13.0	13.4	15.1	15.8	17.2	19.2
Mean shell length (mm) December 13	*	12.0	12.5	13.7	13.9	15.8	16.3	17.0	19.4
Growth (mm) period 1†	6.6	5.5	4.8	3.9	2.6	2.1	0.9	0.4	0
Growth (mm) period 2‡	n.a.	1.4	0.5	0.7	0.5	0.7	0.5	0	0.2
Growth rate $\mu\text{m day}^{-1}$ period 1†	94	79	69	56	37	30	13	6	0
Growth rate $\mu\text{m day}^{-1}$ period 2‡	n.a.	13	5	6	5	6	5	0	2

n.a., not applicable.

* 100% mortality.

† Period 1: June 14 to August 23, 1990.

‡ Period 2: August 23 to December 13, 1990.

Figure 5. Mean growth rate of *Mytilopsis leucophaeata* of different size classes in relation to water temperature in the 1990 experiment (data of one cage).

effect differed between size classes (F value: 3.75, Df: 7, P value < 0.01) (Table 4).

With increasing starting size of *Mytilopsis leucophaeata*, mean summer growth (June to August) decreased significantly (F value: 69.07, Df: 2, P value < 0.001) (Table 3, Fig. 6A). Mean overall growth (June to December) within a year significantly decreased with increasing starting size of *M. leucophaeata* (F value: 142.09, Df: 2, P value < 0.001) (Table 3, Fig. 6B). Most growth occurs during the summer season. Hereafter, growth was negligible for all size classes. The mean summer growth of *M. leucophaeata* was characterized by the equation $Y_1 = 0.214X^2 - 12.05X + 148.18$, with Y_1 = mean summer growth (in $\mu\text{m day}^{-1}$) and X = initial size (in mm). The mean overall growth of *Mytilopsis leucophaeata* was characterized by the equation $Y_2 = 0.135X^2 - 5.43X + 54.415$, with Y_2 = mean overall growth (in $\mu\text{m day}^{-1}$) and X = initial size (in mm). The calculated mean summer growth became zero at a size of 18.1 mm; the calculated mean overall growth became zero at a size of 18.9 mm. Growth decreased with shell length (Table 5).

DISCUSSION

The 1 y and a few months old mussels with a length of 19 mm died off in the months November and December in the docks in Amsterdam according to Vorstman (1933). In the cage experiments, the 16–18 mm class and the 18–22 mm class also showed high mortality at the end of the year. Most probably they do not recuperate enough from the reproduction season to survive another winter season.

In an experimental setup with a water flow rate of $1 \text{ m}^3 \text{ h}^{-1}$ in the harbor of Antwerp, *Mytilopsis leucophaeata* smaller than

5 mm showed a growing period from May to August in 2003 with a growth rate of $30 \mu\text{m day}^{-1}$; in June 2003, a maximum growth rate of $58 \mu\text{m day}^{-1}$; and in 2004, a growing period from May to July with a growth of $23 \mu\text{m day}^{-1}$ (Verween et al. 2006). This leads to an annual shell growth of $3\text{--}6 \text{ mm y}^{-1}$. In the cage experiment in the North Sea Canal started June 14, 1990, the 2–4 mm size class was growing for 70 days with a mean growth rate of $94 \mu\text{m day}^{-1}$. The mean shell growth rate of free-living mussels of this size class mostly living on the undersides of stones in the littoral zone was $69 \mu\text{m day}^{-1}$ in 3 mo (Van der Gaag et al. 2017). This growth rate was lower than that of the caged ones. This indicates good growth conditions in the cages by higher exchange of water and food. In the cage experiment started at August 18, 1992, the annual shell growth rate was $27 \mu\text{m day}^{-1}$ for the 4–6 mm

TABLE 4.

Linear model results of the size class-dependent growth of *Mytilopsis leucophaeata*—dependent variables are water temperature, size class, and the interaction between water temperature and growth of the size class.

Source	Df	F value	Pr (>F)
Size class dependent growth			
NULL	—	—	—
Water temperature	1	41.1548	<0.001
Size class	7	6.2348	<0.001
Water temperature: size class	7	3.7519	<0.01

Figure 6. Mean summer growth rate (A) and mean overall growth rate (B) of *Mytilopsis leucophaeata* in relation to their starting size (grey area: 95% confidence interval) in the two cages in 1990.

size class. This leads to a mean annual shell growth of 10–11 mm y^{-1} .

Mussels settled on panels in the North Sea Canal showed a fast shell growth during July to November, almost no growth during December to May, and again a fast growth during May to July (Van der Gaag et al. 2017). There was a strong difference in growth between individuals. Fast growing individuals reached a maximum shell length of 20.9 mm in 14 mo and the slowest growing or last settled individuals reached in the same period a maximum shell length of 4.1 mm (Van der Gaag et al. 2017). In shunt-placed mussel monitors (Mossel-Monitor) connected to the cooling circuits of the power stations of Velsen and Hemweg (Amsterdam), the fast-growing

mussels reached a shell length of 14 mm in 98 days after settlement, resulting in a growth rate of 133 $\mu m day^{-1}$ (Rajagopal et al. 1995). A review of available data on mean seasonal and annual growth of *Mytilopsis leucophaeata* in canals and harbors of Western Europe reveals high spatial variability (Table 6). The lowest and highest annual growth in experimental setups have been recorded in the harbor of Antwerp and the Kiel Canal (Nord-Ostsee-Kanal), respectively. In the North Sea Canal (Noordzeekanaal), *M. leucophaeata* yielded intermediate values.

In the North Sea Canal, the highest chlorophyll *a* values are always measured before the growing season of *Mytilopsis leucophaeata* and, therefore, a direct correlation could not be found as also found by Verween et al. (2006) in the harbor of Antwerp.

TABLE 5.
Shell growth rate of various size classes of *Mytilopsis leucophaeata* in the North Sea Canal.

Period	mm class										Days
	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–22	Growth rate	
June 14 to August 23, 1990	94	79	69	56	34	27	13	6	0	$\mu m day^{-1}$	70
July 25 to September 6, 1990	–	76	76	38	21	10	5	3	0	$\mu m day^{-1}$	42
August 18 to October 7, 1992	–	55	27	18	15	9	9	9	0	$\mu m day^{-1}$	50
April 21 to September 22, 1993	–	62	56	37	19	17	7	14	6	$\mu m day^{-1}$	154
Mean growth rate	94	68	57	37	22	16	7	7	2	$\mu m day^{-1}$	n.a.
SD	n.a.	11	22	16	8	8	5	6	3	$\mu m day^{-1}$	n.a.

n.a., not applicable.

TABLE 6.

Mean seasonal and annual shell growth of *Mytilopsis leucophaeata* in canals and harbors in Western Europe.

Sample area/substratum	Summer growth (mm)	Days	Summer growth rate ($\mu\text{m day}^{-1}$)	Annual growth (mm)	Annual growth rate ($\mu\text{m day}^{-1}$)	References
North Sea Canal*, Oosterdok, Amsterdam/glass slides	7	± 60	110	11	30	Vorstman (1933)
North Sea Canal*/littoral stones	8.5	± 100	89	10–15	27–41	Van der Gaag et al. (2017)
North Sea Canal*/panels	6.4	51	125	11.4	32	Van der Gaag et al. (2017)
North Sea Canal*/cages	6.5	70	94	10–11	27	This publication
Harbor of Antwerp (Belgium)/experimental setup	5	± 120	30	3–6	8–16	Verween et al. (2006)
Kiel Canal† (Germany)/piles	9	± 100	90	15–18	41–49	Schütz (1969)
North Sea Canal*/mussel monitor	14	98	133	–	–	Rajagopal et al. (1995)

* Noordzeekanaal (in Dutch).

† Nord-Ostsee-Kanal (in German).

Shell length growth of *Mytilopsis leucophaeata* was significantly correlated with water temperature. The highest growth was in June and not in August when the temperature was at its peak (Verween et al. 2006). The cage experiment showed higher than 18°C for the classes 2–14 mm a strong growth, for the class 14–16 mm a slight growth, and for the classes longer than 16 mm a negligible or no growth. At water temperatures between 9 and 18°C, a slow or no growth was recorded. At less than 9°C, no or a very low growth occurs. A threshold temperature of 9°C was also found for shell growth of *M. leucophaeata* on the stones in the littoral zone (Van der Gaag et al. 2017). The influence of the temperature on the shell growth is strong, especially for the small mussels.

In a growth experiment of 22 mo with *Mytilopsis leucophaeata* in the harbor of Antwerp using three shell size groups with mean lengths of 4.2, 9.8, and 15 mm, the first two classes grew to a mean length of 12.6 mm and the latter to 15.2 mm, respectively (Verween et al. 2006). This results in an annual growth rate of 11.4 and 7.5 $\mu\text{m day}^{-1}$, respectively. The 15 mm class had a negligible growth and many individuals of this size class died (Verween et al. 2006). Shell length growth decreases with shell length. The third-order polynomial regression for results of the cage growth experiment reveals a summer growth rate of 94 $\mu\text{m day}^{-1}$ for the 2–4 mm

class, 37 $\mu\text{m day}^{-1}$ for the 10–12 mm class, and no growth for the 18–22 mm class.

CONCLUSIONS

A significant positive interaction was found between temperature and shell growth. Shell growth increased strongly at water temperatures higher than 18°C, in particular for the small individuals. Mean shell growth rates were highest during the summer months. A maximum annual growth rate was observed in the cages for the size class 2–4 mm. Growth was size dependent and decreased with increasing shell length. It showed a strong decline at shell sizes between 18 and 22 mm, corresponding with a maximum recorded size of 23 mm. Mortality increased with increasing temperature, although this effect differed between size classes.

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