In situ feeding rates of the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella*, in a temperate, temporarily open/closed Eastern Cape estuary

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Size-fractionated chlorophyll-*a* (chl-*a*) concentrations and the *in situ* grazing rates of the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella*, were assessed seasonally at the temporarily open/closed Kasouga estuary situated along the southeast coast of southern Africa. Total integrated chl-*a* concentration ranged between 1.17 and 12.18 mg chl-*a* m^{-3} and was always dominated by small phytoplankton cells (<20 *μ*m), which comprised up to 86% (range 64–86%) of the total pigment. Total zooplankton abundance ranged between 2676 and 62 043 individuals m^{-3}. These copepods numerically dominated the zooplankton counts, accounting for between 79% and 91% of the total. Gut pigment concentrations of the two species at night were significantly higher than the daytime values ($P < 0.05$ in all cases). The observed pattern could be related to the marked diurnal vertical migration patterns exhibited by the copepods. Gut evacuation rates of *P. hessei* during the study ranged between 0.29 and 0.77 h^{-1} and between 0.39 and 0.58 h^{-1} for *A. longipatella*. The rate of gut pigment destruction for *P. hessei* and *A. longipatella* ranged between 55% and 81% and between 88% and 92% of the total chl-*a* ingested, respectively. The combined grazing impact of the two copepods ranged between 0.65 and 4.37 mg chl-*a* m^{-3}, or between 4.3% and 35.9% of the available chl-*a* in the water column. Variations in the grazing activity of the two species could be attributed largely to seasonality in water temperature and shifts in the phytoplankton community structure and zooplankton abundance.

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Introduction

The copepods, *Pseudodiaptomus hessei* and *Acartia longipatella,* are major contributors to total zooplankton standing stock in a variety of permanently open southern African estuaries.[1] Peaks in the abundance and biomass of both species correspond to freshwater pulses rather than to seasonal changes in temperature.[1] These copepods contribute substantially to the total zooplankton standing stock, and represent an important prey item in the diets of a variety of predators including invertebrates (e.g. mysids)[2] and vertebrates (fish larvae)[3] in southern African estuaries. Estimates of the grazing impact of *P. hessei* and *A. longipatella* on the phytoplankton standing stock in permanently open estuaries, although variable, range from <1% to ~30% of the available chl-*a* in the water column.[4] Temporal variability in the grazing impact of these copepods in permanently open estuaries has been linked to several factors including water temperature, phytoplankton community size structure and feeding history.[4,5]

Some 70% of all southern African estuaries can be classified as temporarily open/closed systems.[6] In the absence of freshwater inflow, these estuaries are separated from the sea by an extensive sandbar. After periods of high rainfall and freshwater run-off, the volume of the estuary rises until it exceeds the height of the sandbar, which is then breached. This results in a dramatic decrease in the water levels of the estuary. During this phase, river conditions dominate throughout the system.[7–11] The development of a sandbar within weeks of the breaching due to along-shore sand movement in the surf zone, however, results in the estuary rapidly being closed off from the sea. During the subsequent closed period, seawater flows in by wash-over during peaks in spring tides or in severe storms.[8,9,12,13]

The zooplankton community structure in temporarily open/closed estuaries has been described on several occasions.[11,13–15] These studies indicate that the zooplankton biomass, particularly during the closed phase, may at times attain levels in excess to those found in the more productive, permanently open estuaries within the same geographic region.[14,15] Among the zooplankton, copepods of the genera *Pseudodiaptomus* (mainly *P. hessei*) and *Acartia* (*A. longipatella* and *A. natalensis*) dominate the total zooplankton both numerically and by biomass.[11,14,15] Locally, mysids may also contribute to the total zooplankton

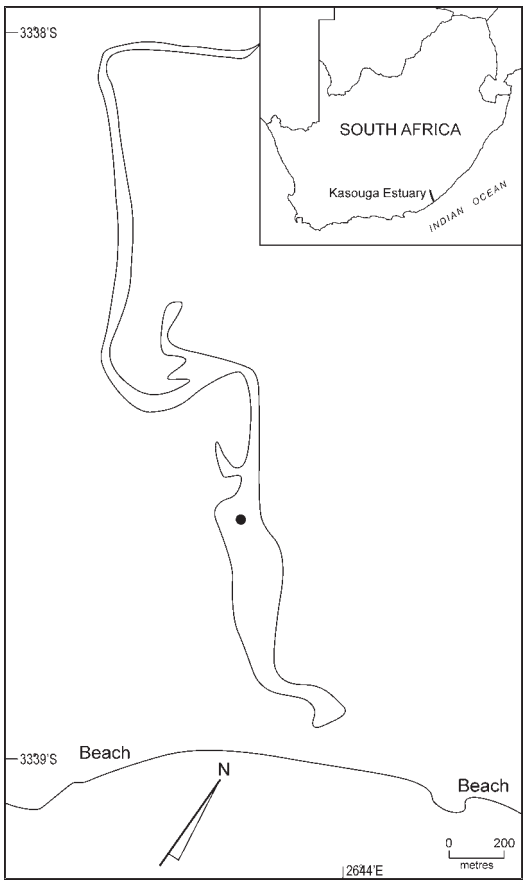

Fig. 1. Map of the temporarily open/closed Kasouga estuary, with position of sampling station indicated by a black dot.

abundance and biomass.[14,15] With one exception,[14] there are currently no published data on the species-specific grazing rates of copepods in temporarily open/closed southern African estuaries. To provide further information this study investigated the *in situ* seasonal patterns in the feeding activity of *Pseudodiaptomus hessei* and *Acartia longipatella* in such an estuary situated along the southeastern coast of southern Africa.

Materials and methods

Temporal patterns in size-fractionated chlorophyll-*a* (chl-*a*) concentration and the abundance and grazing activity of the copepods *P. hessei* and *A. longipatella* were investigated at a single station occupied in the middle reaches of the Kasouga estuary over the period from November 2001 to September 2002 (Fig. 1). Only a single station was investigateded as recent studies conducted in the estuary demonstrated that there are no significant spatial differences in the biology of the system.[11,13,15] The lack of any marked spatial variability in the biology can be related to the virtual absence of a horizontal gradient in salinity and temperature due to reduced freshwater inflow resulting from the small catchment size of the estuary and strong coastal winds, which facilitate the horizontal and vertical mixing of the water column.[13]

Study site

The Kasouga estuary (33°39′S, 26°44′E) is classified as a medium-sized, temporarily open/closed estuary (Fig. 1). Its surface area is approximately 22 ha excluding the shallow salt marsh areas, which are inundated only during periods of high water. The estuary is navigable for approximately 2.5 km and the widest part is about 150 m. The system is mostly shallow, with the depth of the main channel varying between 0.5 and 1.5 m.[13] The catchment area of the estuary is estimated at 39 km^2. Most of this area is used primarily for cattle farming. The nearby stream and river valleys within the catchment area are, however, relatively undisturbed and covered by Valley Bushveld vegetation.

Depending on the rainfall received by the catchment, average monthly water temperatures and salinities in the Kasouga estuary range from 10°C to 30°C and from 0 to 40‰, respectively. Mouth-opening events occur during or shortly after periods of high rainfall (usually in months with sustained rainfall exceeding 100 mm). The estuary mouth rapidly closes off from the sea due to extensive sandbar development caused by along-shore drift. During the subsequent closed period, seawater inflow into the estuary occurs only during peak spring tides and severe storms.[13]

Trophic environment

Salinity and water temperatures at the grazing stations were investigated using a YSI 610 water quality logger. Only subsurface (0.5 m depth) values were measured as previous studies demonstrated that the water column of the estuary is well mixed with no clear stratification evident.[13]

In situ *chlorophyll*-a *concentrations*

Water samples were collected from the surface (0.5 m depth) using a 5-litre Niskin sampling bottle. For the determination of size-fractionated chlorophyll-*a,* a 250-ml subsample from each depth was serially filtered (vacuum <5 cm Hg) through 20.0-μm (Nitex mesh), 2.0-μm (Nucleopore) and GF/F filters and extracted in 90% acetone for 24 h in the dark. Chl-*a* concentrations were then determined fluorometrically (Turner Designs 10AU fluorometer) before and after acidification.[16]

Zooplankton community structure

For the determination of zooplankton community structure, three net tows each season were conducted during the day (09:00 to 12:00) and night (19:00 to 21:00) using a modified WP-2 net (nominal mouth size 0.20 m^2; mesh size 60 μm), fitted with a flow meter (General Oceanics) to determine the amount of water filtered during each tow. The upper part of the net was kept 5–10 cm below the surface during each tow. Towing speed varied between 1 and 2.5 knots. The samples collected were immediately fixed in 4% buffered formalin (hexamine) for the analysis of zooplankton in the laboratory. Zooplankton species composition and abundance at each station was determined from a 1/8 subsample examined using a Heerenburg dissecting microscope at ×100 magnification.

Feeding experiments

Grazing rates of *Pseudodiaptomus hessei* and *Acartia longipatella* (copepodid stages III to adult) were estimated using the gut fluorescent technique.[17] To assess variability in feeding activity, animals were collected at 4-h intervals over 24 h using the sampling gear described above. Samples collected were immediately anaesthetized in a solution of soda: seawater (1:5 volume ratio),[18] before being filtered (vacuum <1 cm Hg) onto GF/C filters, placed in Petri dishes and frozen for later analysis. In the laboratory, filters were thawed and individuals of the copepod species quickly sorted under low light conditions using a Nikon dissection microscope operated at ×100 magnification. Ten individuals were placed in plastic centrifuge tubes (10 ml) with 8 ml 90% acetone and stored at –20°C for 24 h. After centrifugation (5000 rpm), the pigment content of the acetone

extract was measured, before and after acidification, using a Turner Designs 10AU fluorometer.[17] Pigment contents were expressed as chl-*a* equivalents per individual.[19,20]

To calculate the gut evacuation rate, freshly caught zooplankton were gently placed in a 20-l plastic bucket filled with filtered seawater (0.2 μm) to which non-fluorescent charcoal powder was added.[21,22] Sub-samples were collected every 10 min for the first hour and every 15 min thereafter, and stored as above. The total incubation time was 2.5 h. The gut evacuation rate was derived from the slope of the regression of the change in gut pigment versus time.[23]

Estimates of the gut pigment destruction rate during each season were determined using the two-compartment approach.[21] Prior to the experiments, the copepods were allowed to empty their guts for 24 h in particle-free water to which charcoal powder was added. Triplicate bottles (1 litre), each containing 15 copepods, were then incubated for 45 min with naturally occurring phytoplankton concentrations. A further three replicates were incubated without grazers (control). A comparison of pigment budgets in the control (without grazers) and experimental treatments was then carried out. Any decrease in the pigment concentrations in the grazing bottles (water and grazers) was attributed to gut pigment destruction.[21]

Daily ingestion rates [I, ng (pigment) ind^{-1}day^{-1}] were estimated from the equation[22]: $I = kG/(1 - b)$, where k is the gut evacuation rate (h^{-1}), G is an integrated value (over 24 h) of gut pigment contents [ng (pigm) ind^{-1}] and b is a non-dimensional index of pigment destruction. Community grazing impact was calculated as the product of night-time zooplankton abundance (ind m^{-2}) and individual ingestion rates [ng (pigm) ind^{-1} day^{-1}]. Community grazing impact was then expressed as a percentage of the integrated phytoplankton standing stock consumed per day.

Carbon-specific daily rations, expressed as percentage body carbon consumed per day, were calculated by determining the dry weight of individual copepods and assuming a carbon content of 40% dry weight and a chl-*a*: carbon ratio of 50 (ref. 4). To determine individual dry weights, 10 to 20 individuals were placed on a pre-weighed GF/C filter and oven-dried at 60°C for 36 h. Dry weights of copepods were then calculated by subtracting the initial weight of the filter from the final. Weights were determined using a Sartorius microbalance.

Statistical analyses

To assess if there were any significant temporal differences in the biological variables, a Newman-Keuls test was performed after one-way analysis of variance (ANOVA). Homogeneity of the data was achieved after log transformation. The analysis was conducted using the computer package, Statistica, version 6.

Results

Trophic environment

Estuarine water temperatures during the study demonstrated a distinct temporal pattern with maximum values recorded during summer (28.9°C) and minimum values in winter (13.6°C). In spring and autumn, the corresponding water temperatures were 22.8°C and 19.7°C, respectively (Table 1). Salinity values (practical salinity units) were lowest during spring (13.5) and highest in summer (32.7). In autumn and winter these values were 29.3 and 28.7, respectively (Table 1).

Chlorophyll-*a* concentrations

Total chlorophyll-a concentration during the study ranged between 1.17 and 12.18 mg chl-*a* m^{-3} (Fig. 2). Newman-Keuls tests performed afterANOVA indicated that the total chl-*a* concentration during spring was significantly higher than those obtained in the other seasons ($F = 22.1$; $P < 0.05$). The nanophytoplankton (2–20 μm) usually represented the largest contributor to the total chl-*a* concentration, comprising between 34% and 75% of the total pigment. An exception was recorded during winter, when the picophytoplankton (<2.0 μm) represented the largest contributor to total integrated phytoplankton biomass. Concentrations of nanophytoplankton during the study ranged from 0.42 to 6.47 mg chl-*a* m^{-3}. With the exception of spring, when microphytoplankton (>20 μm) represented the second largest contributor to total pigment, the picophytoplankton represented the second largest contributor to total chl-*a* concentration. Concentrations of the picophytoplankton ranged between 0.63 and 1.47 mg chl-*a* m^{-3}. Microphytoplankton concentrations during the four seasons ranged between 0.12 and 4.25 mg chl-*a* m^{-3}.

Table 1. Summary of environmental conditions during grazing experiments conducted in the temporarily open/closed Kasouga estuary of the southeastern coastline of southern Africa.

Date	Season	Temperature (°C)	Salinity (practical units)
23 Nov 2001	Summer	28.9	32.7
16 May 2002	Autumn	19.7	29.3
18 July 2002	Winter	13.6	28.7
29 Sept 2002	Spring	22.8	13.5

Zooplankton community structure

Total zooplankton abundance demonstrated a distinct diel pattern with daytime abundances 2–3 times lower than the nocturnal values (Fig. 3). During the day, total zooplankton abundances ranged between 2676 and 7992 ind m^{-3} and between 5391 and 62 043 ind m^{-3} by night. A distinct temporal pattern in zooplankton abundance by day and by time was observed. Total zooplankton abundances were highest in spring (62 043 ind m^{-3}) and lowest in winter (2676 ind m^{-3}). In summer, the mean zooplankton abundance by day was 7581 ind m^{-3} and 32 373 ind m^{-3} at night. Mean average zooplankton abundance during autumn was 5202 ind m^{-2} by the day and 10 620 ind m^{-3} at night. Newman-Keuls tests performed after ANOVA indicated that the springtime zooplankton abundances were significantly higher than during the three other seasons ($F = 167.1$, $P < 0.001$).

Total zooplankton abundance during the entire investigation

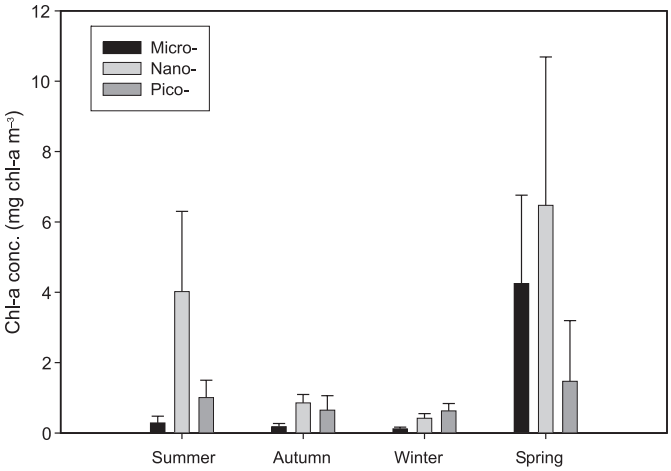

Fig. 2. Size-fractionated chlorophyll-*a* analysis at grazing stations occupied in the temporarily open/closed Kasouga estuary. Error bars are standard deviations; $n = 3$ for each station.

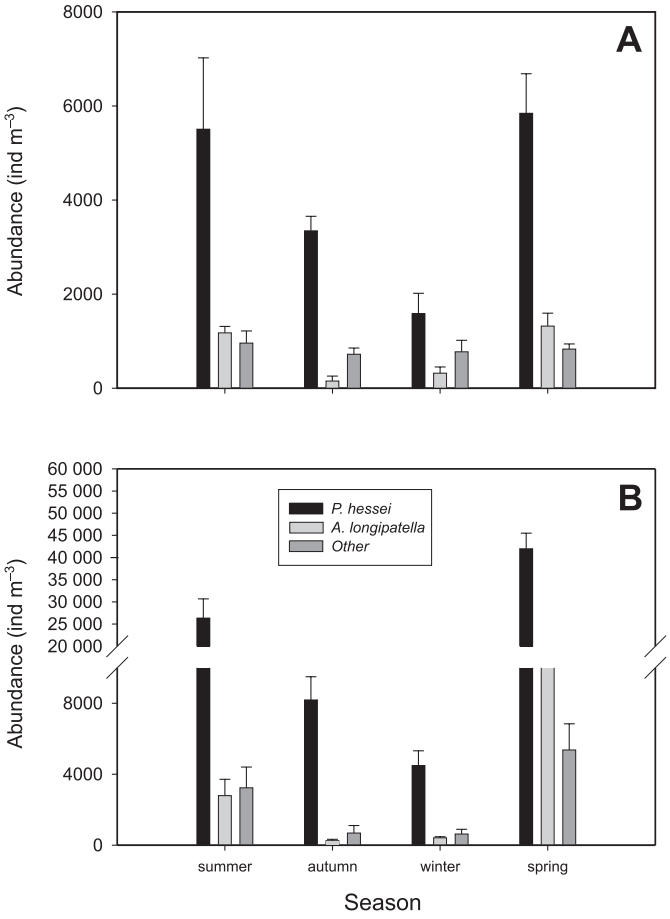

Fig. 3. Zooplankton abundance and community structure during the day (**A**) and night (**B**) at grazing stations occupied in the Kasouga estuary. Error bars are standard deviations; $n = 3$ for each station. Note different scales on *y*-axes.

was numerically dominated by *P. hessei* and *A. longipatella*, which collectively comprised between 79% and 91% of all zooplankton counted. Also well represented among the copepods were *Oithona nana, O. brevicornis* and *Halicyclops* species, although their contribution was <5% of the total at all stations (Fig. 3). Among the larger zooplankton, the cumacean, *Iphinoe truncata,* and the amphipod, *Grandidirella lignorum,* were well represented. Abundances of these zooplankton species were, however, always <150 ind m^{-3}.

Feeding experiments

Night-time gut pigment contents for both *P. hessei* and *A. longipatella* were significantly higher than the daytime values (Fig. 4A,B; $P < 0.05$ in all cases). During spring and summer, mean gut pigment concentrations of *P. hessei* were estimated at 0.52 (s.d. ±0.09) and 0.47 (s.d. ±0.13) ng pigm ind^{-1} during the day and between 1.16 (s.d. ±0.18) and 1.06 (±0.38) ng pigm ind^{-1} at night (Fig. 4A). The corresponding values in winter, for *P. hessei* ranged from 0.11 ng pigm ind^{-1} during the day to a maximum of 0.27 ng pigm ind^{-1} at night. Values in autumn ranged from 0.19 to 0.47 ng pigm ind^{-1}, with the highest values consistently recorded at night (Fig. 4A).

Mean daytime gut pigment concentrations of *A. longipatella* in summer ranged between 0.20 and 0.29 ng pigm ind^{-1} and between 0.38 and 0.46 ng pigm ind^{-1} at night (Fig. 4B). In autumn, the corresponding values by day ranged between 0.11 and 0.16 ng pigm ind^{-1} and between 0.21 and 0.30 ng pigm ind^{-1} at night. In winter and spring, these values were estimated at 0.07 (s.d. ±0.02) and 0.32 (s.d. ±0.08) ng pigm ind^{-1} during the day and between 0.18 (s.d. ±0.03) and 0.98 (±0.23) ng pigm ind^{-1} at night, respectively (Fig. 4B).

Table 2. Seasonal estimates of gut evacuation rate (k, h^{-1}), gut passage time (1/k, h) and gut pigment destruction (b) for the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella* in the temporarily open/closed Kasouga estuary. Values in brackets are standard deviations.

Season	k (h^{-1})	1/k	b
P. hessei			
Summer	0.773	1.29	64.8 (±9.9)
Autumn	0.755	1.32	58.2 (±10.6)
Winter	0.287	3.48	73.2 (±8.7)
Spring	0.642	1.56	80.5 (±4.5)
A. longipatella			
Summer	0.578	1.73	87.2 (±5.7)
Autumn	0.474	2.11	83.5 (±4.2)
Winter	0.392	2.55	71.4 (±6.7)
Spring	0.536	1.87	91.6 (±2.1)

An exponential model provided the best fit (R^2 ranged between 44% and 94%; $P < 0.05$) for the decline in gut pigment over time during the gut evacuation experiments for both copepod species (Fig. 5A,B). These experiments for *P. hessei* demonstrated a strong temporal pattern with the highest rate recorded in summer ($k = 0.77$ h^{-1}) and the lowest in winter ($k = 0.29$ h^{-1}) (Table 2). In spring and autumn, the corresponding values were 0.64 h^{-1} and 0.76 h^{-1}, respectively. These estimates correspond to a gut passage time (1/k) of 1.21 h in summer, 3.48 h in winter, 1.56 h in spring and 1.32 h in autumn. Gut evacuation rates for *A. longipatella* were estimated at 0.58 h^{-1} in summer, 0.47 h^{-1} in autumn and 0.39 h^{-1} in winter. In spring, the corresponding rate was 0.54 h^{-1} (Table 2). These rates correspond to a gut passage time of between 1.73 h and 2.55 h (Table 2).

Estimates of the gut pigment destruction rate for *P. hessei* were highly variable during the study (Table 2). During summer, it ranged between 54.9% and 74.7% (mean = 64.8; s.d. ±9.9) and between 63.6% and 81.2% (mean 73.2; s.d. ±8.7) during winter. In spring and autumn, the corresponding rate was equivalent to 80.5 (s.d. ±4.7) and 58.2% (s.d. ±10.6), respectively. For *A. longipatella,* the mean gut pigment destruction rate was 87.2% (s.d. ±5.5) in summer and 91.6% (s.d. ±2.1) in spring (Table 2). The corresponding rates in autumn ranged between 79.3% and 87.7% and between 64.7% and 76.3% in winter (Table 2).

The daily ingestion rate of *P. hesssei* was highest in spring (68.7 ng pigm ind^{-1} day^{-1}) and lowest in winter (5.1 ng pigm ind^{-1} day^{-1}) (Table 3). During summer and autumn, these values were equivalent to 21.1 ng pigm ind^{-1} day^{-1} and 12.4 ng pigm ind^{-1} day^{-1}, respectively (Table 3). The ingestion rate of *A. longipatella* in summer and spring was estimated at 34.2 ng pigm ind^{-1} day^{-1}and 100.1 ng pigm ind^{-1} day^{-1}, respectively (Table 3). In autumn and winter, the corresponding rates were estimated at 13.6 and 4.1 ng pigm ind^{-1} day^{-1}, respectively (Table 3).

The combined grazing impact of the two copepod species ranged between 0.65 and 4.37 mg chl-*a* m^{-3}, or between 4.3% and 35.9% of the available chl-*a* in the water column (Table 4). The highest grazing impact was recorded during spring and the lowest in winter. In summer and autumn, zooplankton grazing removed on average 12.1% and 8.3% of the total water column chlorophyll-*a,* respectively (Table 4).

Mass-specific ingestion rates

Mass-specific ingestion rates of *P. hessei* during the study ranged between 4.2% and 64.0% of body carbon per day (Table 3). The highest rate was recorded in spring and the lowest in winter. The autumn and spring mass-specific ingestion rate of was equivalent to <20% of body carbon per day. For *A.*

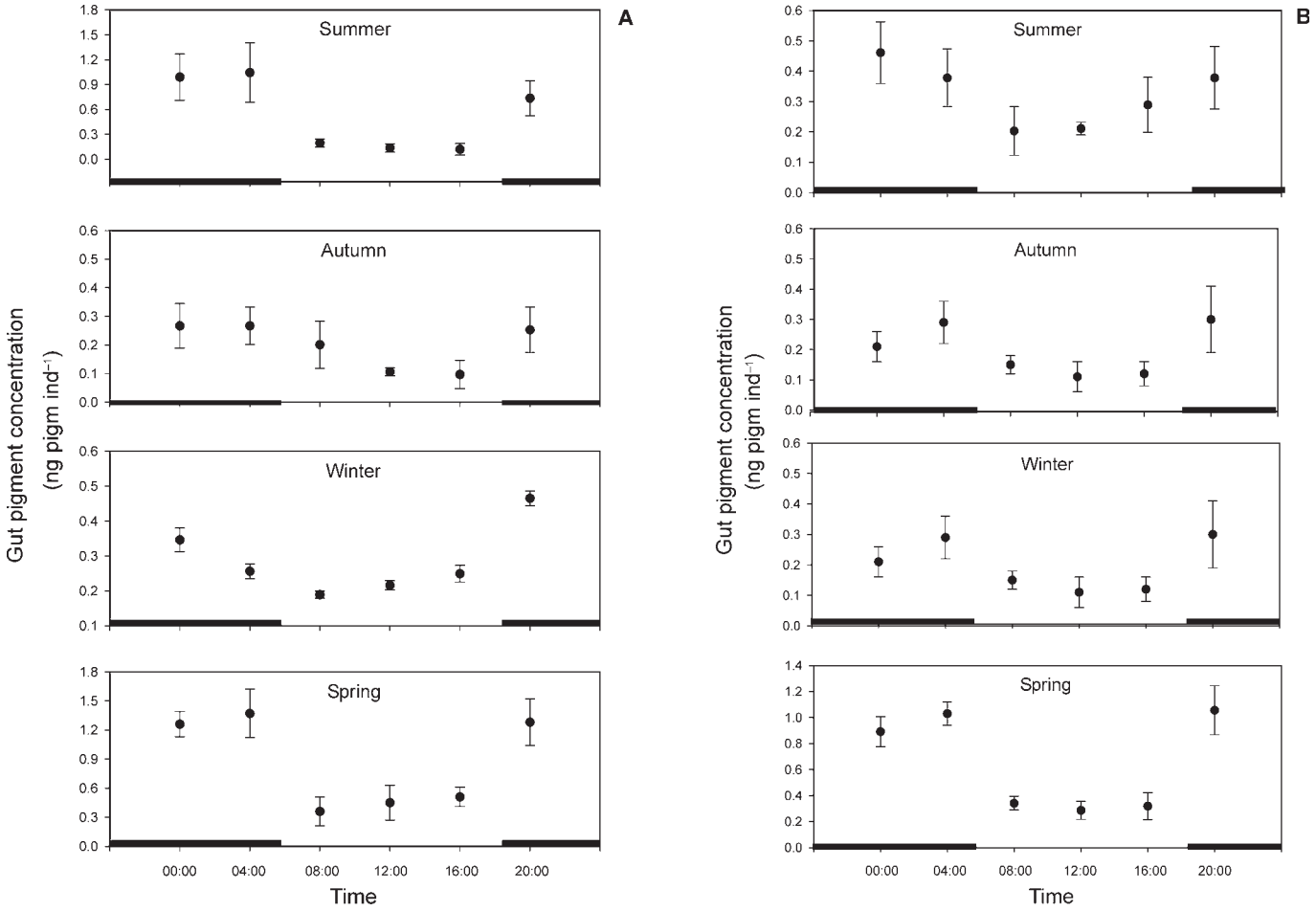

Fig. 4. Diel gut pigment concentrations of the copepods, (**A**) *Pseudodiaptomus hessei* and (**B**) *Acartia longipatella*, at grazing stations occupied in the Kasouga estuary. Error bars are standard deviations. Periods of darkness are indicated by a thickening of the horizontal axis.

longipatella, the mass-specific ingestion rate in summer was equivalent to 47.5% body carbon and 143.1% in spring (Table 3). The corresponding rates in autumn and winter were equivalent to 19.4% and 7.5% body carbon, respectively (Table 3).

Discussion

The influence of riverine inflow on the primary production rates of phytoplankton in a variety of southern African estuaries is now well documented.[24–27] Freshwater inflow into estuaries is the primary source of macronutrients necessary to sustain the growth of phytoplankton.[26,27] The elevated chl-*a* concentrations following freshwater inflow (as evident from the reduced salinity in the estuary) during spring is, as a consequence, not unexpected. The high contribution of the microphytoplankton to total chl-*a* concentration during this period can be related to the increased availability of macronutrients, which promotes the growth of large phytoplankton.[11,28] In the absence of freshwater inflow into the estuary, the total chl-*a* concentration was dominated by small phytoplankton cells, reflecting low macronutrient availability (Fig. 2). The reduced chl-*a* concentrations during the colder winter months can in part also be attributed to the effect of lower water temperatures on the growth rates of phytoplankton.[28] The increase in total zooplankton abundance during spring is consistent with previous studies as

Table 3. Seasonal estimates of the ingestion rate, body carbon content and daily ration of the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella*, in the temporarily open/closed Kasouga estuary. Carbon-specific daily rations, expressed as percentage body carbon consumed per day, were calculated by determining the dry weight of individual copepods and assuming a carbon content of 40% dry weight and a chl-*a* : carbon ratio of 50.[11] Values in brackets are standard deviations ($n = 10$).

Season	Ingestion rate (ng pigm ind^{-1} day^{-1})	Ingestion (g C ind^{-1} day^{-1})	Dry weight (g dwt ind^{-1})	Carbon content (g C ind^{-1})	Daily ration (% body carbon)
P. hessei					
Summer	21.14	1.06	13.6 (±2.8)	5.4 (±1.1)	19.4 (±3.3)
Autumn	12.36	0.62	12.9 (±3.3)	5.2 (±1.3)	11.9 (±2.4)
Winter	5.10	0.26	15.4 (±1.9)	6.1 (±0.7)	4.2 (±0.4)
Spring	68.66	3.43	13.3 (±2.7)	5.4 (±1.1)	64.0 (± 10.7)
A. longipatella					
Summer	34.22	1.71	9.0 (±0.5)	3.6 (±0.2)	47.5 (±2.5)
Autumn	13.56	0.68	8.7 (±0.3)	3.5 (± 0.1)	19.4 (±0.5)
Winter	4.11	0.21	6.9 (±0.6)	2.8 (±0.2)	7.5 (±0.5)
Spring	100.12	5.01	8.8 (±1.1)	3.5 (±0.5)	143.1 (±17.9)

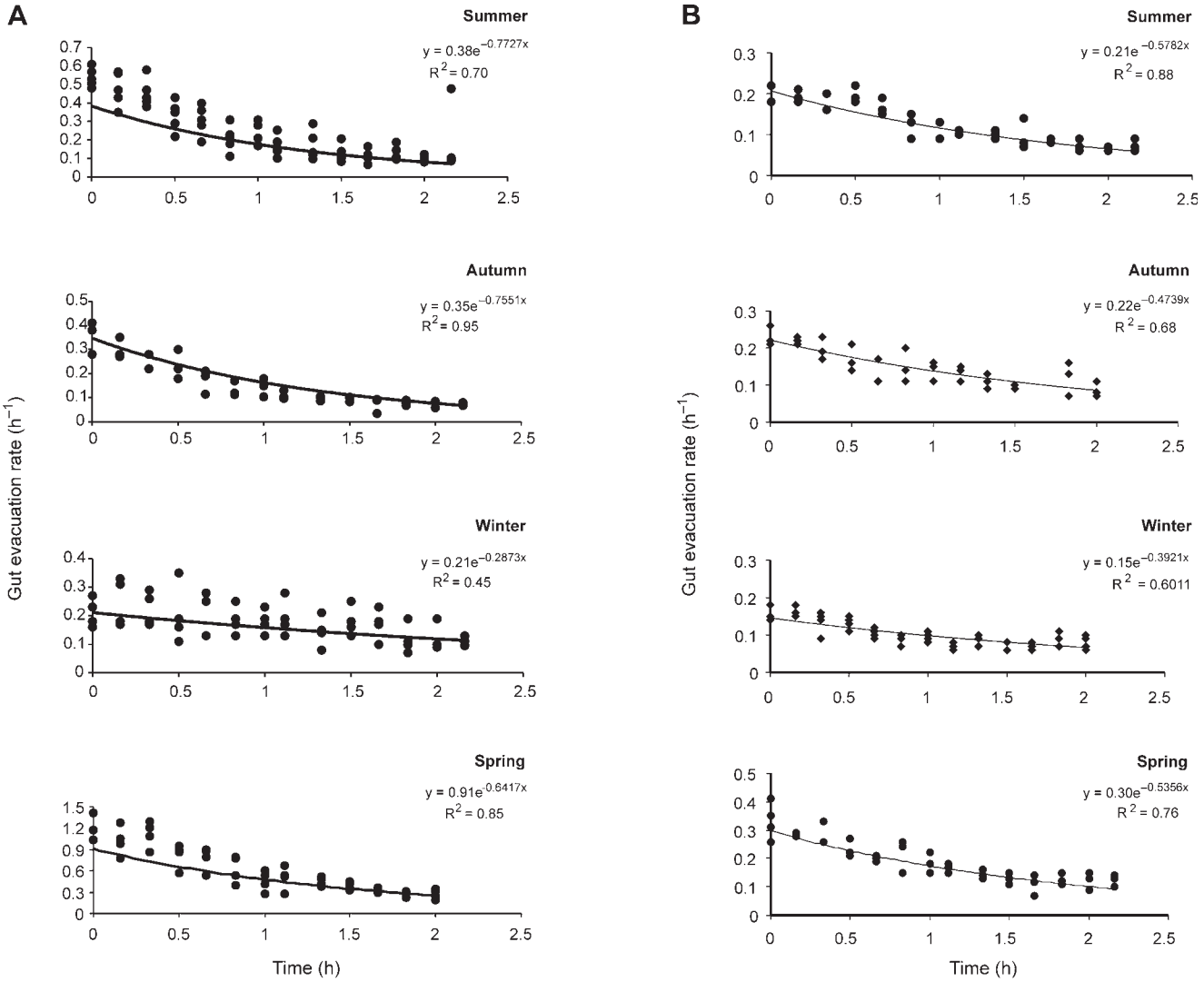

Fig. 5. Gut evacuation rates of (**A**) *Pseudodiaptomus hessei* and (**B**) *Acartia longipatella* during the four seasons ($P < 0.05$ in all cases).

peaks in the abundance and biomass of both *P. hessei* and *A. longipatella* coincide with freshwater inflow into permanently open southern African estuaries.[1]

Gut pigment concentrations of *P. hessei* and *A. longipatella* demonstrated a strong diel pattern during all four seasons, with maximum values recorded at night and minimum values during the day (Fig. 4). The observed pattern is consistent with previous studies conducted in a variety of estuaries along the southern African coast and can be related to the distinct daily vertical migration patterns demonstrated by both copepod species.[1,4,14] This diel vertical migration pattern is generally thought to be a predator avoidance strategy, although factors such as moonlight and water currents may also influence the distribution of zooplankton within the water column.[1]

The strong seasonal pattern in gut evacuation rates for both copepod species observed during this study can likely be related to the influence of the higher water temperatures on the metabolic activities of the copepods in summer.[23] The gut evacuation rates for the two species presented here are in the range recorded in the permanently open Kariega estuary in the same geographic region.[4] On the other hand, the values for *P. hessei* reported here are generally higher than those found in the temporarily open/closed Mepanjati estuary (range 0.42–0.48 h^{-1}) along the east coast of southern Africa.[14] Gut evacuation rates of zooplankton vary according to prey type, food concentration, temperature and feeding history.[23,29,30] The plethora of possible factors that influence the gut evacuation rate of zooplankton makes any comparison impossible. Nonetheless, it is worth noting that the estimates of this rate for the two species in this study are in the range reported for similar-sized copepods in a variety of aquatic environments.[21,29–31]

The estimates of the mean gut pigment destruction rate for the

Table 4. Grazing impact of the dominant zooplankton species on phytoplankton in the temporarily open/closed Kasouga estuary.

Season biomass	Phytoplankton (mg chl-*a* m^{-3})	*Pseudodiaptomus hessei* (mg pigm m^{-3} day^{-1})	*Acartia longipatella* (mg pigm m^{-3} day^{-1})	Grazing impact (% total chl-*a*)
Summer	5.31	0.56	0.09	12.1
Autumn	1.68	0.11	0.02	8.3
Winter	1.17	0.03	0.02	4.3
Spring	12.18	2.88	1.49	35.9

copepods reported here (range 58.2–80.5%) match the estimates reported for the permanently open Kariega estuary within the same geographic region.[4] Gut pigment destruction rates of copepods are highly variable, ranging between 0 and 100% of the total pigment.[14,32–34] The variable estimates of gut pigment destruction reported for different studies can be related to various factors including prey type, feeding history, ingestion rate and temperature.[33]

Although the grazing impact of only two species was considered here, collectively these copepods accounted for between 79% and 91% of the total zooplankton abundance (Fig. 3). The grazing estimates are in the range reported for the oligotrophic, permanently open Kariega estuary in the same geographic region[4] and, indeed, in estuaries in the northern hemisphere.[35] On the other hand, the estimates for the Kasouga estuary are substantially lower than those obtained in the temporarily open/closed Mepanjati estuary (east coast of southern Africa), where the zooplankton at times removed more than 100% of the available water column chl-*a*.[14] Differences in the results of the two studies can in part be attributed to the size structure of the phytoplankton. In autumn and winter, picophytoplankton (<2 μm), which are poorly utilized by copepods,[36] contributed substantially to total chl-*a* concentration in the Kasouga estuary (Fig. 2A). These data suggest that in autumn and winter, much of the chl-*a* was not available to the zooplankton. In contrast to the Mepanjati estuary, the available chl-*a* in the water column was largely composed of nanophytoplankton (2–20 μm), which is regarded as the optimum particle size for copepods.[36] The elevated grazing impact of the zooplankton in the Mepanjati estuary is, therefore, not unexpected.

The daily carbon requirement of copepods, although variable, is thought to be in the order of about 30% of body carbon per day.[1] These results suggest that carbon derived from the consumption of phytoplankton was sufficient to meet the basic metabolic requirements of *P. hessei* during spring and in summer and spring for *A. longipatella.* At other times, the copepods must consume alternative carbon sources to meet their metabolic requirements. It has recently been suggested that the elevated zooplankton stocks recorded in the temporarily open/closed Mepanjati estuary were sustained by the substantial microphytobenthic stocks within the system.[14] Within the Kasouga estuary, microphytobenthic algal concentrations are typically 2–3 orders of magnitude higher that the water column chl-*a* concentrations.[13] These observations suggest that microphytobenthic algae probably represent an important carbon source for the numerically dominant copepods in the Kasouga estuary. However, the low pigment concentrations in the gut observed for both copepods during the day suggest that the microphytobenthic algal stocks are utilized via the detrital food web rather than by direct ingestion. Alternatively, the copepods may obtain carbon by consuming protozooplankton to meet their basic metabolic requirements.[37]

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