Polar Biol (2005) 28: 776–783
DOI 10.1007/s00300-005-0003-7

ORIGINAL PAPER

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# Population dynamics of *Themisto gaudichaudii* in Kerguelen Islands waters, Southern Indian Ocean

Received: 23 December 2004 / Revised: 6 April 2005 / Accepted: 8 April 2005 / Published online: 20 July 2005


**Abstract** Fieldwork was carried out at Kerguelen Islands. Two groups of stations in a coastal area, the Morbihan gulf, were surveyed. At both stations, macroplankton biomass ranged from 2.3 mg dry weight $m^{-3}$ to 89 mg dry weight $m^{-3}$ and consisted mostly of *Themisto gaudichaudii* with values ranging from 1.9 mg dry weight $m^{-3}$ to 50.6 mg dry weight $m^{-3}$. Biomass was high for sub-Antarctic waters with marked seasonal and inter-zone differences. Biomass minima were observed at the end of the winter, from September to November, while maxima were recorded in summer and in early fall at the beginning of the year between January and April. *T. gaudichaudii* showed a recruitment of new size classes, mainly from November to January, followed by a rapid growth phase in summer, which slowed down during the southern winter period. Individuals breed after 1 year. Large individuals, older than 1 year, were not a significant presence in the gulf of Morbihan. The main pattern of the population dynamics were characterised by an univoltine life cycle with a very high biomass marked by a strong seasonal signal linked with the hydrological and trophic parameters of the Gulf.

**Keywords** Population dynamics amphipod · Kerguelen Islands · *Themisto gaudichaudii*

## Introduction

The hyperiid amphipod, *Themisto gaudichaudii*, is present in large areas of the Southern Ocean, Kane (1966).
*T. gaudichaudii* is a predator of different mesozooplankton species. In South Georgia, *T. gaudichaudii* adults play a major role in the control of the local mesozooplankton community and contribute significantly to the downward flux of biogenic carbon (Pakhomov and Perissinotto 1996). Schneppenheim and Weigmann-Haass (1986) have shown than the southern form of *Themisto* was *T. gaudichaudii* and was different from the northern counterpart, *T. compressa*.

In the Southern Ocean, high densities were found between the sub-tropical convergence (STC) and the Antarctic polar front (APF) (Pakhomov et al. 1994; Pakhomov and McQuaid 1996). The largest biomass was found in the coastal waters of the Antarctic and sub-Antarctic zone (Piatkowski 1985), and in the neritic waters of the west coast of South Africa (Siegfried 1965). In the sub-Antarctic trophic web, T. gaudichaudii is a food source for myctophids (Pakhomov et al. 1996) and other fishes (Kock et al. 1994; Arkhipkin et al. 2001), squids (Ivanovic and Brunetti 1994); Phillips and Nichols 2003) and birds. For this last group, the nutritional role of hyperiids is particularly important during the chick-rearing period (Bost et al. 1994; Green et al. 1998; Bocher et al. 2000, 2001; Cherel et al. 2002a, b).

Descriptions of the population dynamics of T. *gaudichaudii* are limited to two reports which, while covering the entire seasonal cycle, are limited to two geographical areas: the coastal zones of South Africa and the waters between 0°E and 20°E of the Southern Ocean (Siegfried 1965; Kane 1966). To our knowledge, no data are available for the sub-Antarctic Indian sector.

In the present paper, we present the results of a multi-year study of the size structure kinetics of *T. gaudichaudii* for the coastal area of the Kerguelen archipelago. We describe the main features of the population dynamics such as recruitment period, annual size structure variability, relationship between the two study sites and links with environmental parameters.

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## Material and methods

Fieldwork was carried out at “Kerguelen Islands“, Southern Indian Ocean (Fig. 1a). Sampling was conducted at two groups of stations in the Bay of Morbihan, with different bathymetric and hydrological characteristics. The “Bay of Morbihan” is a large gulf (about 700 km$^2$) located in the eastern part of the archipelago (Fig. 1b). The first set of stations (stations 1 and 2) was located in the northern part of the bay, outside the group of inner islands, with maximum depths of 60 m and with a sill entrance open to the Indian Ocean. This group is referred to as “Open gulf stations”. The second set of stations (stations 6–10) was located around the “Ile Longue” in the western part of the Bay of Morbihan, which is characterised by deep submarine valleys (up to 190 m depth) and numerous inner islands (Fig. 1b). This group is referred to as “Ile Longue stations”.

The studies period extended from June 1995 to December 1997, with 41 sampling dates in the “Open gulf” stations and between 35 and 38 sampling dates at the “Ile Longue” stations.

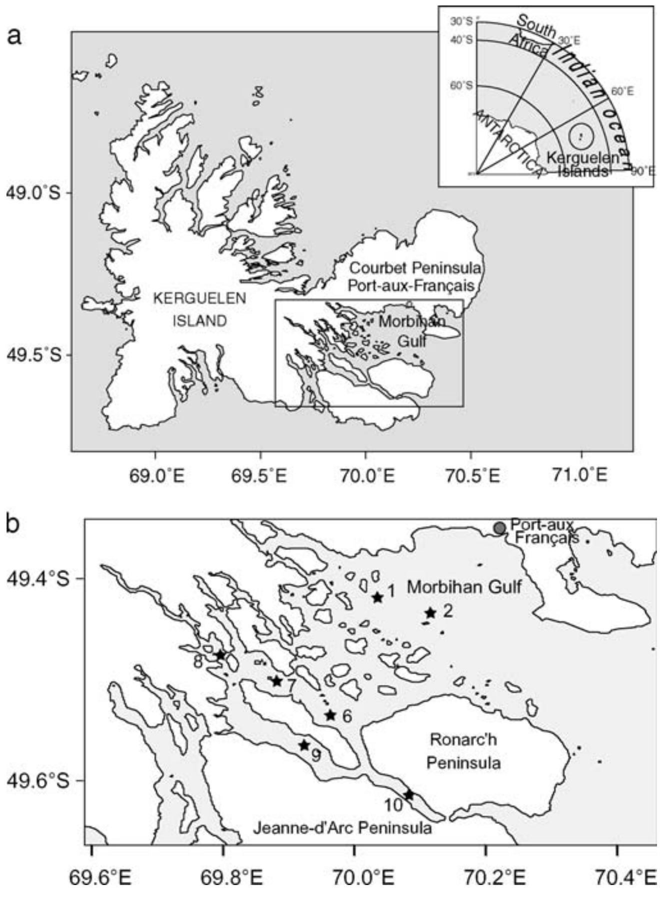



**Fig. 1** Map of the localisation of the sampled stations. **a** Kerguelen islands, **b** Gulf of Morbihan

Macrozooplankton were collected at night by oblique hauls (bottom-surface using an Omori net (1-mm mesh, 1.6 m diameter). Volumes sampled were cross-computed from General Oceanic flow-meter data and GPS track records. Two consecutive samplings were performed at each station. One sample was preserved on board in 5% buffered formalin–water solution and the other one kept alive in cooled seawater. Back to the laboratory, living individuals of *T. gaudichaudii* were sorted out and dried for biomass measurements in order to quantify the absolute and relative importance of this species in the macrozooplankton community. Formalin samples were sent to Villefranche-sur-Mer, France for size structure analysis. Temperature and salinity profiles were recorded at each station with a CTD probe, SBE 25 Seabird technology.

### Biomass measurements

All individuals of the hyperiid *T. gaudichaudii* were separated from the rest of the zooplankton, rinsed with distilled water and dried at 60° C until constant weight was attained. Population biomass was expressed per unit of volume sampled (milligram of dry weight per cubic meter, DW mg m$^{-3}$).

### Length measurement and sex determination

Size structure was analysed at two stations where T. gaudichaudii was continuously abundant, i.e., station 2 and station 8 (Fig. 1b). At these two stations, *T. gaudichaudii* was present all the year round and accounted for the largest proportion of the macrozooplankton community. Total samples were divided using a Motoda box to obtain sub-samples of 150–200 specimens. In each sub-sample, individuals were counted, sized and sexed. Standard length measurements corresponded to total body length (BL), measured directly from the front of the eye to the tip of the uropods, L1 length of Pakhomov and Perissinotto (1996). Sexes were determined using secondary sexual characters: males were identified by the flagellum of the second antennae which become filamentous and divided into many segments, while females displayed short and unsegmented second antennae, Kane (1966). Animals with broken antennae were labelled as undefined. Small *T. gaudichaudii* (BL < 12 mm) were considered as juveniles.

### Data analysis

For the biomass time series, the data were smoothed using moving average, $B_t = 0.25B_{t-1} + 0.5B_t + 0.25B_{t+1}$ where $B_t$ is the biomass at time $t$. To determine the difference between independent samples, Wilcoxon–

Mann–Whitney test was used (Siegel and Castellan (1988).

### Correspondence analysis

The variability of the size structure was analysed using a multivariate analysis that was able to synthesise the key features. Correspondence analysis (CA) (Benzecri 1973) is an ordination method which has been widely used to analyse ecological data (Gower 1987) and, among others, to describe size structures (Badia and Do-Chi 1976). Its aim is to describe the total inertia of a multi-dimensional set of data, in a sample of fewer dimensions (or axes) that is the best summary of the information contained in the data. Among the inertia methods, CA employs contingency tables and uses a Chi-square metric. Starting from the cloud of samples within the space of size classes, and the cloud of size classes within the space of the samples, this factorial analysis provides the best possible summary of the kinetics of the size structure of a population over time. The position of a sample in the multivariate space is defined using all the size classes: proximity reflects similar abundance while distance reflects scarcity. To avoid the over representation of classes with few individuals, classes of sizes above 22 mm were pooled in a single group. CA and graphical representations were computed with Matlab 6.5.

## Results

### Hydrological characteristics

Figure 2 shows the temperature and salinity at three depths (surface, −30 m, −60 m) during the sampling period. Stations 2 and 8 show a similar annual cycle for the temperature, with maxima observed between January and March and minima in August or September. In terms of salinity, a large difference occurred between the two stations. Station 2 was clearly related to open ocean waters with relatively constant values. Station 8 displayed lower salinity with a surface layer strongly influenced by fresh water inputs from rivers. Hence, the annual variation in salinity should be related to the pattern of rainfall with maximum inputs during the winter period.

### Biomass

Biomass values were averaged from the 3 years of observations sampled in the seven stations. Total macrozooplankton and *T. gaudichaudii* biomass ranged from 2.3 to 89 mg dry weight $m^{-3}$ and from 1.9 mg dry weight $m^{-3}$ to 50.6 mg dry weight $m^{-3}$, respectively . In percentage, *T. gaudichaudii* accounted for 39.3% at

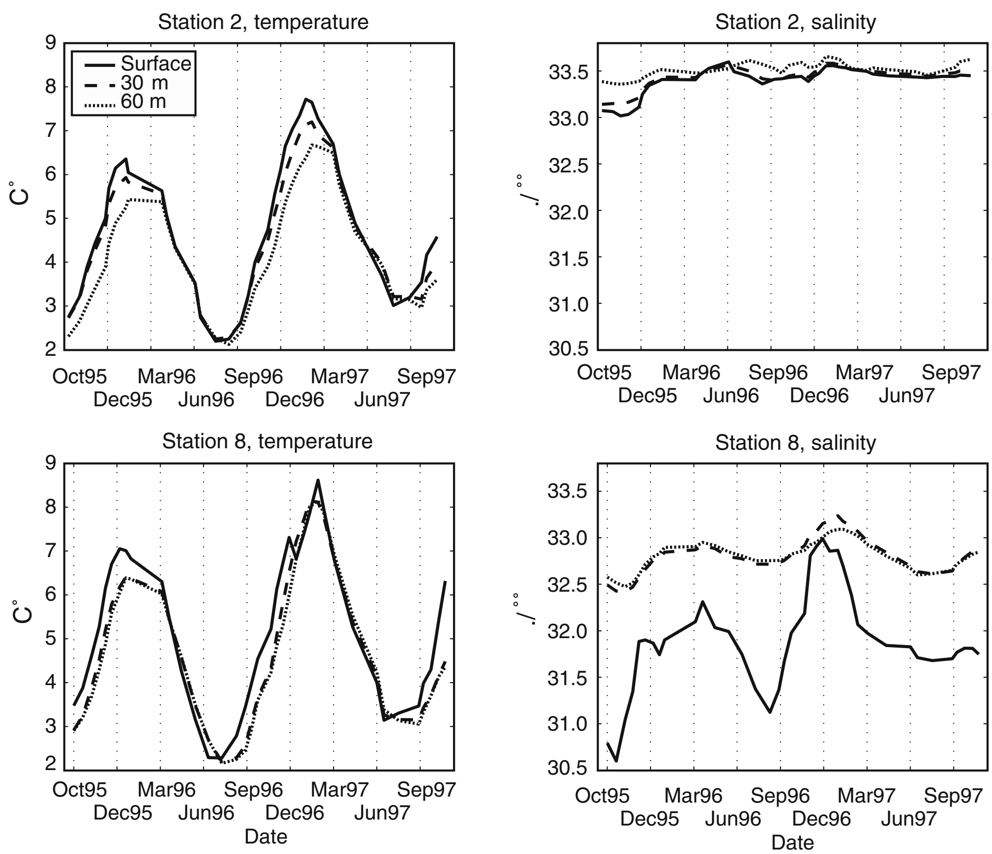



**Fig. 2** Temperature and salinity at the stations 2 and 8 during the sampling cycle at three depths

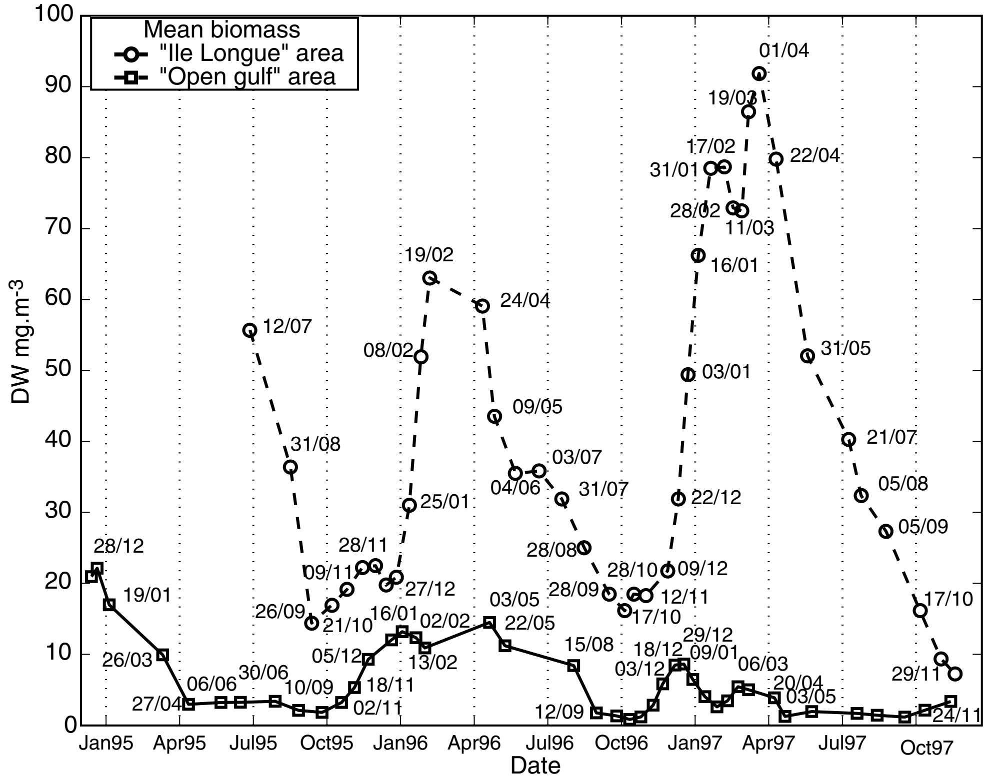



Fig. 3 Mean biomasses, in DW mg m$^{-3}$, for the "Open gulf" and the "Ile Longue" areas of the Gulf of Morbihan. (Means are computed from the two stations in 'Open gulf' area and from the five stations in "Ile Longue" area)

station 7 to 92.9% at station 2, of the total community sampled with the Omori net.

The total and *T. gaudichaudii* biomasses were clearly larger within the "Ile longue" area than in the "Open gulf" area ($P < 0.05$, Wilcoxon–Mann–Whitney), but in proportion *T. gaudichaudii* is the largest representative of the community in the "Open gulf" area ($P < 0.05$, Wilcoxon–Mann–Whitney).

Averaging the data for each of the two areas (Fig. 3), *T. gaudichaudii* biomass showed a distinct seasonality and inter-zone differences. Higher values and a stronger seasonal signal were recorded for the "Ile Longue" area. The lowest values of biomass were observed during the end of the winter, from September to November. In spring, a steep increase was recorded from November to December. The maximum values were observed in summer and in early fall at the beginning of the year, between January and April. In the fall, the decline took place over a larger period than during the increase that took place in the spring . In 1995 and 1997, the minimum values occurred earlier in the "Open gulf" area, between April and May.

## Sex-ratio

The sex ratio (expressed as the ratio of the females to all individuals in percentage) was determined on a sample of 1,029 individuals larger than 12 mm, pooled from different stations where large individuals were well represented. Undetermined individuals with broken flagellum antennae represented 16% of the individuals. The rest was sexed and yielded a ratio of 47%. This ratio is not statistically different from 50%, i.e., an equal ratio between males and females.

## Size structure

Figure 4a and b illustrate the size structure (normalised in percent) for station 2 in the "Open gulf" area and for station 8 in the "Ile Longue" area. The start of the recruitment period, marked by the arrival of the cohort of small-size individuals, and the growth effect, as seen by the size shift over time towards larger size, were evident in the two areas during the southern summer. Some difference exists between the two zones: small- and large-size classes are better represented in station 2 and in station 8, respectively.

## Correspondence analysis (CA) results

Correspondence analysis was performed on the contingency crossing 65 rows (samples) and 19 columns (size classes). The first two factorial axes accounted respectively for 45.4% and 27.1% of the inertia (72.5% for plane 1–2). The third axis explained only 11.8%. Figure 5 shows the topology of the size classes (round label) and the dates (square label) on the plane defined by axes 1, 2. The size of the label is proportional to the quality of the representation of each object (square cosines index).

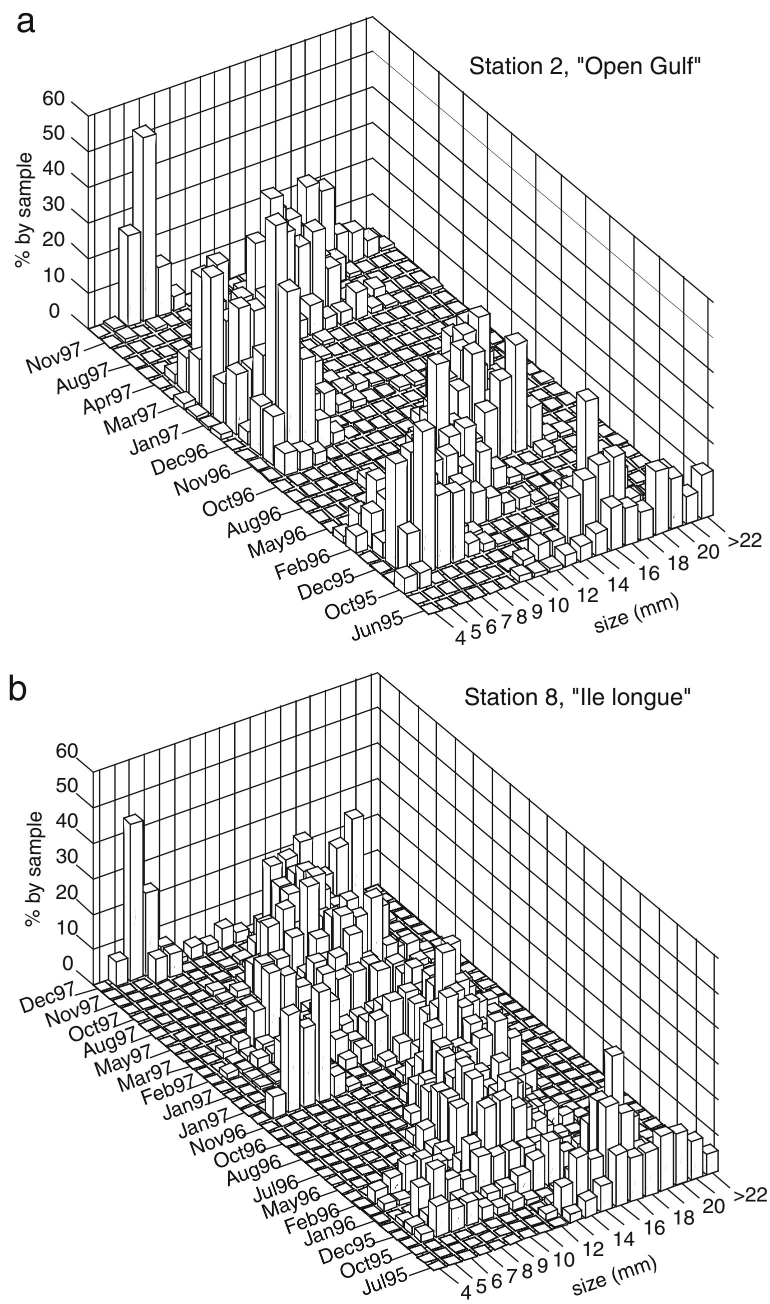



**Fig. 4** Size structures. **a** at station 2, "Open gulf" area **b**; at station 8, "Ile Longue" area

Axis 1 shows an opposition on the negative part of the axis between the smaller sizes classes, 4–11 mm, and the higher than 12-mm size classes on the positive part. Axis 2 shows an opposition between the larger than 15-mm size class and the others. In the 1–2 plane, ordination of the size classes and of the samples shows the result of the growth and the recruitment effects on the size structure kinetics during the annual cycles. The pattern of the plan 1, 2 is clearly the result of the dynamics of a univoltine population.

Figure 6 represents the value of the coordinates of the two stations plotted in axis 1 versus the time-sampling scale. As shown in Fig. 5, axe 1 illustrates the opposition of small-size classes in the negative part with large-size classes in the positive part. The time signal observed in Fig. 6 must be viewed in the context of such size opposition. The global shape, maximum and minimum positions, of this signal is very close for stations 2 ("Open gulf" area) and 8 ("Ile longue" area), but station 2 showed more extreme negative values, associated with a larger contribution of the small-size classes (annual recruitment). This pulse starts in October and ends in March (in 1997) and is maximum from November to January. The difference between the stations, e.g., earlier and more intense recruitment of the small-size class at station 2, suggested that recruitment was essentially associated with the "Open gulf " area.

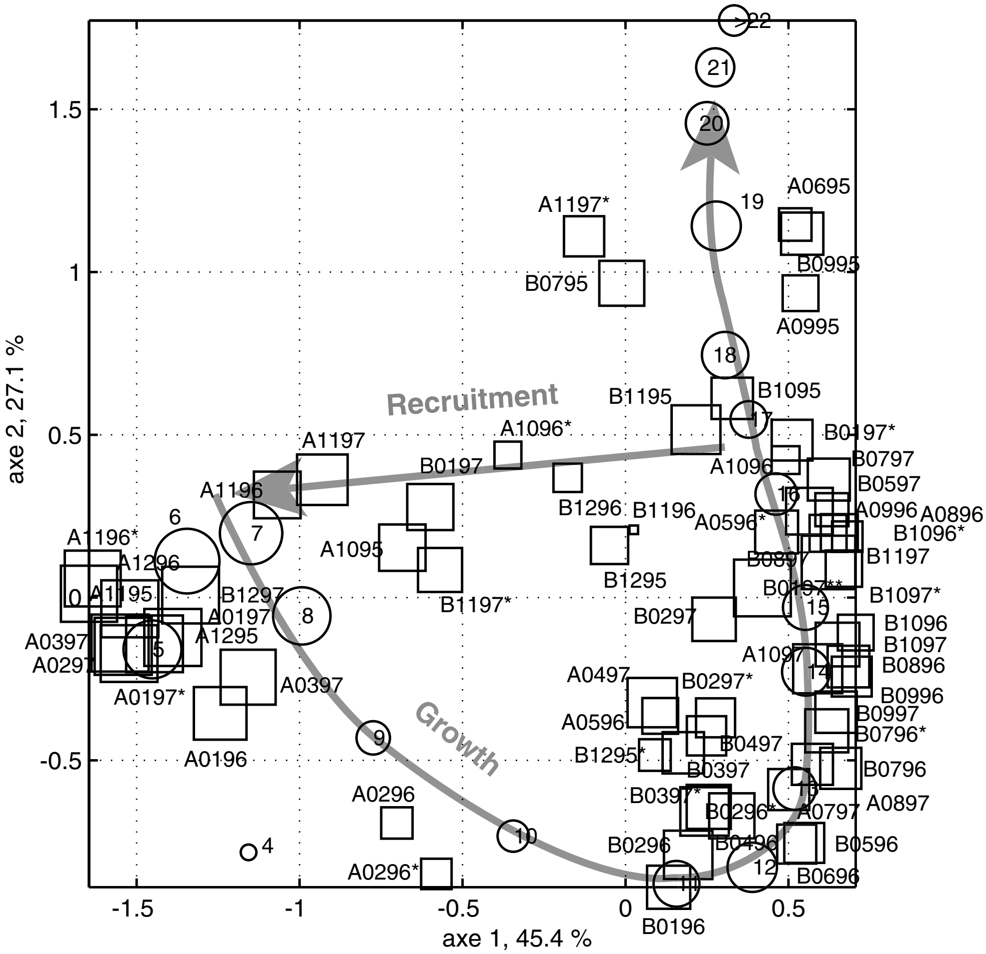



**Fig. 5** Plan defined by the1–2 axes of the correspondence analysis (CA). Size of the *circles* are proportional to the quality of the representation. Samples are represented by *squares*, whose sizes are also proportional to the quality of the representation. Symbols: *A* station 2, *B* station 8, *four next digit* month–year (“*“ added for the second sample within the same month when needed)

## Discussion

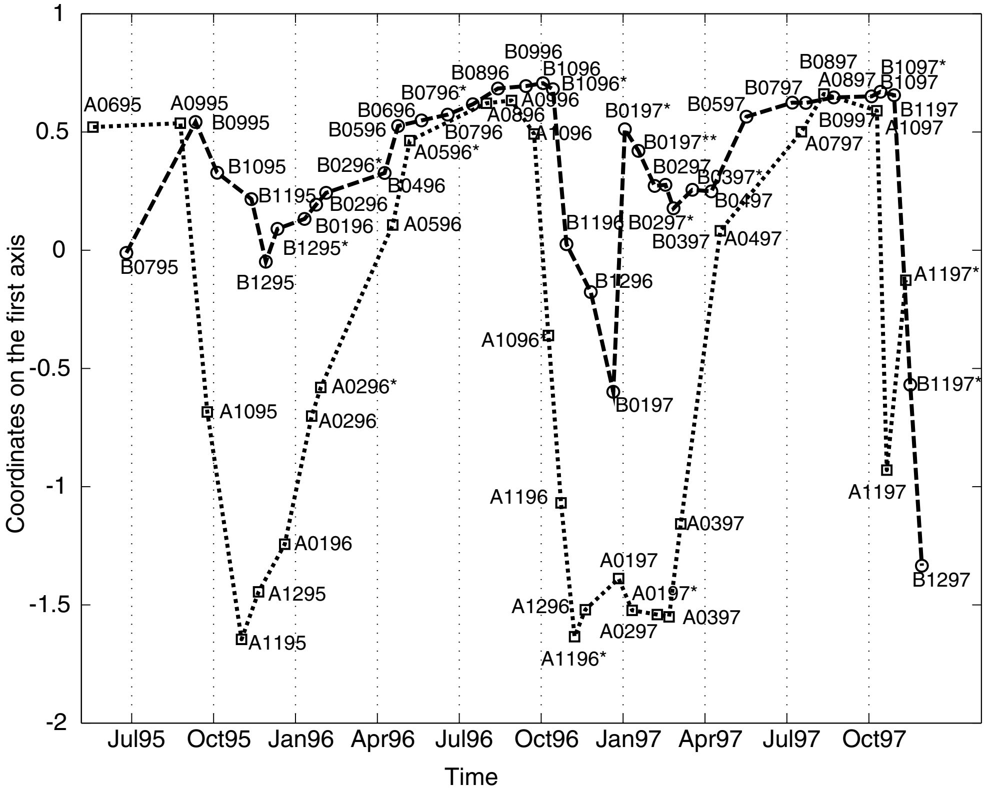
Total zooplankton biomass recorded in the Gulf of Morbihan, particularly around the Ile Longue area, are higher than the values reported for other sub-Antarctic waters (see Pakhomov et al. 1994). More specifically, *T. gaudichaudii*, within Kerguelen coastal waters, also displayed biomass higher than the values reported by Pakhomov and McQuaid (1996) for open ocean between Mc Murdo Sound and New Zealand (0.53 DW mg $m^{-3}$), between the sub-tropical convergence and the APF (1.6 DW mg $m^{-3}$), as well as around Prince Edward Islands, 0.7 DW mg $m^{-3}$ (Hunt and Pakhomov 2003).

The general pattern of the *T. gaudichaudii* population dynamics that we describe is in agreement with the observations of Kane (1966) for sub-Antarctic waters between 0°E and 20°E, that is, recruitment of new size classes in November and December followed by a rapid growth phase in summer. However, low growth characterised the southern winter period. This pattern contrasts with the report by Siegfried (1965) of a continuous reproduction and a fluctuating but permanent recruitment throughout the year in the northern part of the sub-Antarctic area. In Kerguelen, the recruitment and the increase of the biomass of *T. gaudichaudii* seemed to be synchronised with the initial increase of seawater temperature (Fig. 2) and with the bloom of phytoplankton and the corresponding increase in zooplankton, which usually takes place in October (Razouls et al. 1997). The strong seasonal signal of the environmental parameters certainly exerts a strong control on the cycle of this species through the temperature effect on growth rate and food resource availability.

The life cycle observed for the Kerguelen islands in the sub-Antarctic area corresponds with the general point of view of Ikeda et al. (1992) on the life cycle of the genus *Themisto*: the number of generation per year is decreasing with the extreme latitude, e.g., *T. libellula* and *T. abyssorum* with one generation per 2 year for the arctic areas and *T. japonica*, *T. pacifica* and *T. compressa* with several generations per year for lower latitude areas. For *T. gaudichaudii*, in our studies, we observe one generation per year with a recruitment during the summer.

The changes in biomass and size structure in the two areas of the Kerguelen Islands system suggested re-

**Fig. 6** Coordinates (scores) of stations 2 (*label A*) and 8 (*label B*) on the axis 1 of the CA versus a time scale, labelled as Fig. 5




cruitment in the "Open gulf" zone and a migration of an important part of the population of young individuals to the "Ile Longue" area. The early emergence of the smaller size class in the "Open gulf" area is followed by an clear increase in the biomass of small size individuals in the "Ile Longue". The slight increase in size supports the hypothesis of active migration associated with growth.

In the Kerguelen Islands system, comparison of the size structures of *T. gaudichaudii* population derived from net catches with the gut content of major predators has shown a good agreement (Bost et al. 1994; Bocher et al. 2000, 2001) with the individuals mainly distributed between 11 mm and 20 mm. Interestingly, such size pattern also agreed with the data reported for the coastal waters of Heard Islands (Green et al. 1998) and South Georgia (Kock et al. 1994). Open ocean sampling revealed the presence of larger size (> 22 mm) in *T. gaudichaudii* (Briesley et al. 1998) or in the stomachs of bird feeding outside the Island system (Bocher et al. 2001). Such large size, older age classes were very rarely found in the Gulf of Morbihan, and may be interpreted as an emigration of individuals after the first-year period towards the open ocean. How representative is this migrating part population remains an open question. If so, the stock of young coastal individuals could be seen as a nursery of *T. gaudichaudii* for the open Southern Ocean.

In conclusion, the general pattern of *T. gaudichaudii* in the Kerguelen coastal water begins with recruitment from October to March, followed by growth during the winter month and at the beginning of spring, producing adults of reproductive age. In coastal waters, population is more concentrated in sheltered areas than in the more open area of the Morbihan gulf. Absence of large individuals in the coastal waters, known from the open waters of the ocean, suggest an emigration from the coastal zone for the individuals older than 1 year.

**Acknowledgements** The authors thank F. Alonzo, G. Fradet, N. Gasco, L. Guérin, F. Jiguet, B. Labidoire, G. Roudaut and the crew of the research vessel *La Curieuse* for their work in the field. Analysis of the data was supported financially by a grant from the Groupement de Recherche en Environnement 1069 ''Ecosystèmes Polaires et Anthropisation" from the C.N.R.S. (Programme IOZ: Interactions Oiseaux-Zooplancton). Field work was supported financially and logistically by the Institut Français pour la Recherche et la Technologie Polaires (IFRTP, Programmes N°109 and 166), and the Terres Australes et Antarctiques Françaises.

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