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Temporal patterns of change in the necrophagous hyperbenthic zooplankton community of Lobster Bay, Cape d'Aguilar Marine Reserve, Hong Kong

Christine N.W. Lee*† and Brian Morton*‡

*The Swire Institute of Marine Science, The University of Hong Kong, Cape d'Aguilar, Shek O, Hong Kong.
Present addresses: †C545, Kwun Lung Lau, 20 Lung Wah Street, Kennedy Town, Hong Kong.
‡The Western Australian Museum, Frances Street, Perth, Western Australia, Australia.

Crab-baited traps, with a 5-mm diameter opening, were deployed 90 mm off the seabed monthly at Lobster Bay, Hong Kong, for one year between 1998 and 1999. Visitors drawn to the traps were mainly species of *Ceradocus* (Gammaridea: Melitidae), *Tisbe* (Harpacticoida: Tisbidae) and *Nebalia* (Leptostraca: Nebaliacea). Apart from *Ceradocus* sp., all were scavengers with catches using baited traps significantly exceeding unbaited controls. *Ceradocus* sp. was apparently drawn to traps for refuge. The trapped scavenger community composition changed with deployment duration in the presence of bait. *Nebalia* sp., *Neanthes cricognatha* (Polychaeta: Nereidae) and *Lepedepecreum* sp. (Gammaridea: Lysianassoidea) were identified mostly two/three-days post-deployment, exhibiting a potential preference for rotten organic matter. Seasonal catches were also identified for all three visitors with maxima between October 1998 and April 1999. Such seasonal patterns might be related to either turbulence destabilizing the substratum during this period or life cycle patterns in the study area.

INTRODUCTION

In the deep sea and/or at high latitudes, necrophagous zooplankters captured using baited traps are usually dominated by lysianassoid amphipods (Sainte-Marie et al., 1989). There is, nonetheless, growing evidence to demonstrate that the preponderance of lysianassids attracted to traps in boreal waters (Sainte-Marie et al., 1989) progressively gives way to other crustaceans in subtropical regions (Biernbaum & Wenner, 1993).

In Hong Kong (22°12′N 114°15.5′E), necrophagous scavenging studies have mainly focused upon gastropods (Morton & Chan, 2000). Only Lee & Morton (in press) have concerned themselves with scavenging hyperbenthic zooplankters. These authors sampled a zooplankton community at depths of between 6 and 17 m during the winter of 1998 dominated by species of *Tisbe* and *Nebalia*. Their studies also showed that the trapped fauna at depths of <2 m chart datum (CD) mostly comprised a species of *Ceradocus* which is probably not a scavenger.

Massive human intervention in the marine ecosystem, caused by fishing and pollution, has enhanced scavenging, particularly in coastal waters (Britton & Morton, 1994). Detailed seasonal investigations of macrophagous scavenging zooplankters in shallow waters should therefore be conducted to determine if community structure has changed, as on the seabed itself (Morton, 1993). The aims of the present study were, thus, as follows:

1. to investigate if the spatial pattern identified by Lee & Morton (in press) from Lobster Bay in winter persisted throughout the year;
2. to investigate if catches change with deployment duration;
3. to examine seasonal variations in the community composition of captured scavengers.

MATERIALS AND METHODS

Site and station descriptions

Hong Kong is subtropical and experiences a sea-surface temperature range of between 15.6°C in February (winter) and 29.1°C in August (summer) (Lee, 2002). Concomitantly, sea-surface salinities vary from 23 psu in the latter to 35 psu in the former (Lee, 2002). The Cape d'Aguilar Marine Reserve is remote from a significant human population, industries and farmlands, and thus locally experiences the least amount of anthropogenic pollution with high hyperbenthic dissolved oxygen concentrations ($3.3–9.9\,\mathrm{mg\,l^{-1}}$; Lee, 2002).

Lobster Bay is an embayment of the marine reserve (Lee & Morton, in press). It encloses a sea area of six hectares and is open to the South China Sea through two gaps: to the east and south-west, respectively. Because of the island of Kau Pei Chau, Lobster Bay is partly sheltered from the north-east monsoon, particularly during winter, and is therefore semi-exposed. The substratum here chiefly comprises a mixture of coarse sand (median grain size=406–1238 μm) and large boulders >1.5 m in diameter (Lee, 2002) contained within a shallow lagoon which is partly bordered by two rocky ramparts. Station L1 was situated on the sand in the middle of the lagoon at a depth of -1.5 m CD, ~100 m from the south-western rampart. Beyond this rampart, there is a large expanse of sand with median grain sizes ranging between 1030–1288 μm (Lee, 2002). Stations M1 and M2, ~100 m apart, were situated on this sand at a depth of ~-6 m

CD. Both were located ~100 m from the southwestern rampart.

Trap design

The 250-ml traps with a 5 mm opening deployed in this study were described by Lee & Morton (in press). A trap set included three baited and two unbaited cylinders, regularly spaced but in a random order on a wooden board (Lee & Morton, 2003). Two one-kilogram weights were tethered beneath the board to lift the trap openings 90 mm off the seabed to minimize entry by unwanted benthic scavengers.

Prior to the experiments, ~10 g of *Charybdis feriatus* (Linnaeus, 1758) (Crustacea: Decapoda) was put into 4-mm mesh bags (5×6 cm) which prevented it from fragmenting and clogging the finer mesh net at one end of each trap. Empty mesh bags were placed in vacant control traps. Ten grams was chosen because approximately four grams of bait usually remained in the trap at the end of the experiments.

Trapping experiments

Three sets of five traps which collectively held nine baited and six empty controls were placed on the seabed at each station, i.e. L1, M1 and M2, with the openings paralleling the direction of the prevailing current. They were placed at a distance of ~30 cm from each other. Every trap was assigned a number (1–15), in conjunction with the corresponding station code. One-day post-deployment, three baited traps and two unbaited ones were chosen from each station using a random table, regardless of the rack, and SCUBA divers sent to retrieve the traps inserted a plug into the selected bottles. This eliminated the possibilities of a rack effect which would imply that catches of any animals might be biased for traps on certain racks. Although two baited traps from the same rack were occasionally selected for a given soak time, the possibility that three such traps were chosen from the same rack for a given soak time was not allowed. Similarly, two unbaited ones were never selected from the same rack for a given soak time. The same process was repeated at two- and three-days post-deployment.

In the laboratory, both the interiors of the traps, baited and unbaited, and the bait were rinsed thoroughly with filtered seawater into Petri dishes. The baits were examined carefully under a dissecting microscope to collect every possible scavenger. This experiment was carried out on a monthly basis from June 1998 to June 1999.

Statistical analyses

Catches were described as individuals per trap, regardless of deployment duration. As the composition of the captured fauna differed with location within Lobster Bay (Lee & Morton, in press), total catches and catches of dominant species were analysed separately for each station. A two-way analysis of variance (ANOVA) was carried out upon the dominant species caught every month to identify differences between trap type (baited/control) and deployment duration (1–3 days) at a significance level of $P=0.05$. Statistical analyses were hence conducted only for the months when considerable numbers of zooplankters were captured. If no individuals were recorded from unbaited controls, only baited trap data were examined for any significant catch differences among deployment durations using one-way ANOVA. Because the data matrix were neither normally distributed nor had equal variance, data were (x+0.5)-transformed, as suggested by Moore & Wong (1995). *Post-hoc* comparisons of catches were undertaken using the Student–Newman–Keuls correction. All the aforementioned statistical analyses were conducted using the SAS Release 8.02 software.

In addition, the data matrix was fourth-root transformed before undertaking a one-way analysis of similarity (ANOSIM) to identify any trapped faunal composition differences between baited and unbaited controls, again at a significance level of $P=0.05$. Traps with no caught animals were excluded from the analyses. Species which largely accounted for any detected community differences were identified using the SIMPER (similarity percentages) routine. Both ascending hierarchical agglomerative clustering analysis and non-metric multidimensional scaling were also done to detect any possible faunal community differences according to deployment duration and sampling month for baited trap samples. The above multivariate analyses were conducted using the PRIMER (Plymouth Routines in Multivariate Ecological Research) 5.2.0 software.

RESULTS

Overall composition of the captured fauna

Among a total of 7247 collected zooplankters, the major visitor group was *Tisbe* sp. (76.6%), followed by *Ceradocus* sp. (13.2%) and *Nebalia* sp. (6.0%). In addition, a polychaete (*Neanthes cricognatha* (Ehler, 1904)) and eight species of gammariid amphipods, including one lysianassoid (*Lepedepecreum* sp.), were captured, besides the minor and sporadic occurrences of isopods, ostracods and cumaceans. The latter were rarely obtained over the study period and captured exclusively in unbaited controls. Among the eight species of amphipods caught, four were different from those obtained in the spatial heterogeneity experiments (Lee & Morton, in press).

Over the study period, traps deployed at Station L1 attracted most *Ceradocus* sp. (89.4%); whereas 34.6% and 51.3% of *Tisbe* sp. and 36.0% and 56.2% of *Nebalia* sp. were obtained from Stations M1 and M2, respectively. The faunal composition at Station L1, hence, differed substantially from M1 and M2. *Tisbe* sp. (48.8%) and *Ceradocus* sp. (44.8%) dominated the first station. At the latter two stations the trapped fauna was overwhelmingly dominated by *Tisbe* sp. (87.6% and 86.4%, respectively), followed by *Nebalia* sp. (7.1% and 7.4%, respectively).

Station L1 (at −1.5 m CD)

Baited traps generally attracted more zooplankters (mean ±standard deviation=13 ±19 individuals·trap^{-1}) than unbaited controls (3 ±4). Such a difference increased with deployment duration from 2 to 18 individuals·trap^{-1} (Figure 1). Catches peaked from November 1998 to March

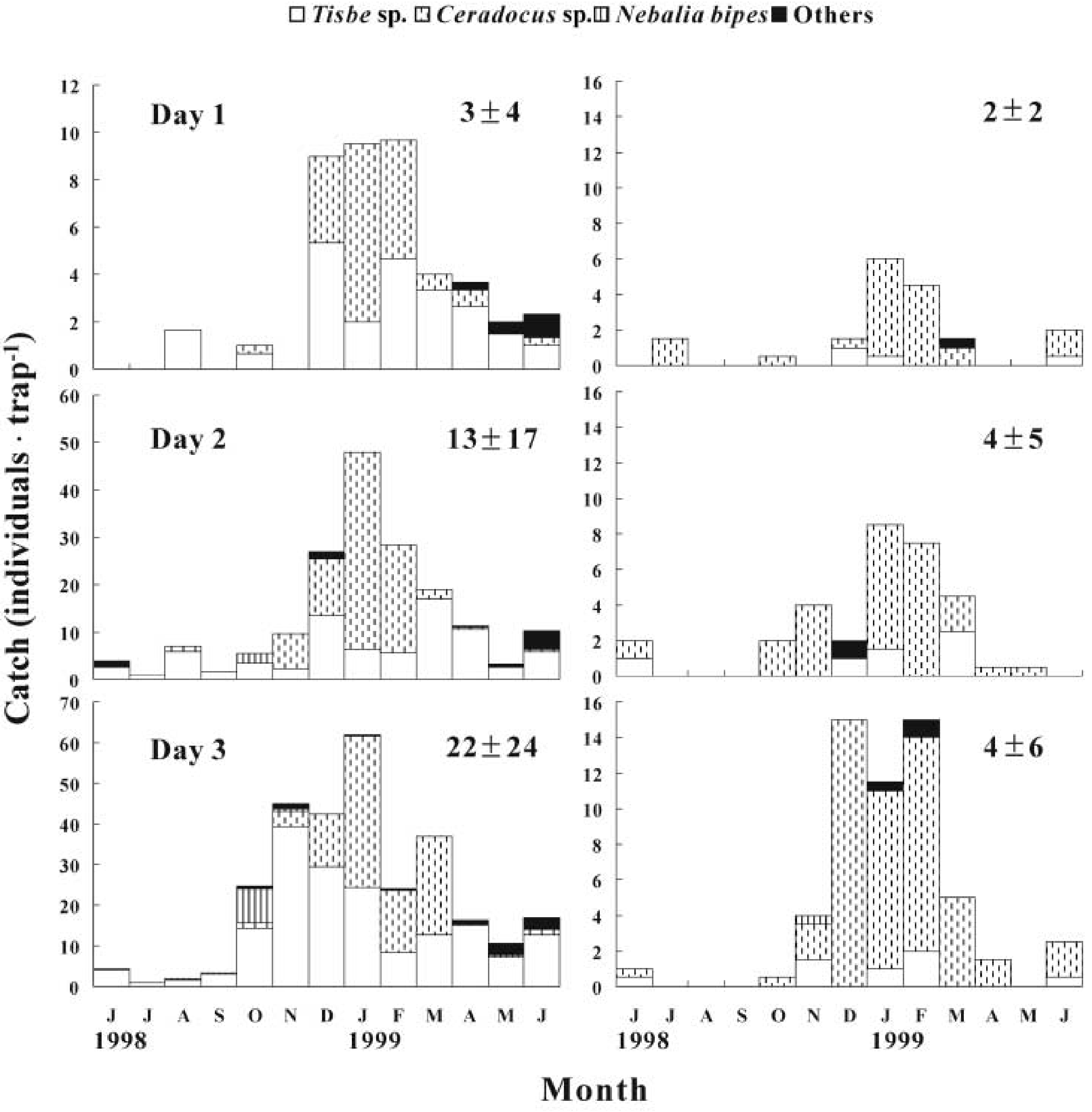

Figure 1. Temporal variations in mean total catches using tree baited (left) and two unbaited control (right) traps 1-, 2- and 3-days post-deployment at Station L1 in Lobster Bay. Means and standard deviations are also shown.

1999 and were minimal between June and September 1998, regardless of the presence of bait.

From November 1998 to March 1999, baited traps yielded significantly more *Tisbe* sp. than controls, except in January 1999. Overall, the proportion of *Tisbe* sp. in baited traps changed with deployment duration from 55.6% after Day-1 to 59.3% after Day-3. In the presence of bait, Day-3 traps contained significantly more *Tisbe* sp. than Days-1 and 2 ones only in November 1998 (df=2; MS=23.02; F=13.56; P=0.0096). In March 1999, Days-2 and 3 traps also contained more *Tisbe* sp. than Day-1 ones (df=2; MS=3.20; F=4.41; P=0.0463) for both baited and control traps. Catches in Day-3 baited traps peaked between November 1998 and January 1999.

Conversely, although mean *Ceradocus* sp. catches in baited traps numerically exceeded those of controls, significant differences between them occurred only in January 1999 (df=1; MS=16.34; F=5.99; P=0.0401). Indeed, most trapped zooplankters in controls were usually *Ceradocus* sp., accounting for an average of 83.0% of the total number of zooplankters caught using unbaited traps, as compared with baited ones (39.7%). Between baited traps, catches in Day-3 traps were significantly higher than Day-2 ones in March 1999 only (df=2; MS=13.32; F=39.64; P=0.0003). Monthly catches peaked between November 1998 and March 1999.

Catches of *Nebalia* sp. were low (2.1% of all zooplankters caught). Most occurred in Day-3 traps from August to November 1998 and May 1999. Peak abundances were identified in October 1998.

Apart from the three dominant visitors to the baited traps, 35 individuals of *Neanthes cricognatha* were captured exclusively from baited traps, albeit accounting for only 2.1% of total zooplankters captured here. Only three *N. cricognatha* were trapped one-day post-deployment but numbers rose to 12 and 20 individuals in Day-2 and 3 traps, respectively. Most individuals (40%) were obtained in June 1999, followed by May 1999 (23%).

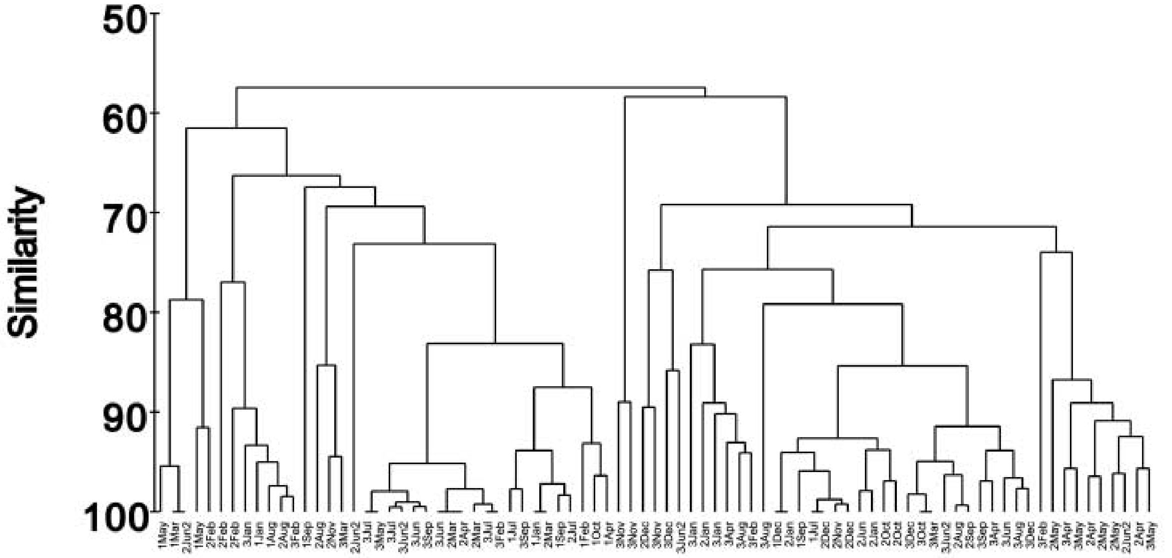

Figure 2. A dendrogram of ascending hierarchical agglomerative clustering analysis of faunal community composition identified using baited traps at Station L1. The vertical scale indicates similarity levels. Symbols are presented as deployment duration (in days) followed by sampling month. Because notations for samples collected in June 1999 overlapped with June 1998, the former was identified as "June2".

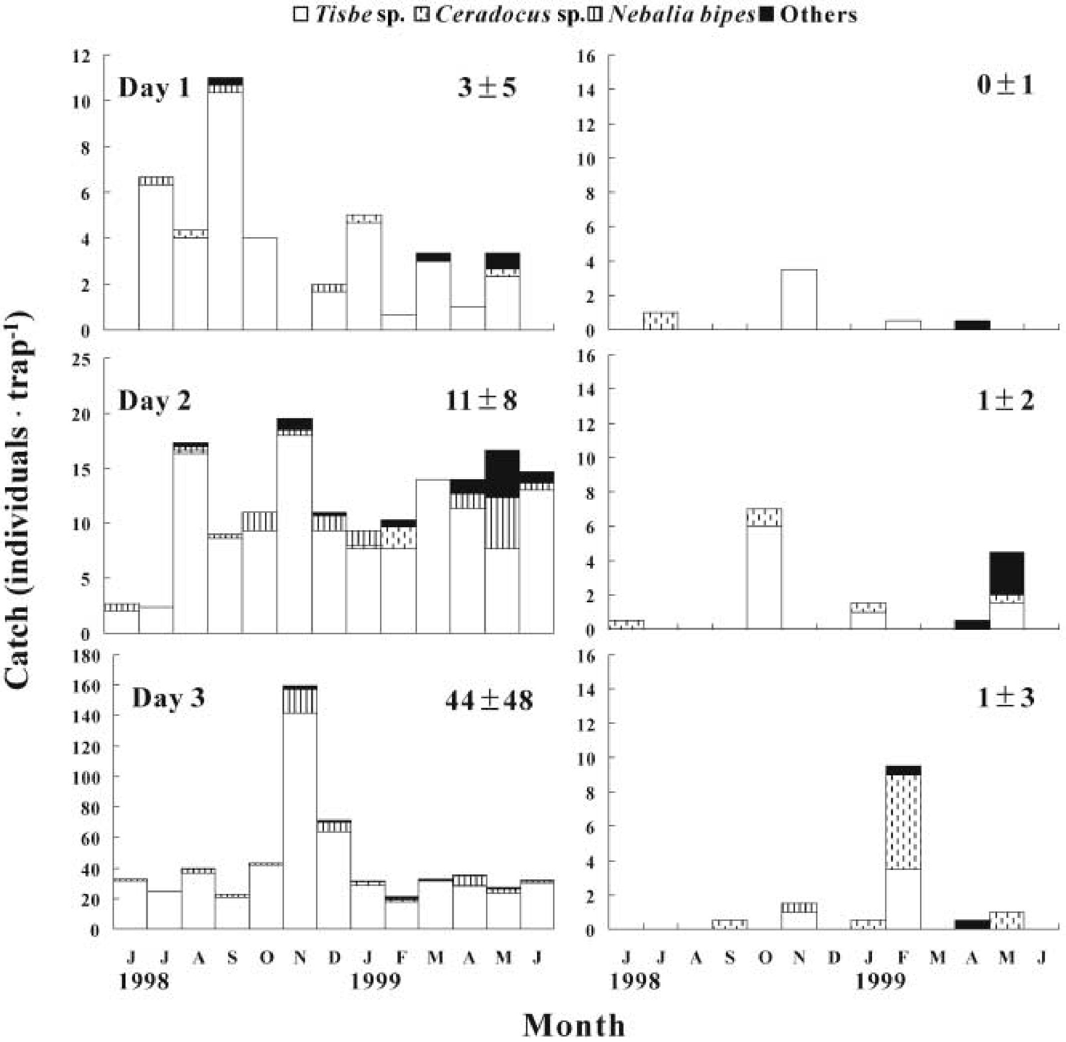

Figure 3. Temporal variations in mean total catches using baited (left) and unbaited control (right) traps 1-, 2-, and 3-days post-deployments at Station M1 in Lobster Bay. Same notations as in Figure 1.

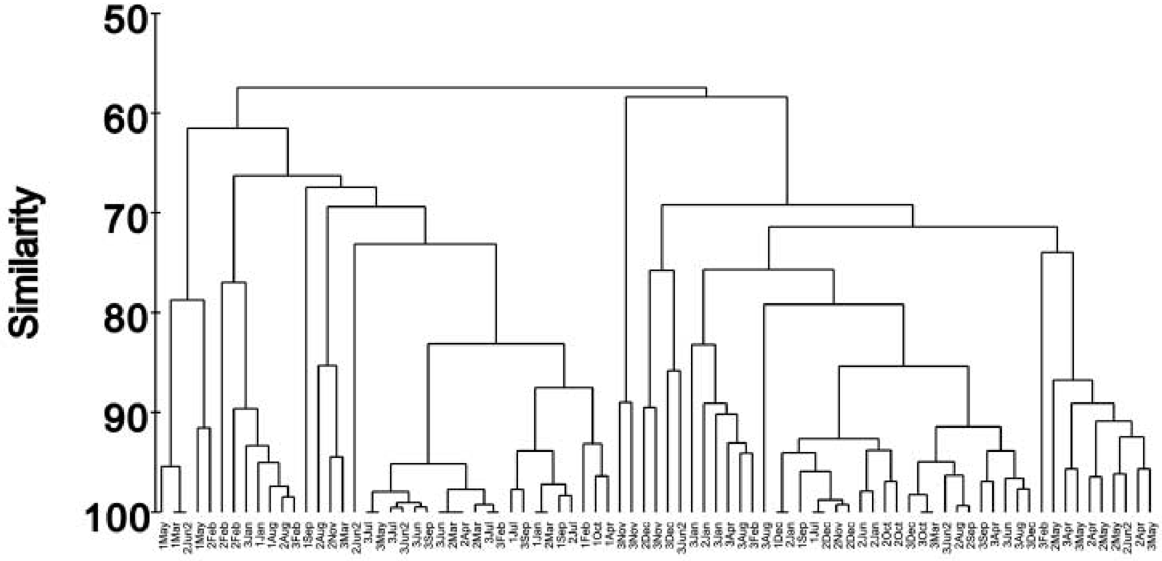

Figure 4. A dendrogram of ascending hierarchical agglomerative clustering analysis of faunal community composition identified using baited traps at Station M1. Same notations as in Figure 2.

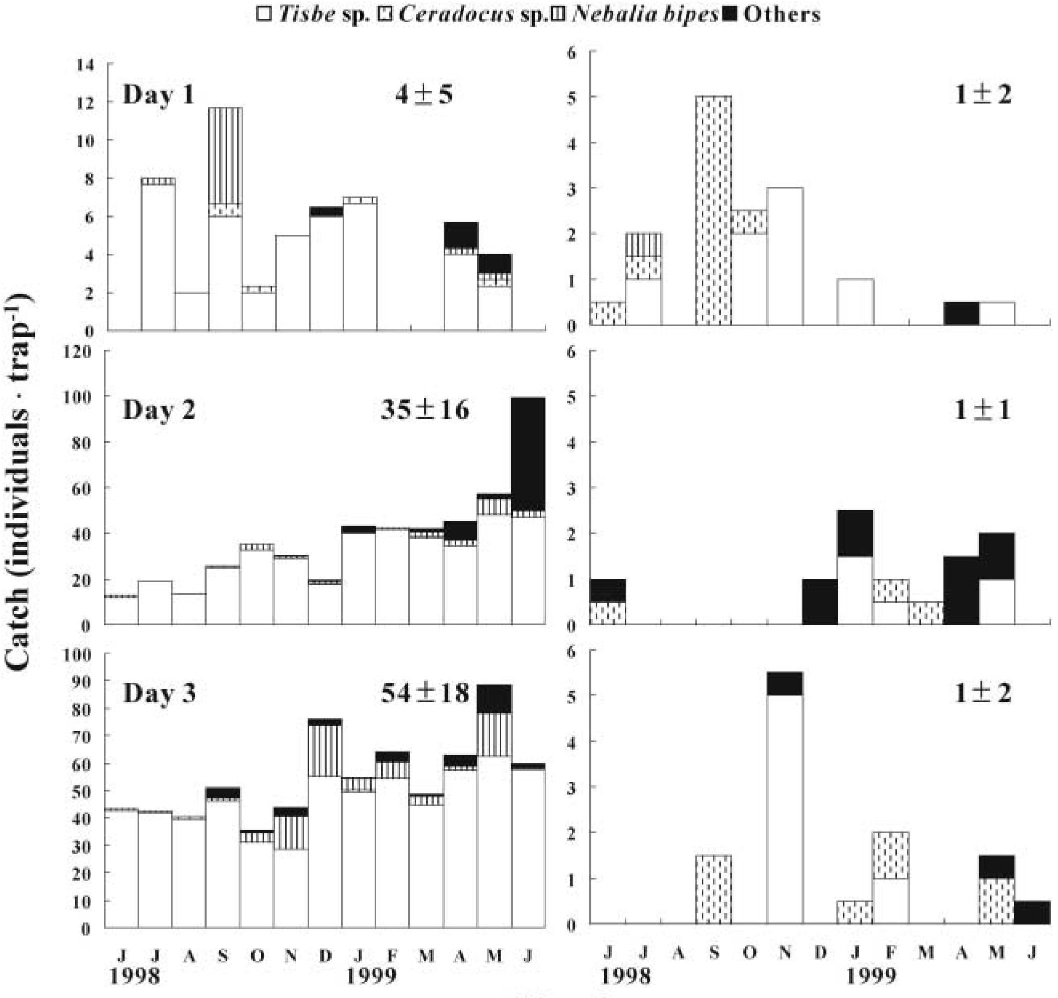

Figure 5. Temporal variations in mean total catches using baited (left) and unbaited control (right) traps 1-, 2- and 3-days post-deployment at Station M2 in Lobster Bay. Same notations as in Figure 1.

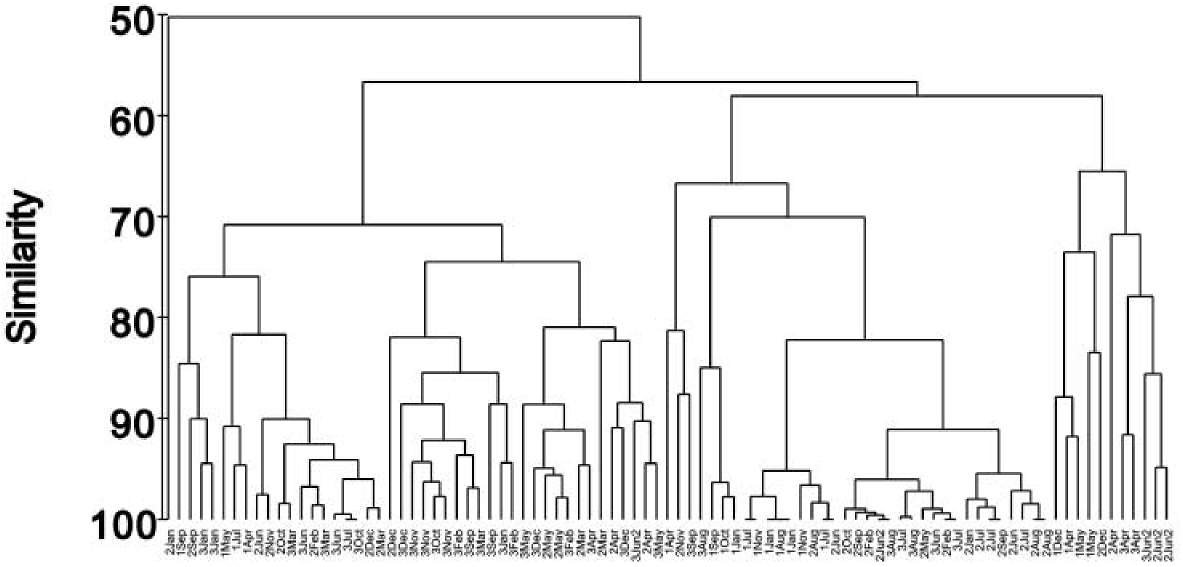

Figure 6. A dendrogram of ascending hierarchical agglomerative clustering analysis of faunal community composition identified using baited traps at Station M2. Same notations as in Figure 2.

A significant faunal community difference was obtained between baited and control traps deployed (global R=0.41; P=0.001) at a 60.6% dissimilarity level because of the relatively abundant *Ceradocus* sp. and *Tisbe* sp. in baited traps, as compared with the controls. These species, together, accounted for ~ 70% of the contribution to the dissimilarity value. Among all baited trap samples, two groups were delineated at the ~50% dissimilarity level, according to deployment duration (Figure 2), differentiating mainly Days-1 and 2 and mainly Days-2 and 3 samples. No temporal nor seasonal variations were identified for the empty controls.

Station M1 (at –6 m CD)

Total catches were numerically higher in baited (30 ±25 individuals·trap^{-1}) than unbaited (1 ±2) traps. Differences increased from seven times higher catches in the former for Day-1 post-deployment to 43 times on Day 3. The seasonal pattern for baited traps at this station was not as unequivocal as Station L1, with a single peak identified between August and November 1999 for all three day post-deployment traps (Figure 3). Low catches occurred in June and July 1998 and June 1999.

Ninety-nine per cent of caught *Tisbe* sp. were recorded from baited traps. Catches were always significantly higher in baited traps than unbaited controls, except in October 1998. Also, values for Day-3 baited traps usually significantly exceeded Days-1 and 2. A seasonal peak in *Tisbe* sp. catches was identified in November 1999.

Nebalia sp. was almost exclusively obtained using baited traps (99.6% of the total number of individuals trapped), except one from an unbaited control in November 1999. In addition, of the 160 individuals captured using baited traps here, only three were obtained from Day-1 traps, while 38 and 119 individuals were captured in Days-2 and 3, respectively. Three peaks of catches were identified among Day-3 baited traps, i.e. in August 1998, November 1998 and April/May 1999.

Ceradocus sp. rarely occurred in deployed traps, accounting for only 2% of the total number of zooplankters captured here. Total catches using baited traps over the study period (24 *Ceradocus* sp.) approximated unbaited controls (21). None was captured in November and December 1998.

A species of *Lepedepecreum* was captured at this station, but not L1. Notwithstanding, only one individual was obtained throughout the study: from a baited trap deployed for three days in August 1998. In addition, 16 *Neanthes cricognatha* were captured. All were trapped from baited traps on either Days-2 (4 individuals) or 3 post-deployment (12). In terms of a seasonal pattern, half were captured in November 1998, followed by 25% in December 1998.

Significant differences in faunal community structure between baited and control traps were identified (global R=0.64; P=0.001) at a 77% dissimilarity level. The preferences of *Tisbe* sp. and *Nebalia* sp. for bait (>50% of contribution to the dissimilarity) principally accounted for this dissimilarity. As with Station L1, baited traps deployed here could be generally demarcated into two groups, i.e. Days-1 and 2 and Days-2 and 3 (Figure 4). No such groupings were identified among unbaited controls.

Station M2 (at –6 m CD)

As at Station M1, captured zooplankters at M2 generally exhibited a preference for baited traps (30 ±25 individuals·trap^{-1}) over controls (1 ±2), regardless of deployment duration (Figure 5). Numbers accumulated with deployment duration but only for the baited traps, i.e. from 4 to 54 individuals·trap^{-1} at Days-1 and 3, respectively. The seasonal pattern was most obvious for Days-2 and 3 traps with lower catches occurring between June and November 1998.

Ninety-nine per cent of *Tisbe* sp. were caught using baited traps. Its abundance was frequently low from Day-1

(3 ±4 *Tisbe* sp.·trap^{-1}), as compared with Days-2 (30 ±15) and 3 (47 ±14). Catches were generally higher between December 1998 and June 1999. Of the 251 *Nebalia* sp. captured, only one was recorded from unbaited controls in July 1999, indicating its preference for the provided bait. In the presence of the bait, 7.2%, 20.0% and 72.8% of the total captured were recorded from Days-1, 2 and 3 traps. Catches peaked in September and December 1998 and February and May 1999. None was recorded in August 1998.

A total of 42 *Ceradocus* sp. was captured, accounting for 1.2% of the total number of zooplankters caught here. Baited and unbaited traps captured a total of 14 and 28 individuals, respectively. None was recorded in November 1998 and June 1999 using both traps.

Similar to Station M1, a single individual of *Lepedepecreum* sp. was captured in September 1998 using baited traps on Day-3 post-deployment. A total of 50 *Neanthes cricognatha* was also captured again exclusively using baited traps. Eighty-six per cent of them were captured three days post-deployment, followed by 12% on Day-2 post-deployment. Fifty-six per cent of *N. cricognatha* were obtained between September and December 1998, while not one individual was trapped between June and August 1998.

Results of ANOSIM confirmed the influence of bait upon the faunal community composition of the traps (global R=0.55; P=0.0001). Paralleling the results obtained for Station M1, such a difference at M2 was principally explained by the preference of both *Tisbe* sp. and *Nebalia* sp. for baited traps. Figure 6 demonstrates that faunal community differences in baited traps at Station M2 were determined mainly by deployment duration. Baited traps attracted a statistically different faunal community at Days-1 and 2 post-deployment from Days-2 and 3 at ~45% of the dissimilarity level. No such temporal pattern in terms of the unbaited control traps was identified.

DISCUSSION

Trapped faunal community composition in Lobster Bay

The results of the present study generally agree with those of Lee & Morton (in press). That is, *Tisbe* sp., *Ceradocus* sp. and *Nebalia* sp. were the three major hyperbenthic components of the trapped fauna in Lobster Bay. The spatial segregation of the trapped fauna identified by Lee & Morton (in press) in winter was also evident in this study. For baited traps, the trapped fauna at Station L1 was dominated by *Ceradocus* sp. and *Tisbe* sp., except for summer (April–June) when catches of the former were low; while the latter and *Nebalia* sp. were the major components at M1 and M2 throughout the year. Lee & Morton (in press) attributed this spatial pattern to changing patterns of water flow in the shallow lagoon of Lobster Bay (L1). For unbaited controls, on the other hand, trapped zooplankters were usually either *Ceradocus* sp. or *Tisbe* sp. at all the three sampling stations.

Although Lee & Morton (in press) identified insignificant differences in *Ceradocus* sp. catches between baited (13 ±7 *Ceradocus* sp.·trap^{-1}) and control (25 ±16) traps, in the present study catches using bait were numerically higher (5 ±12) than without it (2 ±4) at Station L1 and significant differences were identified, albeit only in January 1999. As reported by Lee & Morton (in press), it appears that *Ceradocus* sp. is attracted to the traps as refuges. No significant negative relationship between *Tisbe* sp. and *Ceradocus* sp. was obtained (r=−0.18; P=0.1271), contrary to the results obtained by Nishida et al. (1999) who suggested that predation by amphipods upon copepods occurs within baited traps.

Temporal patterns identified for the three trap deployment days

The present study demonstrated that baited traps, excluding fish, were initially and mostly visited by *Tisbe* sp. Catches increased with soak time. Concomitantly, *Nebalia* sp. and *Neanthes cricognatha* began to occur in baited traps on Day-2 post-deployment and increased in abundances on the third, while *Lepedepecreum* sp. occurred only in Day-3 traps.

In subtidal Gullmar Fjord, Sweden, Eriksson et al. (1975) showed that a suite of scavengers arrive at bait in a definable sequence and suggested that a wider range of scavengers come to carrion on flood tides, as compared with the ebb. Hong Kong, however, experiences unequal semi-diurnal tides, i.e. two high and two low tides of unequal size almost every day (Morton & Morton, 1983). The local tidal cycle might therefore not explain such a sequential change in faunal community composition.

Apart from the tidal cycle, Sainte-Marie (1986) suggested that the catchability of scavengers might also depend on substratum topography, sex, developmental stage, degree of starvation, scavenger efficiency in locating carrion, swimming ability and current speed. Increasing catches with deployment duration might relate to the limited swimming abilities of *Tisbe* sp., but not the other scavenging taxa because they are agile and active. Sainte-Marie & Hargrave (1987) reported that arrival sequence, times of first arrival at bait and instantaneous numbers of animals on bait may indicate the abundance and attraction distance of scavengers. However, it is doubtful that only ten grams of the bait could be detected far away (Sainte-Marie, 1986).

Although the availability of carrion in the sea is largely unpredictable and its bacterial decomposition rapidly renders it unpalatable and even inedible for most macrophagous scavengers, carrion is generally regarded as good, nutritious food which requires minimal effort to handle and consume (Britton & Morton, 1994). Scavengers therefore normally respond to the occurrence of carrion as soon as they can. The rising catches of *Tisbe* sp. with time and the trapping of *Nebalia* sp. and *Neanthes cricognatha*, however, two-day post-deployment is, therefore, puzzling.

At shallower depths, such as on the continental shelf, fish and sharks are always important primary consumers of carrion (Hill & Wassenberg, 1990), while invertebrate scavenging is negligible (Britton & Morton, 1994). The trapped fauna identified in this study, therefore, with the exclusion of fish, represents secondary arrivals upon carrion (Britton & Morton, 1993). In order to alleviate the high predation risk by fish when consuming carrion in shallow waters, these secondary scavengers might therefore be adapted to saprophagous scavenging. Most scavengers in the sea prefer fresh moribund tissues to those in an advanced state of saprophytic disintegration (Moore & Wong, 1995), except for amphipods, polychaetes (Britton & Morton, 1994) and, in this case, leptostracans and copepods. After the bait has leached into the sea for either one or two days, its tissues become partly decomposed by bacteria and gradually deteriorate to an advanced state of saprophytic disintegration. Eventually, the putrefying flesh becomes unattractive to fish and allows the approach of another array of scavengers, such as *Nebalia* sp., *Neanthes cricognatha* and *Lepedepecreum* sp. Further studies regarding the possible saprophagous preferences of these scavengers are needed to confirm this hypothesis.

Seasonal patterns

The present study shows that data from Day-1 post-deployment were highly variable, possibly due to unpredictable daily effect, such as sun/moonlight intensity. The results from Day-3 post-deployment traps, however, included the widest diversity of trapped fauna and hence were used to identify any seasonal pattern. With a constant supply of carrion throughout the year, catches of *Tisbe* sp., *Ceradocus* sp. and *Nebalia* sp. were generally high in Lobster Bay from October 1998 to April 1999 and low in summer (June–September 1998 and June 1999) at all stations.

Since natural moribund animal tissues were rarely observed on the seabed throughout the course of this study, it is unlikely that such carrion would attract scavengers from the baited traps.

Intensive wave activity in Lobster Bay under the influence of the north-east monsoon between October and May (Lee, 2002) might be responsible for the identified seasonal pattern. Although orbital wave velocities decay exponentially with depth, storm-induced disturbances can reach 100 m (Hall, 1994). Winter storms might, therefore, wash populations of *Nebalia* sp. from the deeper waters of Lobster Bay (Stations M1 and M2) to the shallow lagoon at L1, leading to a peak catch there in October 1998. This is particularly true for taxa, such as *Nebalia* sp., which do not exhibit curling behaviour that acts as an anchor to help stop them being washed out of the sediment (Hall, 1994). Winter storms might be responsible for the higher catches of non-scavenging *Ceradocus* sp. at Station L1. Because the shallow lagoon is open to 'The Gap' in the east (Lee & Morton, in press), current velocities and turbulence here are relatively powerful, particularly during the north-east monsoon in winter. *Ceradocus* sp., therefore, might seek refuge in the traps to prevent it being washed away at this time.

Moore & Wong (1995) also identified an analogous seasonal pattern in catches using baited traps in Scotland, i.e. a peak between September and November, and correlated this with high sea-surface temperatures which accelerate the metabolic rates of lysianassoids and, hence, foraging activities. In Hong Kong, however, sea-surface temperatures fall from 28°C in August to 15.9°C in February (Lee, 2002), indicating that other factors, such as species-specific biological cycles of the trapped fauna, might operate here. Further studies relating to the life cycles of the scavengers trapped in this study of Lobster Bay are therefore required.

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