Zoological Studies

# Distribution of Necrophagous Copepods in the Cape d'Aguilar Marine Reserve, Hong Kong

Christine N.W. Lee

The Swire Institute of Marine Science, University of Hong Kong, Cape d'Aguilar, Shek O, Hong Kong Tel: 852-6271-9312. Fax: 852-2809-2197. E-mail: leptostracan@yahoo.com or h9305583@graduate.hku.hk

(Accepted February 2, 2004)

**Christine N.W. Lee (2004)** Distribution of necrophagous copepods in the cape d'Aguilar marine reserve, Hong Kong. *Zoological Studies* **43**(2): 304-313. Unbaited traps and traps baited with crushed crabmeat were deployed 60 mm off the seabed of Lobster Bay, the Cape d'Aguilar Marine Reserve, for 3 d in the winter 1999. Each trap had a 5-mm-diameter opening. A common visitor to the bait was a species of *Tisbe* (Copepoda: Harpacticoida). Baited traps usually contained more *Tisbe* than unbaited ones. A spatial distribution of *Tisbe* was also identified within the study area, i.e., a greater catch was recorded from deeper waters outside the bay. A significant positive correlation between the number of *Tisbe* trapped and sediment organic content was identified. Simultaneously, *Tisbe* catches corresponded negatively to the median grain size of the substratum, implying that the distribution of scavenging *Tisbe* is inversely related to sediment physiography in Lobster Bay. http://www.sinica.edu.tw/zool/zoolstud/43.2.304.pdf

Key words: Baited traps, Scavengers, Tisbidae.

he Copepoda, with high species richness in the sea, is comprised of members occupying various feeding guilds, including herbivores (Guisande et al. 1996, Calbet et al. 2000), detritivores (Boak and Goulder 1983, Gyllenberg 1984, Steinberg et al. 1998), bacterivores (Gowing and Wishner 1992, Turner and Roff 1993, Webber and Roff 1995), ciliates (Jonsson and Tiselius 1990, Siaz and Kiørboe 1995) and cyanobacteria consumers (Tokioka and Bieri 1966, Ingólfsson and Ólafsson 1997), and carnivores (Ohtsuka et al. 1987, Uye and Kayano 1994, Kurashov 1996). Notwithstanding, feeding in the natural environment is probably opportunistic, and copepods generally rely on mixed diets (Raymont 1983, Turner 1984a b, Mauchline 1998).

In contrast, necrophagous scavenging copepods are rarely recorded. The 1st description of harpacticoid scavenging behavior was by Garstang (1900). *Tisbe furcata* (Baird, 1837) was seen to attach by its antennae and maxillipeds to dead fish larvae and use its mandibles to consume them. *Tisbe furcata* also attacks living fish larvae but prefers either moribund or dead prey. In addition, Seifried and Dürbaum (2000) observed *Ectinosoma carnivora* Seifried and Durbaum, 2000 ingesting deceased ostracods and fish in the laboratory. Several predatory calanoids also consume dead animals. Recently, other marine copepods, such as *Xanthocalanus gracilis* Wolfenden, 1911, through an analysis of oral appendage structure, have been suggested to be macrophagous scavengers, particularly those inhabiting the hyperbenthon (Ohtsuka 1984 1985, Ohtsuka and Mitsuzumi 1990, Ohtsuka et al. 1991). Some freshwater cyclopoids feed upon fish carrion (Kaestner 1970, Britton and Morton 1993 1994).

Carrion feeding occurs unambiguously in all marine habitats (Biernbaum and Wenner 1993, Britton and Morton 1993 1994). Congregations of zooplanktonic necrophages have been well documented in 2 areas: at high latitudes, regardless of water depth (Bowman 1974, Thurston 1979, Lampitt et al. 1983, Sainte-Marie 1986a b, Biernbaum and Wenner 1993) and in waters deeper than the mesopelagic stratum at low latitudes (Hessler et al. 1978, Sekiguchi and Yamaguchi 1983, Tso and Mok 1991). Areas, other than the aforementioned, however, have received either little or no study for the possible occurrence of these animals (Biernbaum and Wenner 1993). The aims of this study were, thus:

1. to trap and identify necrophagous copepods in the shallow waters of subtropical Hong Kong;

2. to determine whether or not such trapped copepods have a spatial distribution pattern; and

3. to identify possible factors determining any spatial pattern of such scavenging copepods in the study area.

## MATERIALS AND METHODS

#### Site description

Cape d'Aguilar is the only marine reserve in Hong Kong and was designated on 5 July 1995 because of its variety of habitats and diversity of associated flora and fauna (Morton and Harper 1995). It is situated on the southeastern tip of Hong Kong Is. (22°12'N, 144°15.5'E) (Fig. 1) and is remote from population centers, with no industry or farmland nearby, indicating a low degree of anthropogenic influence (with an annual mean nitrate concentration of 0.48 mg  $\cdot$  L<sup>-1</sup> and an annual mean chlorophyll *a* concentration of 0.37 µg  $\cdot$  L<sup>-1</sup>; Lee 2002). Stratification of the water mass in the study area occurs in summer with dissolved oxygen concentrations at the bottom always > 3.30 mg · L<sup>-1</sup> (Chiu et al. 1985, Leung 1994). The southeastern waters of Hong Kong in winter are mainly subjected to the Zhejiang-Fujian Longshore Current from the East China Sea and the Kuroshio from the eastern Philippines which keep local sea temperatures at > 15°C. In summer, the South China Sea Surface Waters raise local sea temperatures to ~28°C (Clark 1997, Hawkins 1998, Lee 2002). The study area, therefore, constantly experiences various oceanic current intrusions and is considered to have the cleanest waters in Hong Kong (Morton and Morton 1983, Environmental Protection Department 2001).

In this study, all samplings were conducted within Lobster Bay with a sea area of approximately 6 ha (Fig. 2). Lobster Bay is a semi-exposed marine embayment with water depths ranging from 0.8 to 7 m. The northeast monsoon creates a seasonal movement of water, which may reach velocities of 0.63 m  $\cdot$  s<sup>-1</sup> (Clark 1997). The sediments of the bay are mainly comprised of large rocks, interspersed with sand patches (Hodgson 2000). The sediments here are well-sorted with a median  $\Phi$  value of 1.3, i.e., medium sand (Wells 1994). They consist of pale, yellowish-gray sand with an oxygenated surface layer at between 2 and 3 cm.



Fig. 1. Map of Hong Kong showing the location of the Cape d'Aguilar Marine Reserve.

Stations L1, L2, L3, M1, M2, and D1 were selected in accordance with an envisaged transect line shown in fig. 2. This transect stretched from the western shore of the Cape d'Aguilar Peninsula seaward in a southwesterly direction. It crossed stations at different water depths, including those of between -0.8 m C.D. on the western rampart at station L3 and -17 m C.D. at D1. Stations L1 and L2 were situated in a shallow lagoon at a depth of -1.2 m Chart Datum; M1 and M2 were at -6 m C.D.

## Sediment physiography

Both median grain size and organic content of the substratum were examined at the 6 sampling stations. The former was determined using a graded series of sieves of 63, 125, 250, 500, 1000, and 2000  $\mu$ m (Percival and Lindsay 1996). Approximately 500 g samples of sediments were collected and oven-dried at 80°C to a constant weight. The dried sediments were subsequently



Fig. 2. Map of Lobster Bay, the Cape d'Aguilar Marine Reserve, Hong Kong, showing the location of the 6 sampling stations (after Hodgson 2000).

weighed using an electronic balance and soaked with freshwater for 2 h before undergoing a 15 min wet sieving on a mechanical sieve shaker (E.V.T.1, Endecotts). The sorted samples were oven-dried again to a constant weight. The median grain size of the sediment samples is reported in micrometers.

The organic content of the sediment was determined by placing ~5 g of sediment into a preweighed aluminum cup, weighing it using an electronic balance, and combusting the sample at 550°C in a muffle furnace for 4 h. The samples were then cooled to room temperatures in a desiccator. The percentage organic content of dried sediment was calculated from the weight difference between the pre-combusted and ashed samples. Both granulometric parameters measured were run in triplicate for each station on 6 randomly selected days between June 1998 and July 1999.

## Trap design

Traps used in this study were modified from Morton and Chan (2000) and made from 250 ml, transparent "Farlin" baby feeding bottles with the bottom cut off and fitted with an inverted plastic funnel, with an opening of 5 mm (Fig. 3A). The inverted funnel was also covered by a screen with a mesh size of ~4 mm, to keep gastropods, fish, crabs, and prawns out of the trap because these are numerous in the study area (Morton and Chan 2000). The other opening of the bottle was shielded with a finer 80  $\mu$ m mesh net held in place using a screw cap with a 25-mm-diameter aperture.

Two weights, each of approximately 1 kg, were tethered beneath both ends of a wooden board  $(0.6 \times 0.4 \text{ m})$  (Fig. 3B). Each thus-constructed rack held 5 traps fastened with plastic cable ties. Of these, 3 were baited, with the other 2 act-



**Fig. 3.** Basic design of (A) a trap and (B) the arrangement of traps on a wooden board.

ing as unbaited controls. The 5 traps were positioned randomly on each wooden board. The weights kept the traps just off (60 mm) the seabed to minimize the numbers of unwanted scavengers. The openings of the traps were, as a result, situated ~90 mm above the level of the substratum, and the centers of the funnels were 60 mm apart. The traps were not, therefore, expected to capture individuals of benthic copepods which are incapable of swimming. Raising the traps off the seabed excluded scavenging gastropods, such as *Ergalatax contractus* L.A. Reeve, 1846 and *Thais luteostoma* Holten, 1802, which are known to be numerous in the study area (Morton and Chan 2000).

Ten-gram pieces of moribund, crushed crabs, *Charybdis feriatus* (Linnaeus, 1758), were used as bait within 4 mm mesh bags (5 x 6 cm). These prevented fragments of the bait from detaching and clogging the finer-mesh net at 1 end of each trap. Such clogging would hamper ventilation inside the traps and, in turn, curtail stimuli emanating from them to attract potential scavengers. Notwithstanding, the pore apertures of the bags were still large enough for scavenging copepods to access the bait within. Control traps did not come into contact with bait and contained empty mesh bags. Traps and bait bags were thoroughly washed between deployments.

## Sampling

Two sets of traps were deployed at each station. They were placed at a distance of between 20 and 30 cm from each other. The traps were set on the sea floor by scuba divers to make sure that they were positioned in equivalent habitats, i.e., open, soft bottom, with the trap openings oriented parallel to the direction of prevailing currents. Three days after deployment, which encompassed a range of tidal conditions, scuba divers returned to the traps and inserted a chopstick into the entrance of each bottle to prevent further intrusions while they were retrieving them with the jammed opening facing upward. In the laboratory, the interiors of the traps were thoroughly rinsed with filtered seawater into petri dishes. Any captured copepods were identified to species level, where possible, and counted under a dissecting microscope. The bait was also carefully examined to confirm that no living creatures either clung to it or were hidden inside. This experiment was replicated 3 times during the winter 1998.

# **Statistical analyses**

Catches (individuals · trap-1) were calculated for every sampling station. Values of the 3 baited traps and 2 unbaited controls in each set were averaged separately to give a better mean to mitigate for any possible within-set pseudo-replication. Median grain size and sediment organic content were compared separately between the 6 sampling stations using a one-way analysis of variance (ANOVA), while a two-way ANOVA was employed for catch differences between baited and unbaited controls and between sampling stations at a significance level of p = 0.05. Before these tests, the data matrix was examined for both normality and heterogeneity using Shapiro-Wilk's and Bartlett's tests, respectively. If data distributions were either non-normal or of unequal variances, median grain size and organic content were log-transformed, while catches were ( $\sqrt{(x + 0.5)}$ )-transformed, following the method of Moore and Wong (1995) and Morritt (2001) before further comparisons were made. A posteriori pair-wise multiple comparisons were conducted if significant differences between the 6 stations were obtained using Student-Newman-Keul's (SNK) correction at p = 0.05. Correlations between catches and both medium grain size and organic content were examined using a non-parametric Spearman correlation analysis at p = 0.05. SAS vers. 8.02 software (SAS Institute 2001) was used to carry out the statistical analyses.

## RESULTS

## Sediment physiography

Table 1 and fig. 4 summarize both mean sediment granulometry and organic content for the 6 sampling stations in Lobster Bay. The median grain size at station L3 was significantly coarser than the others (M.S. = 1356; d.f. = 5; F = 6.48; p =0.0005) and defined as "very coarse sand", according to Percival and Lindsay (1996). Sediments at station D1 were finest and described as "fine sand". Values at the remaining 4 stations did not significantly differ from each other (~1000  $\mu$ m). Notwithstanding, on the basis of definitions of Percival and Lindsay (1996), sediments at station L1 were "medium sand", while the others were "coarse sand".

A gradation of decreasing organic content from station D1 shoreward was generally recorded along the hypothesized transect, as shown in fig. 2. The muddy substratum at station D1 was significantly more organically enriched than the remaining stations (*MS*. = 0.46; *d.f.* = 5; *F* = 28.70; *p* = 0.0001) (Fig. 4B).

## **Copepod trapping**

In total, 180 traps, 108 baited, and 72 unbaited, were deployed. Large pieces of crab tissues were still present at the time of trap recovery, indicating that surplus food was provided over the deployment duration. This is important because it might have helped reduce chances of cannibalism between trapped visitors in the same container. Regardless of trap type, the faunal community captured was monopolized by the Copepoda (72%, with a total of 1409 individuals). All copepods obtained were exclusively a species of *Tisbe* (Harpacticoida: Tisbidae).

Both the presence of bait and sampling station significantly determined the catches of *Tisbe* (Table 2A). The overall mean number of Tisbe captured using baited traps was 36 ± 34 individuals · trap-1 (Fig. 5). In contrast, the number of Tisbe retained in the empty controls averaged 2 ± 5 individuals · trap-1. Although the catches also varied with sampling station, a significant interaction between the presence of bait and sampling station was identified in the two-way ANOVA. Further analysis of the data revealed that the values differed between the 6 stations only if baited traps were used (Table 2B). No significant inter-station variations were identified for the controls. Statistical analysis clearly demonstrated that, in every case, significantly more numbers of Tisbe were attracted to baited traps at sta-

Table 1. Summary of substratum characteristics at the 6 sampling stations in Lobster Bay

Station		L1	L2	L3	M1	M2	D1
Median grain size ( $\mu m$ )	Mean ± s.d.	755 ± 346	1238 ± 588	2116 ± 231	1288 ± 575	1030 ± 434	194 ± 23
Organic content (%)	Min Max. Mean ± s.d.	406 - 1189 1.98 ± 0.17	707 - 2000 $1.92 \pm 0.09$	2000 - 2462 $2.55 \pm 0.33$	574 - 2000 2.69 ± 0.51	574 - 1866 2.79 ± 0.36	177 - 210 $4.08 \pm 02.4$
<b>J</b>	Min Max.	1.83 - 2.28	1.83 - 2.06	2.14 - 3.13	1.92 - 3.6	2.14 - 3.17	3.79 - 4.35



**Fig. 4.** Spatial distribution of (A) median grain size and (B) organic content at the 6 sampling stations in Lobster Bay during the winter 1998. Vertical lines indicate standard deviations.

tions deeper than -6 m C.D., such as stations M2 (mean, 67 ± 61 individuals · trap<sup>-1</sup>) and D1 (mean, 59 ± 30 individuals · trap<sup>-1</sup>), as compared with identical traps deployed at similar sites, but at the shallowest depths, i.e., station L3 (mean, 17 ± 6 individuals · trap<sup>-1</sup>). A significant negative correlation between *Tisbe* catch and median grain size was identified at r = -0.43 and p = 0.0096. On the contrary, *Tisbe* catches increased with sediment organic content (r = 0.59; p = 0.0001).



**Fig. 5.** Catches of a species of *Tisbe* using baited and unbaited traps deployed in Lobster Bay. Vertical lines indicate standard deviations.

**Table 2.** Statistical analyses of *Tisbe* catches between the 6 sampling stations in Lobster Bay. As the data matrix was neither normally distributed (*F* = 78.89; *p* < 0.0001) nor had equal variances (*W* = 0.78; *p* = 0.0001), data were ( $\sqrt{(x + 0.5)}$ )-transformed. (A) Results of a two-way ANOVA test, examining the effects of both spatial patterns and trap type upon *Tisbe* catches. (B) Results of an one-way ANOVA of copepod catches evaluating the possible spatial distribution for each trap type. \**p* < 0.05; \*\**p* < 0.01; \*\*\**p* < 0.001

A. Two-way ANOVA

Variable	Source of variation	d.f.	<i>M</i> .S.	F	р
Copepod catch	Main effect				
	Trap (T)	1	334.13	148.17	0.0001***
	Station (S)	5	8.88	3.94	0.0037**
	Interaction effect				
	T*S	5	6.43	2.85	0.0224*
	Residuals	60	2.25		

B. One-way ANOVA for each trap type

Variable	Source of variation	d.f.	M.S.	F	p	Ranks
Baited trap	Main effect Station Residuals	5 31	15.33 4.08	6.05	0.0089**	M2, D1, M1, L3, L1, L2
Control trap	Main effect Station Residuals	5 30	1.65 0.81	0.73	0.6010	Not significant

## DISCUSSION

Macrophagous scavenging is a common trophic strategy. Almost all animal phyla have representatives which scavenge, although obligate scavengers are difficult to identify (Britton and Morton 1993 1994). Britton and Morton (1994) reviewed scavenging in various animal phyla, including macrophagous zooplankton. Lysianassid amphipods are always well represented among trapped zooplankters (Dahl 1979, Sainte-Marie 1984 1986a, Biernbaum and Wenner 1993). Scavenging copepods, on the other hand, have received scant attention. This is probably because fishermen have frequently reported on the consumption of both bait and trapped lobsters by large numbers of lysianassids (> 100 individuals · trap-1) (Lampitt et al. 1983, Kikuchi et al. 1990, Morritt 2001).

Table 3 lists previous records of copepod trapping using bait. Virtually all studies, except for that of Sainte-Marie (1986b), were conducted at abyssal depths. Also, most were undertaken in boreal waters. Although Schulz (1990) captured a calanoid, *Pterochirella tuerkayi*, from tropical waters (the Gulf of Aden) using baited traps, Ohtsuka et al. (1998) doubted its regular occurrence there because the only specimen was an adult male with reduced mouthparts. The present study is, therefore, probably the 1st record of scavenging copepods in coastal waters of the subtropics (latitude 22°12'N).

Table 3 also shows that copepods drawn into baited traps are usually either calanoids (representatives of the Phaennidae and Tharybidae) or harpacticoids (Tisbidae). In this study, the only copepod recorded was *Tisbe* sp., i.e., a member of the Tisbidae. Significantly higher Tisbe catches in baited traps than empty controls suggest that it is a scavenger. Representatives of the Tisbidae are known to be omnivorous and opportunistic (Hicks and Coull 1983) and have been reported frequently from baited traps indicating that necrophagy is certainly one of their feeding modes. Tisbe was the only copepod recorded in the present study. This is opposite to the fauna captured from boreal waters in which more than 1 scavenging copepod species is usually obtained (Table 3). More-intensive trapping experiments are necessary to demonstrate possible latitudinal

**Table 3.** A review of copepod trapping using baited traps

Location	Latitude	Depths	Species identified	Reference
On the Ross Ice Shelf in the Antarctic	82°22.5'S	597 m	Longipedia weberi Scott A, 1909, Tharybis magna Bradford- Grieve and Wells, 1983, Tisbe prolata Waghorn, 1979, Tisbe spinulosa Bradford-Grieve and Wells, 1983, Xanthocalanus gracilis Wolfenden, 1911, Xanthocalanus harpagatus Bradford-Grieve and Wells, 1983	Bradford-Grieve and Wells (1983)
Lützow-Holm Bay, Antarctica	68°55.3'S - 69°00.1'S	171-659 m	<i>Tharybis magna</i> Bradford- Grieve and Wells, 1983 , <i>Xanthocalanus gracilis</i> Wolfenden, 1911	Ohtsuka et al. (1998)
Saint Lawrence Estuary	47°57'30''N	0.1-5 m	Unidentified harpacticoids	Sainte-Marie (1986b)
Northeast Atlantic Ocean	37°47.5'N	4855 m	Unknown calanoids	Thurston (1979)
Sagami Bay, central Japan	35°00'N	1445 m	<i>Tharybis</i> sp., <i>Undinuella</i> sp., Unidentified harpacticoids	Nishida et al. (1999)
About 700 km north of Oahu, Hawaii, Central North Pacific Gyre	28°00'N	5720 m	<i>Tisbella</i> sp.	Shulenberger and Hessler (1974)
Gulf of Aden	12°30.7'N	1318 m	<i>Pterochirella tuerkayi</i> Schulz, 1990	Schulz (1990)

differences in scavenging copepod composition.

Members of the Harpacticoida are always recorded from the seabed as benthos. No copepods, however, have been reported from previous benthos studies in Lobster Bay (Wells 1994, Morton and Harper 1997). The trapped *Tisbe* has, however, been recorded in daytime plankton sampling studies using a 125 µm mesh net in the study area at an annual mean abundance of < 1% of total adult copepod numbers (Lee 2003). Chan (1995), using a 75 µm mesh net, did not record this species from the study area, indicating that the water column might not be the primary habitat for Tisbe. The baited traps in this study were deployed at 90 mm above the seabed. Tisbe should, therefore, be, at least, a member of the temporary hyperbenthos.

Spatial segregation of *Tisbe* was evident in the study area. *Tisbe* catches progressively increased seaward with depth. The factors regulating Tisbe catches in terms of water depth are unknown. Significant correlations between the catch and sediment physiography implied that *Tisbe* might favor organically enriched habitats and deeper waters. Conversely, the low abundance of Tisbe at the lagoon stations might have been due to the shallow depths. Sediment distribution in Lobster Bay is consistent with circulation patterns and the degree of exposure, whereby fine sediments are transported from high-energy shallower environments and deposited in deeper areas (Robertson et al. 1989, Hall 1994). Individuals might not be able to tolerate wave-induced bottom disturbance as they cannot establish themselves and maintain populations in frequently perturbed sediments (Hall 1994).

It is, however, worth noting that results from baited trap studies might lead to inaccurate dietary assessments. Bait might aggregate the potential prey of Tisbe and attract it to the traps. This is called the "trap effect" (Griffiths et al. 2000). An assessment of the diets of *Tisbe* should, therefore, be identified using an alternative sampling method, such as feeding experiments in the laboratory. The scavenging behavior of *Tisbe* may also be compounded by different food preferences exhibited by age classes, gender, and reproductive states within various habitats, as reported for lysianassids (Sainte-Marie 1986b). Further studies using various taxa as bait might also provide more information on feeding preferences, as reported for lysianassids (Morritt 2001). Overall, the results of this study demonstrate that baited traps are effective in collecting copepods which are rarely captured from the water column using plankton nets.

Acknowledgments: I would like to thank Prof. B. Morton for his constructive comments on the 1st drafts of the manuscript of this paper. Thanks are also due to Prof. B. Sainte-Marie for advice on trap design. In addition, I would like to show my gratitude to Mr. M. Cheung and Mr. M.H. Cheung for diving assistance and to Mr. P.C. Chan and Mr. K.K. Wong for trap block construction.

#### REFERENCES

- Biernbaum CK, EL Wenner. 1993. Trapping of necrophagous crustaceans on the upper continental slope off South Carolina, U.S.A. J. Crustacean Biol. **13:** 601-608.
- Boak AC, R Goulder. 1983. Bacterioplankton in the diet of calanoid copepod *Eurytemora* sp. in the Humber Estuary. Mar. Biol. **73**: 139-149.
- Bowman TE. 1974. The sea flea *Dolobrotus mardeni* n. gen., n. sp., a deep-water American lobster bait scavenger (Amphipoda: Eusiridae). Proc. Biol. Soc. Wash. 87: 129-139.
- Bradford-Grieve JM, JBJ Wells. 1983. New calanoid and harpacticoid copepods from beneath the Ross Ice Shelf, Antarctica. Polar Biol. **2**: 1-15.
- Britton JC, B Morton. 1993. Are there obligate marine scavengers? *In* B Morton, ed. The marine biology of the South China Sea. Proceedings of the First International Conference on the Marine Biology of Hong Kong and the South China Sea, Hong Kong 1990. Hong Kong: Hong Kong University Press, pp. 357-391.
- Britton JC, B Morton. 1994. Marine carrion and scavengers. Ocean. Mar. Biol. Ann. Rev. **32:** 369-434.
- Calbert A, MR Landry, RD Scheinberg. 2000. Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock. Mar. Ecol.-Prog. Ser. **193**: 75-84.
- Chan ALC. 1995. The ecology of marine plankton in Tai Tam Bay, Hong Kong, with special reference to barnacle (Arthropoda: Cirripedia) larvae. Ph.D. thesis, Univ. of Hong Kong.
- Chiu MTL, RT Chung, RWK Luk. 1985. Chemical hydrographic observations of the southern and eastern coastal waters of Hong Kong. Asian Mar. Biol. **2:** 37-46.
- Clark TH. 1997. The ecology of indigenous and transplanted corals in the Cape d'Aguilar Marine Reserve, Hong Kong. Ph.D. thesis, Univ. of Hong Kong.
- Dahl E. 1979. Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. Oikos **33:** 167-175.
- Environmental Protection Department. 2001. Marine water quality in Hong Kong, 2001. Hong Kong: Hong Kong Government.
- Garstang W. 1900. Preliminary experiments on the rearing of sea-fish larvae. J. Mar. Biol. Assoc. UK 6: 70-97.
- Gowing MM, KF Wishner. 1992. Feeding ecology of benthopelagic zooplankton on an eastern tropical Pacific seamount. Mar. Biol. **112:** 451-467.
- Griffiths MKP, S Mayfield, GM Branch. 2000. A note on a possible influence of traps on assessment of the diet of *Jasus Ialandii* (H. Milne-Edwards). J. Exp. Mar. Biol. Ecol. 247:

223-232.

- Guisande C, J Sánchez, I Maneiro, A Miranda. 1996. Tradeoff between offspring number and offspring size in the marine copepod *Euterpina acutifrons* at different food concentrations. Mar. Ecol.-Prog. Ser. **143**: 37-44.
- Gyllenberg G. 1984. The role of bacteria in *Eurytemora* feeding behaviour. Crustaceana **7**: 229-232.
- Hall SJ. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Ocean. Mar. Biol. Ann. Rev. 32: 179-239.
- Hawkins ST. 1998. The epibenthic colonization of artificial subtidal habitats at the Cape d'Aguilar Marine Reserve, Hong Kong. Ph.D. thesis, Univ. of Hong Kong.
- Hessler RR, CL Ingram, AA Yayanos, BR Burnett. 1978. Scavenging amphipods from the floor of the Philippine Trench. Deep-Sea Res. 25: 1029-1047.
- Hicks GRF, BC Coull. 1983. The ecology of marine meiobenthic harpacticoid copepods. Ocean. Mar. Biol. Ann. Rev. 21: 67-175.
- Hodgson PA. 2000. Underwater maps of the Cape d'Aguilar Marine Reserve, Hong Kong. *In* B Morton, ed. The marine flora and fauna of Hong Kong and Southern China V. Proceedings of the Tenth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong 1998. Hong Kong: Hong Kong University Press, pp. 301-318.
- Ingólfsson A, E Ólafsson. 1997. Vital role of drift algae in the life history of the pelagic harpacticoid *Parathalestris croni* in the northern North Atlantic. J. Plankton Res. **19:** 15-27.
- Jonsson PR, P Tiselius. 1990. Feeding behaviour, prey detection and capture efficiency of the copepod Acartia tonsa feeding on planktonic ciliates. Mar. Ecol.-Prog. Ser. 60: 35-44.
- Kaestner A. 1970. Invertebrate zoology. Vol. 3. Crustacea. New York: Interscience Publishers.
- Kikuchi T, T Toda, T Nemoto, S Ohta. 1990. Preliminary survey on the deep-sea near bottom zooplankton by means of deep-sea submersible "SHINKAI 2000". JAMSTE-CER Deepsea Res. 1990: 115-122. (in Japanese with English abstract)
- Kurashov EA. 1996. Distribution and summer diapause of Canthocamptus staphylinus (Jurine) (Copepoda: Harpacticoida) in Lake Ladoga. Hydrobiologia **320**: 191-196.
- Lampitt RS, NR Merett, MH Thurston. 1983. Inter-relations of necrophagous amphipods, a fish predator and tidal currents in the deep sea. Mar. Biol. 74: 73-78.
- Lee CNW. 2002. The ecology of planktonic copepods and hyperbenthic communities in the Cape d'Aguilar Marine Reserve, Hong Kong. Ph.D. thesis, Univ. of Hong Kong.
- Lee CNW. 2003. Seasonal changes in the planktonic copepod community of the southeastern coastal waters of Hong Kong. *In* B Morton, ed. Perspectives on marine environmental change in Hong Kong and Southern China, 1977-2001. Proceedings of the Hong Kong International Workshops Reunion Conference: Perspectives on Marine Environmental Change in Hong Kong and Southern China (1977-2001). Hong Kong: Hong Kong Univ. Press, pp. 369-389.
- Leung AWY. 1994. The fish fauna of Lobster Bay, Cape d'Aguilar Marine Reserve. M.Phil. thesis, Univ. of Hong Kong.
- Mauchline J. 1998. The biology of calanoid copepods. Adv. Mar. Biol. **33:** 1-710.

- Moore PG, YM Wong. 1995. Activity and trapping characteristics in the field of *Orchomene nanus* (Krøyer) (Amphipoda: Lysianassoidea) at Millport, Scotland. J. Exp. Mar. Biol. Ecol. **189:** 143-157.
- Morritt D. 2001. The crab carrion-scavenging amphipod, *Orchomene nanus*, in Lough Hyne, Co. Cork, Ireland. J. Mar. Biol. Assoc. UK **81:** 1059-1060.
- Morton B, K Chan. 2000. Scavenging behaviour of *Nassarius pauperus* (Gastropoda: Nassariidae) from the dynamic subtidal sands of Lobster Bay, Cape d'Aguilar Marine Reserve, Hong Kong. *In* B Morton, ed. The Marine Flora and Fauna of Hong Kong and Southern China V. Proceedings of the Tenth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong 1998. Hong Kong: Hong Kong Univ. Press, pp. 255-266.
- Morton B, E Harper. 1995. An introduction to the Cape d'Aguilar Marine Reserve, Hong Kong. Hong Kong: Hong Kong Univ. Press.
- Morton B, E Harper. 1997. An undescribed macrofaunal assemblage from shallow subtidal sands at the Cape d'Aguilar Marine Reserve, Hong Kong. *In* B Morton, ed. The marine flora and fauna of Hong Kong and Southern China IV. Proceedings of the Eighth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong 1995. Hong Kong: Hong Kong Univ. Press, pp. 249-261.
- Morton B, J Morton. 1983. The sea shore ecology of Hong Kong. Hong Kong: Hong Kong Univ. Press.
- Nishida S, T Kikuchi, T Toda. 1999. Efficient capture of deepsea hyperbenthic calanoid copepods with baited traps. Plankt. Biol. Ecol. **46:** 165-168.
- Ohtsuka S. 1984. Calanoid copepods collected from the nearbottom in Tanabe Bay on the Pacific coast of the middle Honshu, Japan. I. Arietellidae. Publ. Seto Mar. Biol. Lab. Kyoto Univ. **29:** 359-365.
- Ohtsuka S. 1985. Calanoid copepods collected from the nearbottom in Tanabe Bay on the Pacific coast of the middle Honshu, Japan. II. Arietellidae (cont.). Publ. Seto Mar. Biol. Lab. Kyoto Univ. **30:** 287-306.
- Ohtsuka S, C Mitsuzumi. 1990. A new asymmetrical near-bottom calanoid copepod, *Paramisophria platysoma*, with observations of its integumental organs, behavior and in situ feeding habit. Bull. Plankton. Soc. Jpn. **36:** 87-101.
- Ohtsuka S, A Fosshagen, A Go. 1991. The hyperbenthic calanoid copepod *Paramisophria* from Okinawa, South Japan. Zool. Sci. **8:** 793-804.
- Ohtsuka S, Y Fukuura, A Go. 1987. Description of a new species of *Tortanus* (Copepoda: Calanoida) from Kuchinoerabu Island, Kyushu (Japan), with notes on its possible feeding mechanism and in-situ feeding habits. Bull. Plankton. Soc. Jpn. **34:** 53-64.
- Ohtsuka S, I Takeuchi, A Tanimura. 1998. *Xanthocalanus gracilis* and *Tharybis magna* (Copepoda: Calanoida) rediscovered from the Antarctic Ocean with baited traps. J. Nat. Hist. **32**: 785-804.
- Percival JB, PJ Lindsay. 1996. Measurement of physical properties of sediments. *In* A Mudroch, JM Azcue, P Mudroch, eds. Manual of physico-chemical analysis of aquatic sediments. Boca Raton, Fla. Lewis Publishers, pp. 4-56.
- Raymont JEG. 1983. Plankton and productivity in the oceans. Vol. 2. Zooplankton. Oxford: Pergamon Press.
- Robertson MR, SJ Hall, A Eleftheriou. 1989. Environmental correlates with amphipod distribution in a Scottish sea

loch. Cah. Biol. Mar. 30: 243-258.

- Sainte-Marie B. 1984. Morphological adaptation for carrion feeding in four species of littoral and circalittoral lysianassid amphipods. Can. J. Zool. **62:** 1668-1674.
- Sainte-Marie B. 1986a. Effect of bait size and sampling time on the attraction of the lysianassid amphipods Anonyx sarsi Steele and Brunel and Orchomenella pinguis (Boeck). J. Exp. Mar. Biol. Ecol. 99: 63-77.
- Sainte-Marie B. 1986b. Feeding and swimming of lysianassid amphipods in a shallow cold-water bay. Mar. Biol. **91:** 219-229.
- Schulz K. 1990. Pterochirella merkayi, new genus, new species, an unusual calanoid copepod from the deep Gulf of Aden (Indian Ocean). Mitteilungen Hamburgischen Zool. Mus. Inst. 87: 181-189.
- Seifried S, J Dürbaum. 2000. First clear case of carnivory in marine Copepoda Harpacticoida. J. Nat. Hist. 34: 1595-1618.
- Sekiguchi H, Y Yamaguchi. 1983. Scavenging gammaridean amphipods from the deep-sea floor. Bull. Fac. Fish. Mie Univ. **10:** 1-14.
- Shulenberger E, RR Hessler. 1974. Scavenging abyssal benthic amphipods trapped under oligotrophic central North Pacific Gyre waters. Mar. Biol. **28**: 185-187.
- Siaz E, T Kiørboe. 1995. Predatory and suspension feeding of the copepod Acartia tonsa in turbulent environments. Mar. Ecol.-Prog. Ser. **122**: 147-158.
- Steinberg DK, CH Pilskaln, MW Silver. 1998. Contribution of zooplankton associated with detritus to sediment trap "swimmer" carbon in Monterey Bay, California, U.S.A.. Mar. Ecol.-Prog. Ser. **164**: 157-166.
- Thurston MH. 1979. Scavenging abyssal amphipods from the northeast Atlantic Ocean. Mar. Biol. **79:** 55-68.

- Tokioka T, R Bieri. 1966. Juveniles of Macrosetella gracilis (Dana) from clumps of Trichodesmium in the vicinity of Seto. Publ. Seto Mar. Biol. Lab. Kyoto Univ. 14: 177-184.
- Tso SF, HK Mok. 1991. Development, reproduction and nutrition of the giant isopod *Bathynomus doederleini* Ortmann, 1894 (Isopoda, Flabellifera, Cirolanidae). Crustaceana **61:** 141-154.
- Turner JT. 1984a. Zooplankton feeding ecology: contents of faecal pellets of the copepods *Temora turbinata* and *T. stylifera* from continental shelf and slope waters near the mouth of the Mississippi River. Mar. Biol. **82:** 73-83.
- Turner JT. 1984b. Zooplankton feeding ecology: contents of faecal pellets of the copepods *Eucalanus pileatus* and *Paracalanus quasimodo* from continental shelf waters of the Gulf of Mexico. Mar. Ecol.-Prog. Ser. **15**: 27-46.
- Turner JT, JC Roff. 1993. Trophic levels and trophospecies in marine plankton: lessons from the microbial food web. Mar. Microbial Food Webs **7**: 225-248.
- Uye S, Y Kayano. 1994. Predatory feeding behaviour of *Tortanus* (Copepoda: Calanoida): life-stage differences and the predation impact on small planktonic crustaceans. J. Crustacean Biol. **14:** 473-483.
- Webber MK, JC Roff. 1995. Annual structure of the copepod community and its associated pelagic environment off Discovery Bay, Jamaica. Mar. Biol. **123**: 467-479.
- Wells FE. 1994. The invertebrate community of subtidal sand habitats at Cape d'Aguilar, Hong Kong, with an emphasis on molluscs. *In* B Morton, ed. The malacofauna of Hong Kong and Southern China III. Proceedings of the Third International Workshop on the malacofauna of Hong Kong and Southern China, Hong Kong 1992. Hong Kong: Hong Kong Univ. Press, pp. 467-477.