

OBSERVATIONS ON THE ECOLOGY OF *PLEUROBRACHIA PILEUS* (CTENOPHORA) IN THE SOUTHERN BENGUELA ECOSYSTEM

M. J. GIBBONS*, E. BUECHER*† and D. THIBAUT-BOTHA*‡

The vertical distribution, abundance and size composition of a population of *Pleurobrachia pileus* was studied during a six-day drogue study conducted off the west coast of South Africa in February 1995. The population was centred in deep water, possibly because of the presence of a potential predator, *Beroe* sp., at shallower depths. The population of *P. pileus* failed to display clear patterns of migration, although nocturnal recruitment from deeper water resulted in a deepening of the depth of occupation then. The population was dominated by individuals <4 mm polar diameter, and large animals were confined to the upper water layers. These results are discussed with reference to possible spawning activities. Using published equations relating size to clearance rates, it was estimated that the population could remove up to 27% of integrated mesozooplankton standing stocks, and in excess of 100% (293%) at some depths.

Key words: feeding impact, *Pleurobrachia pileus*, population size structure, South Africa, vertical distribution and migration

Tentaculate ctenophores of the genus *Pleurobrachia* are common in coastal and neritic seas around the world (e.g. Fraser 1970, Frank 1986, Mutlu and Bingel 1999). They feed on a wide variety of prey (Hirota 1974, Reeve and Walter 1978), and, although their diet generally reflects the ambient food environment (Fraser 1970), prey are likely to be selected on the basis of size and escape response (Greene *et al.* 1986). Species of *Pleurobrachia* exhibit a Type II functional response to prey density (Reeve and Walter 1978, Båmstedt 1998), and daily clearance rates increase markedly with increasing predator size (Gibbons and Painting 1992).

Although lobate ctenophores can have a considerable effect on plankton assemblages (Shiganova *et al.* 2001) and have been implicated in the collapse of some regional fisheries (Travis 1993), the impacts of tentaculate ctenophores are less well known. A number of authors have suggested that the average impact of *Pleurobrachia* populations is relatively small (Båmstedt 1998), perhaps varying between 0.6 and 8.8% of copepod biomass per day (Frank 1986, Miller and Daan 1989, Buecher and Gasser 1998). The impact of *Pleurobrachia* will obviously vary with the abundance of both predator and prey, and although theoretical estimates of consumption by a population may be high, these are not always matched by field observations (van der Veer and Sadée 1984).

Most observations of *Pleurobrachia* have been made over shallow continental shelves and seas in temperate regions. Gelatinous carnivores such as *Pleurobrachia*

are not generally considered to be an important component of pelagic food webs in upwelling ecosystems. This is especially true in such variable regimes as the southern Benguela, where the dynamic physical environment prevents the build-up of extensive populations. However, localized embayments with a restricted circulation may allow ctenophore populations to develop and, within these systems, it has been suggested that *Pleurobrachia* may become an important predator (Gibbons *et al.* 1992).

The importance of *Pleurobrachia* as a predator of zooplankton assemblages in the southern Benguela upwelling system was investigated. Because observations of this predator are rare in this region, general observations on the ecology were also made in order to provide baseline data for future work.

MATERIAL AND METHODS

A six six-day drogue study was conducted in St Helena Bay (32°35'S, 18°07'E) off the west coast of South Africa between 20 and 26 February 1995 on board the F.R.S. *Africana*. A weighted 2-m tetrahedral drogue was positioned at 10 m depth, and connected via line and shock-cord to a surface buoy equipped with a radar reflector and flashing light. The drogue was tracked via the ship's GPS-interfaced radar. Additional drogues were released at 2 and 20 m depth on 24 and 25 Feb-

* Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa. E-mail: mgibbons@uwc.ac.za

† Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa

‡ Present address: Hawaii Institute of Marine Biology, 46-007 Lilipuna Road, Kaneohe, HI 96744 USA

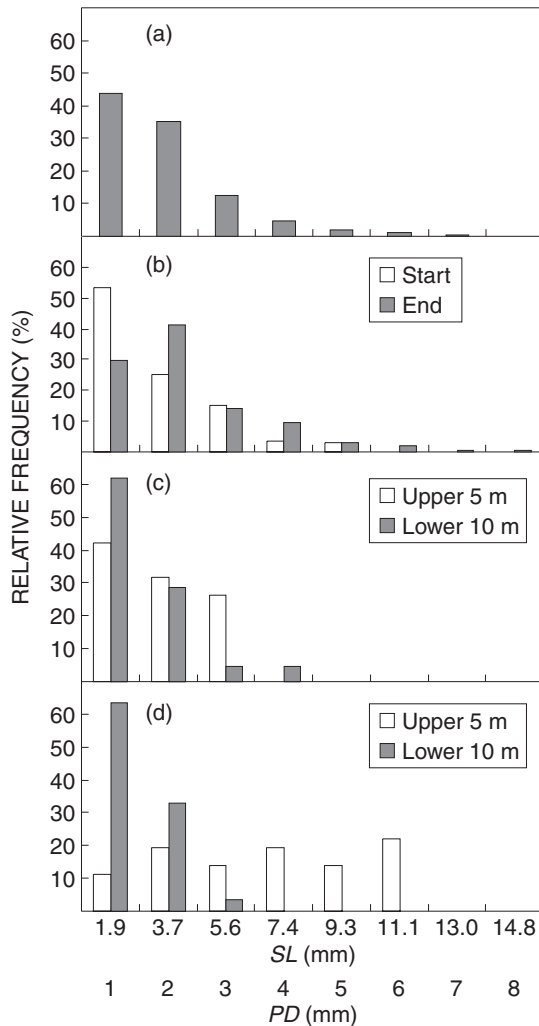


Fig. 1: Size frequency distribution of *P. pileus*: (a) overall, (b) at start and end of study period, (c) at start of study period, in the upper 5 m and lower 10 m of the water column and (d) at end of study period, in the upper 5 m and in the lower 10 m of the water column. Size-classes shown as both SL (mm) and converted PD (mm)

ruary, and were tracked until 26 February.

Environmental variables and plankton samples were collected at regular intervals throughout the day and night. Currents were measured using an RD Instruments 150 kHz Acoustic Doppler Current Profiler

(ADCP) at each station. A Neil Brown Mk 3b conductivity-temperature-depth (CTD) instrument with a 12-bottle rosette was used to profile the water column (5 m from the bottom) at each station. Water samples were taken for the determination of dissolved oxygen at regular depth intervals. The concentration of dissolved oxygen was determined by the Winkler method, using azide to counteract the possible presence of nitrites. Fluorescence profiles were obtained using a Chelsea Instruments Aquatracka submersible fluorometer mounted on a magnum rosette, and water samples were collected at the surface and at the fluorescence maximum for determination of chlorophyll *a*, following the method of Parsons *et al.* (1984).

Zooplankton were collected throughout the day and night using both depth-integrating vertical nets and depth-stratified nets. Paired vertical Bongo nets fitted with 200- μ m mesh were hauled from 5 m above the seabed to the surface at 1 m s⁻¹. A mechanical flowmeter was fitted above the mouth of one of the nets to determine the volume of water filtered. A 1-m² multiple opening-closing rectangular mid-water trawl (RMT 1 \times 6) of 200- μ m mesh size was towed obliquely at 1 m s⁻¹ over 5 depth strata from just above the bottom to the surface. These strata were ~60–40, 40–30, 30–20, 20–10 and 10–0 m. An electronic flowmeter was mounted above the mouth of the net. On retrieval, the zooplankton samples were preserved in 4% buffered saline formalin for later counting.

Within two months of return to the laboratory, all ctenophores were counted from each sample. When high numbers of ctenophores were present, sub-samples were taken using a Folsom splitter, and a minimum of 100 individuals was counted. Data were standardized to numbers per m³ and m² from knowledge of the volume of water filtered.

All counted specimens of *Pleurobrachia pileus* were measured and allocated to 1-mm size-classes. However, because most specimens were damaged during collection, stomach length (SL) was used as an indicator of individual size. Although the size of the stomach is likely to vary with the amount of food eaten, all stomachs inspected were empty at the time of measurement. Subsequent, independent, measurements of live specimens revealed that SL represents 0.54 of the polar diameter (PD; $n = 50$, $r = 0.96$), and all data are presented here as both SL and PD. No adjustments have been made to correct for the effect of shrinkage (Yip 1982), so all measurements represent minima.

The mean vertical position (weighted mean depth, WMD) of *P. pileus* in the water column at any one time was determined using the method of Pearre (1973).

With knowledge of the size structure of the population, the quantity of water filtered by the population of *P. pileus* could be calculated using the equation of Gibbons and Painting (1992):

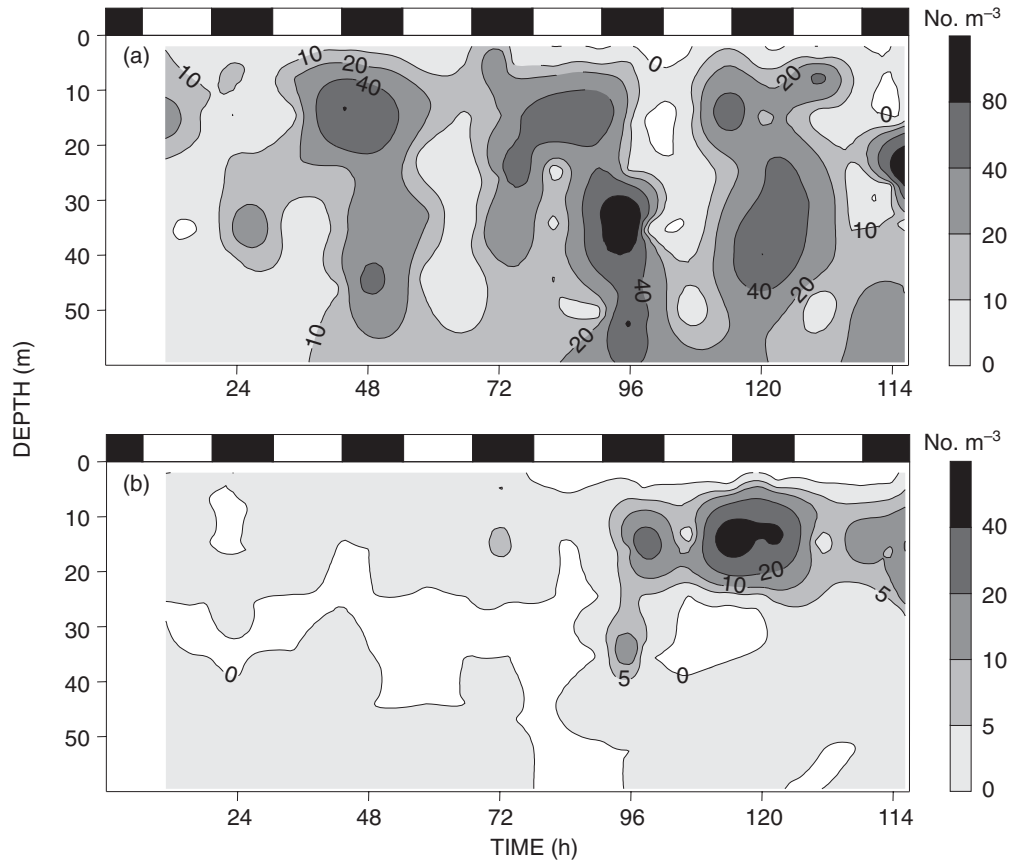


Fig. 2: Vertical distribution of *P. pileus* over the study period: (a) individuals between 0.5 and 1.0 mm *SL* (0.93–1.85 mm *PD*) and (b) individuals >5.0 mm *SL* (9.26 mm *PD*). Time on the *x*-axis refers to hours after the start of the study. Night-time (solid) and day time (open) periods are shown

$$F = 0.01 PD^{3.22}$$

where *F* is daily clearance rate ($\ell \text{ day}^{-1}$) and *PD* is polar diameter (mm).

RESULTS

The physical environment in St Helena Bay during the study period is detailed in Gibbons *et al.* (1999). Of relevance here is the fact that the drogue remained in the bay for the duration of the study, initially moving northwards and offshore before returning southwards and onshore (see Fig. 1 of Gibbons *et al.* 1999). Neither synoptic upwelling nor shelf-wave forcing was ob-

served. Although considerable shear through the water column was noted, currents at 2, 10 and 20 m deep were dominated by diurnally varying winds and inertial oscillations. In other words, water at different depths within the bay stayed within the bay and moved in “independent” inertial circles.

The thermal structure of the water column changed little during the period of study. The base of the thermocline (marked by the 9.5°C isotherm) was between 25 and 35 m. The upper layer, above 12°C at 15–20 m was weakly stratified until Days 4 and 5, when the temperature in the upper 15 m warmed by 1–2°C (to 14.5°C) and the upper layer became more stratified. The entire water column was isohaline for the whole period, with a mean salinity of 34.7, which suggests that, although current shear may have been ubiquitous

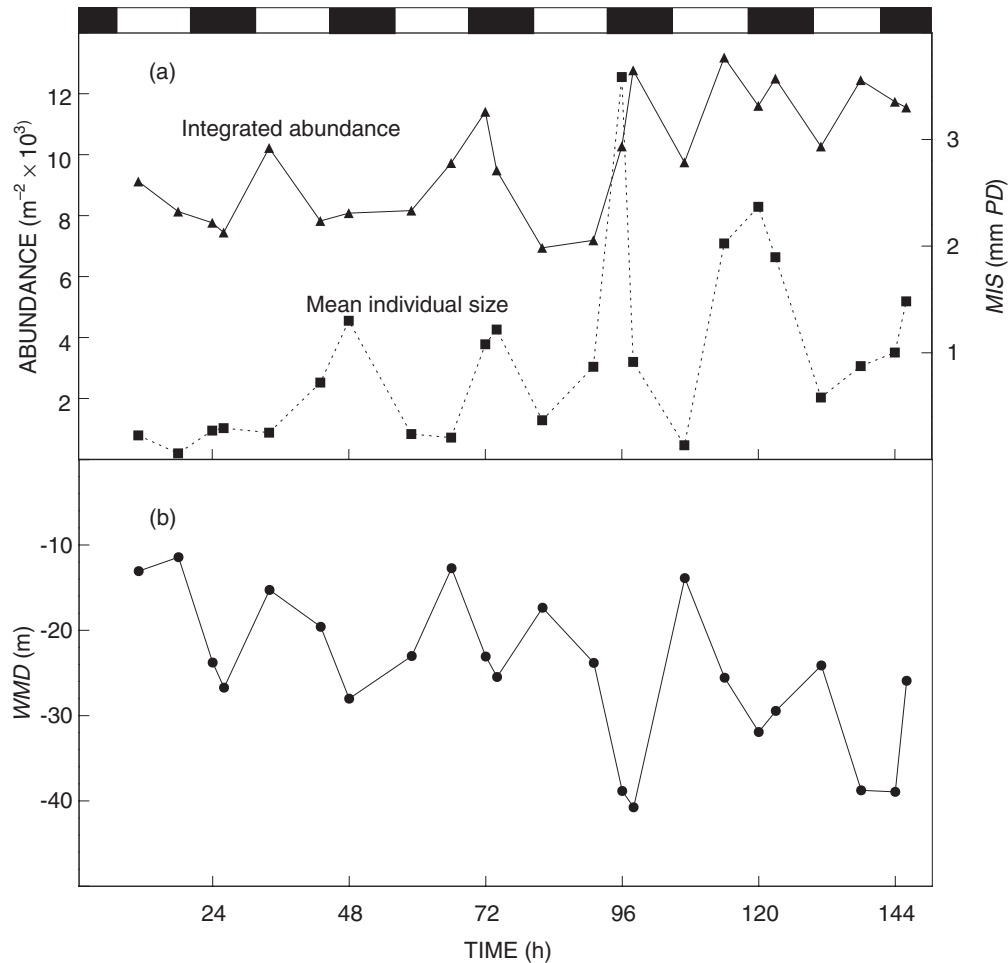


Fig. 3: Changes in the (a) integrated abundance and mean individual size and (b) weighted mean depth (WMD) of the *P. pileus* population over the course of the study. Time on the x-axis refers to hours after the start of the study. Night-time (solid) and daytime (open) periods are shown

in the upper layer, it operated on a small scale and there was no noticeable advection of different water bodies to the vicinity of the drogue. Phytoplankton communities were dominated throughout by diatoms (Kjørboe *et al.* 1998), and the depth-integrated pigment biomass remained more or less constant at $500 \text{ mg Chl } a \text{ m}^{-2}$. Although the depth of the fluorescence maximum increased with time, it did not pass through the thermocline.

The population of *Pleurobrachia pileus* displayed a unimodal size distribution and was dominated by indi-

viduals $< 2 \text{ mm SL}$ (or 3.7 mm PD – Fig. 1). Individuals of between 0.5 and 1 mm SL (0.93 – 1.85 mm PD) represented 44% of the total population sampled (Fig. 1a), whereas cydippid larvae (defined here as individuals $< 0.5 \text{ mm SL}$, 0.93 mm PDI , were not dominant and averaged 7% of the total population (data not shown). Given uncertainties around the successful capture of cydippid larvae, these data are not discussed further. Although the general size structure of the *Pleurobrachia* population did not change appreciably during the study period (Fig. 1b), the proportion of individuals

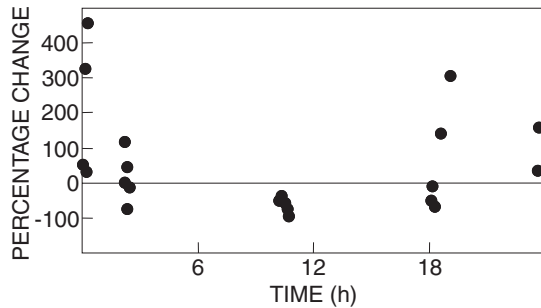


Fig. 4: Percentage changes in the integrated abundance of *P. pileus* between 0.5–1.0 mm *SL* (0.93–1.85 mm *PD*), over the course of a day. All data combined

between 0.5 and 1 mm *SL* (0.93–1.85 mm *PD*) declined between Days 1 and 6 (54 to 28% respectively), and the proportion between 1–2 mm *SL* (1.85–3.70 mm *PD*) increased (25 to 42% respectively). The size structure of the population changed appreciably with depth (Figs 1c, d). Large individuals (>5 mm *SL*, 9.26 mm *PD*) were concentrated near the surface, whereas small specimens (0.5–1 mm *SL*, 0.93–1.85 mm *PD*) were more common in deep water (Fig. 2). This pattern of vertical distribution of the size-classes became more pronounced towards the end of the study period (Fig. 1d).

The numbers of *P. pileus* increased during the study and reached a maximum of 12 712 individuals m^{-2} on the night of 23 February. Nocturnal estimates of abundance (4 903 individuals m^{-2}) of the population were significantly greater than diurnal (1 909 individuals m^{-2}) estimates ($t = -2.68$, $n = 11$, $p = 0.014$; Fig. 3), owing to night-time recruitment of individuals between 0.5 and 1.0 mm *SL* (0.93–1.85 mm *PD*) in deep water (Fig. 4). Although nocturnal recruitment to the sampled population resulted in a significant ($t = -3.47$, $n = 11$, $p = 0.002$) downward shift of the mean population depth at night (19.9 m to 30.3 m; Fig. 3), there was no detectable pattern of DVM amongst individuals >5 mm *SL* (>9.26 mm *PD*). Mean individual size varied in tandem with changes in population size (Fig. 3). Consequently, there was a tendency for individual size to decrease at night owing to recruitment of small individuals to the population.

The potential volume of water cleared by the *P. pileus* population obviously increased with increasing population size, to a maximum of approximately 16 $m^3 m^{-2} day^{-1}$. This value represents an integrated average, and corresponds to 27% of the water column daily. However, it does not take into account the vertical dis-

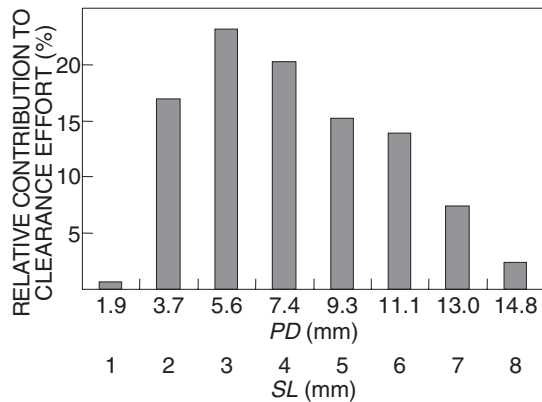


Fig. 5: Relative contribution to clearance effort by different size-classes of *P. pileus*. Size-classes are shown as both *SL* (mm) and converted *PD* (mm). All data combined

tribution of clearance effort. Despite their numerical dominance of the population, small *P. pileus* contributed little towards total clearance (Fig. 5), which was largely undertaken by animals in the size range 2–6 mm *SL* (3.7–11.1 mm *PD*). This means that the greatest clearance effort was concentrated between 10 and 20 m, where daily impacts on zooplankton standing stock were >100% (up to 293%) of the water layer (Fig. 6).

DISCUSSION

The maximum density of *P. pileus* observed in the present study (12 712 individuals m^{-2} , or 212 m^{-3}) is higher than has been reported for many coastal seas (Fraser 1970, Frank 1986). It is also higher than has been reported for areas of localized aggregation following downwelling (Mutlu *et al.* 1994, Mutlu and Bingel 1999) or advection (e.g. van der Veer and Sadée 1984). However, it is not higher than has been observed in shallow estuaries (e.g. Wang *et al.* 1995, Attrill and Thomas 1996), or previously in the southern Benguela ecosystem (Buecher and Gibbons 2000). It is suggested that the high numbers observed here might reflect the local circulation in St Helena Bay, which is retentive owing to the presence of cyclonic eddies and coastally trapped gyres (Holden 1985).

Species of *Pleurobrachia* are prone to inter- (Buecher 1997) and intra-annual (Hirota 1974, Williams and Collins 1985) variations in abundance, which reflect

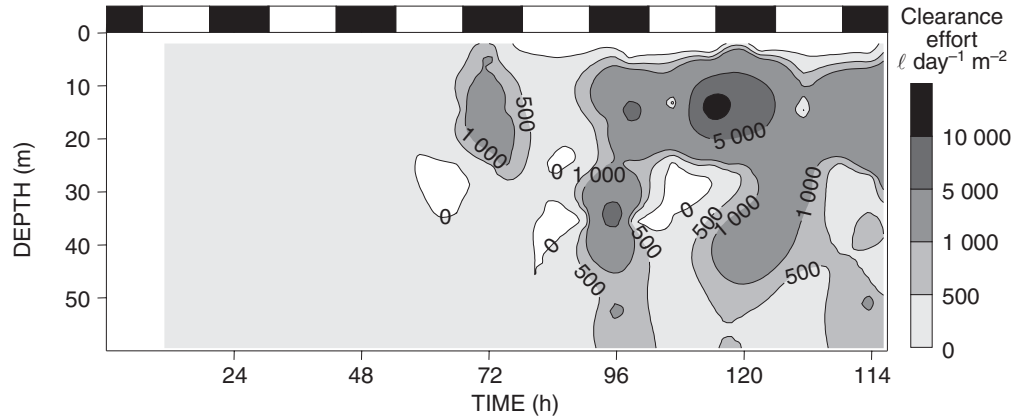


Fig. 6: Vertical distribution of clearance effort by *P. pileus* over the study period. Time on the x-axis refers to hours after the start of the study. Night-time (solid) and daytime (open) periods are shown

patterns of entrainment, reproduction and population growth (Larson 1987). The rapid increase in abundance of the population here, however, cannot be interpreted in terms of intrinsic population growth, but must rather be seen as a function of the interaction between individual behaviour and the physical environment. This hypothesis was proposed by Gibbons *et al.* (1999) to account for the changes in abundance of some macrozooplankton collected (including *P. pileus*) in St Helena Bay. The increases in abundance of *P. pileus* were stepwise, as a consequence of recruitment (and subsequent accumulation) to the population from depth, at a time (night) when the drogue was situated over low low-oxygen bottom water, at the shelf edge. This diel change in abundance is distinct from that observed in shallow coastal areas under the influence of tidal flow, where fluctuations might reflect an interaction between vertical migration and tidal water movement (Dauvin *et al.* 1998). Tidal forcing in St Helena Bay is weak and considered unlikely to have influenced the observations made here (Gibbons *et al.* 1999).

Although a number of studies have shown that species of *Pleurobrachia* are mostly found in the upper water layers (Fraser 1970, Hirota 1974), they may occur throughout the whole water column (Buecher 1997). Populations can extend to depths of 200 m (Mutlu and Bingel 1999), and may over winter in deep water (Runnström 1931, Fraser 1970).

Although it might appear that *P. pileus* undertook regular reverse diel vertical migration (DVM; Fig. 3), this is largely a consequence of the recruitment of individuals from deep water at night, which made the present interpretation of the observations misleading.

Evidence to suggest that species of *Pleurobrachia* undertake DVM is contradictory, and no clear generalizations about this behaviour are possible. For example, Wang *et al.* (1995) observed pronounced migration of *P. pileus* into the surface at night and during periods of flood tide, and argued that this behaviour allowed individuals to maintain their position in their estuarine environment. Those authors also noted that the DVM of *P. pileus* was not related to that of their prey, which supported an observation first reported by Hirota (1974) off the coast of California, although the latter author also noted that populations of *P. pileus* displayed reverse DVM (as Vinogradov *et al.* 1985).

It is not clear from the literature what factors influence the vertical distribution of species of *Pleurobrachia*, and the data provided here do little to support any firm discussions. For example, although salinity has been shown to influence the vertical and horizontal distribution of *Pleurobrachia* (Wang *et al.* 1995, Mutlu and Bingel 1999), the absence of strong salinity gradients in St Helena Bay would suggest that this condition played little role in influencing vertical distribution. Few studies have indicated that temperature *per se* plays an important role in determining vertical distribution.

There is some evidence to indicate that predators might play a role in influencing vertical distribution. Mutlu and Bingel (1999) observed *Aurelia aurita* and *Mnemiopsis* sp. in the waters above those occupied by *P. pileus* in the Black Sea, whereas Bämstedt (1998) noted *Beroe* sp. in the layers immediately below *P. pileus* off the north-west coast of Norway. In both these instances, DVM of *P. pileus* was either not ob-

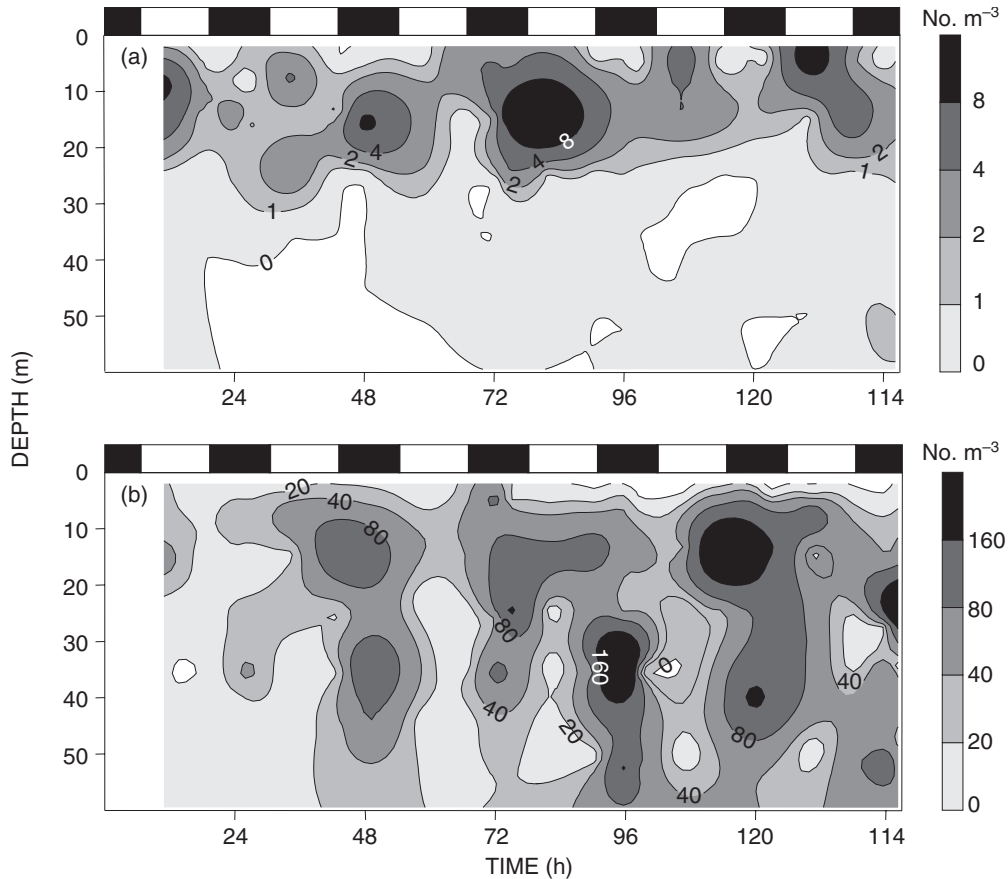


Fig. 7: Vertical distribution of (a) *Beroe* sp. and (b) *P. pileus* over the study period. Time on the x-axis refers to hours after the start of the study. Night-time (solid) and daytime (open) periods are shown

served or was limited. Observations in St Helena Bay indicate that the major part of the *Pleurobrachia* population was concentrated below the layer occupied by *Beroe* sp. (Fig. 7). Although this could account for the absence of any pronounced migration, it is difficult to detect migration if it is an individual and not a population behaviour (Gibbons 1993).

The population of *P. pileus* studied here in summer was dominated by small individuals. The absence of other local data sets precludes comment on reproductive seasonality in the southern Benguela ecosystem, but most studies elsewhere have indicated that small individuals are present for most of the year (van der Veer and Sadée 1984, Mutlu and Bingel 1999), and that they may dominate during periods of maximum abun-

dance (Frank 1986). Because species of *Pleurobrachia* may reproduce within three weeks of hatching (Bigelow and Leslie 1930, Fraser 1970), it has been suggested that spawning occurs as individuals mature and not on a seasonal basis (Fraser 1970). Such an hypothesis could explain the (anecdotal evidence of) year-round presence of *P. pileus* in the region, and is in agreement with the pulsed nature of local upwelling.

As already noted, the data set presented here indicates that large individuals were confined to the near-surface waters, whereas small individuals were in greatest density in deep water. Interpretation of these findings is difficult. It has been suggested that sexually mature individuals spawn in the surface waters (Fraser 1970). That eggs or early larvae were not collected in

the same water layers is most likely attributable to their escapement through the 200- μ m meshed net. If spawning did occur near the surface, then it implies a fairly rapid descent into deep water by the developing cydippids. Alternatively, bigger and more mature individuals might spawn in deep water (Wang *et al.* 1995); large individuals have frequently been recorded at greater depths than smaller individuals (Hirota 1974, Mutlu and Bingel 1999). These individuals might then break up after breeding (Fraser 1970), or re-ascend to the surface waters. It is also possible, as has been noted previously, that individuals are capable of reproducing even at small size, which would imply that the deep-water populations might be self-maintaining. This last explanation can be extended if it is considered that the deep-water individuals represent members of an offshore, possibly dormant population, as suggested by Wang *et al.* (1995). Such individuals need not be of large size (McIntosh 1890), and indeed small individuals would probably survive the low oxygen conditions found offshore occasionally (Bailey and Rogers 1997), better than large individuals. Furthermore, these small individuals might also be better able to cope with the low food concentrations by feeding on microzooplankton (Stoecker *et al.* 1987). Noteworthy in this respect is the fact that *P. pileus* can withstand prolonged periods without food. The present authors have maintained individuals without food in the laboratory for up to 23 days at 16°C, and up to 40 days at 8°C. Greve (1972) noted that *P. pileus* were able to survive starvation for more than three months. Such periods without food result in body shrinkage and a reduction in size. Although this latter hypothesis is not unreasonable, given that surface and deep waters move independently within the study area (Gibbons *et al.* 1999), none of the foregoing can be discounted.

If it is assumed that all mesozooplankton were removed from within the volume of water filtered by *P. pileus* in St Helena Bay, then populations removed up to 27% of the total integrated standing stock, and in excess of 100% of the standing stock between 10 and 20 m deep. On the one hand, these estimates are likely to be conservative, because they are based on preserved material, and ctenophores shrink with time in formalin (Yip 1982). On the other hand, however, not all prey is likely to be eaten, because individuals select food on the basis of size and escape response (Greene *et al.* 1986). Interestingly, the greatest impact on mesozooplankton standing stocks appears to have been made by the less abundant, larger size size-classes of *P. pileus* rather than the more numerous, small individuals. This reflects the near cubic relationship between size and clearance rate (Gibbons and Painting 1992), and results in a vertically stratified predatory impact (Fig. 6 – Båmstedt 1998). However, small individuals were unlikely

to be feeding extensively on mesozooplankton, but rather on microzooplankton (Stoecker *et al.* 1987). The maximum predatory impact suggested here is higher than has been reported in other studies (e.g. Båmstedt 1998, Frank 1986, Miller and Daan 1989, Buecher and Gasser 1998), probably as a result of the high abundances observed. By contrast, Williams and Collins (1985) estimated that the metabolic demands of *P. pileus* in the Bristol Channel might, on occasion, exceed daily copepod production. The impact estimates generated here are to be treated with caution, however, because they are based on extrapolations from laboratory experiments (Gibbons and Painting 1992). Agreement between estimated predation on prey populations and actual change in prey population size has thus far been weak (Sullivan and Reeve 1982), although recent models of Chandy and Greene (1995) hold promise for the future.

ACKNOWLEDGEMENTS

We would like to thank the officers and crew of the F.R.S. *Africana* for their co-operation and assistance in the field. We are also grateful to Drs L. Hutchings and A. J. Richardson, Mesdames J. A. Huggett and S. M. Jones and Mr A. du Randt (Marine & Coastal Management) for assistance in the collection of samples. Professor Prof. U. Båmstedt (University of Bergen, Norway) and an anonymous referee are thanked for their comments on an earlier draft of the manuscript. Financial support from the Benguela Ecology Programme of the National Research Foundation, the University of the Western Cape and the Royal Society (London) is appreciated.

LITERATURE CITED

- ATTRILL, M. J. and R. M. THOMAS 1996 — Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters. *Mar. Ecol. Prog. Ser.* **143**: 25–36.
- BAILEY, G. W. and J. ROGERS 1997 — Chemical oceanography and marine geoscience off southern Africa: past discoveries in the post-Gilchrist era, and future prospects. *Trans. Roy. Soc., S. Afr.* **52**: 51–79.
- BÅMSTEDT, U. 1998 — Trophodynamics of *Pleurobrachia pileus* (Ctenophora, Cydippida) and ctenophore summer occurrence off the Norwegian North-West coast. *Sarsia* **83**: 169–181.
- BIGELOW, H. B. and M. LESLIE 1930 — Reconnaissance of the waters and plankton of Monterey Bay, July 1928. *Bull. Mus. comp. Zool. Harv.* **70**: 429–581.
- BUECHER, E. 1997 — Distribution and abundance of *Pleurobrachia rhodopsis* (cydippid ctenophore) in the Bay of Villefranche-sur-Mer (northwestern Mediterranean) studied using three different planktonic time series. *Annls. Inst. océanogr., Paris*

- 73: 173–184.
- BUECHER, E. and B. GASSER 1998 — Estimation of predatory impact of *Pleurobrachia rhodopsis* (cydippid ctenophore) in the northwestern Mediterranean Sea: *in situ* observations and laboratory experiments. *J. Plankt. Res.* **20**: 631–651.
- BUECHER, E. and M. J. GIBBONS 2000 — Interannual variation in the composition of the assemblages of medusae and ctenophores in St Helena Bay, southern Benguela ecosystem. *Scientia Mar., Barcelona* **64** (Suppl. 1): 123–134.
- CHANDY, S. T. and C. H. GREENE 1995 — Estimating the predatory impact of gelatinous zooplankton. *Limnol. Oceanogr.* **40**: 947–955.
- DAUVIN, J. C., THIÉBAUT, E. and Z. WANG 1998 — Short term changes in the mesozooplankton community in the Seine ROFI (Region of Freshwater Influence) (eastern English Channel). *J. Plankt. Res.*, **20**: 1145–1167.
- FRANK, K. T. 1986 — Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. *Can. J. Fish. Aquat. Sci.* **43**(1): 211–222.
- FRASER, J. H. 1970 — The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters. *J. Cons. perm. int. Explor. Mer* **33**(2): 149–168.
- GIBBONS, M. J. 1993 — Vertical migration and feeding of *Euphausia lucens* at two 72 h stations in the southern Benguela upwelling region. *Mar. Biol.* **116**(2): 257–268.
- GIBBONS, M. J., GUGUSHE, N., BOYD, A. J., SHANNON, L. J. and B. A. MITCHELL-INNES 1999 — Changes in the composition of the non-copepod zooplankton assemblage in St Helena Bay (southern Benguela ecosystem) during a six day drogue study. *Mar. Ecol. Prog. Ser.* **180**: 111–120.
- GIBBONS, M. J. and S. J. PAINTING 1992 — The effects and implications of experimental container volume on clearance rates of the ambush entangling predator *Pleurobrachia pileus* (Ctenophora: Tentaculata). *J. expl. mar. Biol. Ecol.* **163**: 199–208.
- GIBBONS, M. J., STUART, V. and H. M. VERHEYE 1992 — Trophic ecology of carnivorous zooplankton in the Benguela. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 421–437.
- GREENE, C. H., LANDRY, M. R. and B. C. MONGER 1986 — Foraging behavior and prey selection by the ambush entangling predator *Pleurobrachia bachei*. *Ecology* **67**(6): 1493–1501.
- GREVE, W. 1972 — Ökologische Untersuchungen an *Pleurobrachia pileus*. 2. Laboratoriumsuntersuchungen. *Helgoländer Wiss. Meeresunters.* **23**: 141–164.
- HIROTA, J. 1974 — Quantitative natural history of *Pleurobrachia bachei* in La Jolla Bight. *Fishery Bull., Wash.* **72**(2): 295–335.
- HOLDEN, C. J. 1985 — Currents in St Helena Bay inferred from radio-tracked drifters. In *South African Ocean Colour and Upwelling Experiment*. Shannon, L. V. (Ed.). Cape Town; Sea Fisheries Research Institute: 97–109.
- KIØRBOE, T., TISELIUS, P., MITCHELL-INNES, B. A., HANSEN, J. L. S., VISSER, A. W. and X. MARI 1998 — Intensive aggregate formation with low vertical flux during an upwelling induced diatom bloom. *Limnol. Oceanogr.* **43**: 104–116.
- LARSON, R. J. 1987 — Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. *Neth. J. Sea Res.* **21**(1): 35–44.
- MCCINTOSH, W. C. 1890 — On the occurrence of the ctenophores throughout the year. *Ann. Mag. nat. Hist.* **65**: 43–47.
- MILLER, R. J. and R. DAAN 1989 — Planktonic predators and copepod abundance near the Dutch coast. *J. Plankt. Res.* **11**: 263–282.
- MUTLU, E. and F. BINGEL 1999 — Distribution and abundance of stenophores, and their zooplankton food in the Black Sea. 1. *Pleurobrachia pileus*. *Mar. Biol.* **135**: 589–601.
- MUTLU, E., BINGEL, F., GÜÇÜ, A. C., MELNIKOV, V. V., NIERMANN, U., OSTR, N. A. and V. E. ZAIKA 1994 — Distribution of the new invader *Mnemiopsis* sp. and the resident *Aurelia aurita* and *Pleurobrachia pileus* populations in the Black Sea in the years 1991–1993. *ICES J. mar. Sci.* **51**: 407–421.
- PARSONS, T. R., MAITA, Y. and C. M. LALLI 1984 — *A Manual of Chemical and Biological Methods for Seawater Analysis*. New York; Pergamon: [xiv] + 173 pp.
- PEARRE, S. 1973 — Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* **54**(2): 300–314.
- REEVE, M. R. and M. A. WALTER 1978 — Nutritional ecology of ctenophores – a review of recent research. *Adv. mar. Biol.* **15**: 249–287.
- RUNNSTRÖM, S. 1931 — Eine Uebersicht über das Zooplankton des Herdla- und Hjelte-fjordes. *Bergen Mus. Arb.* **7**: 67 pp.
- SHIGANOVA, T. A., MIRZOYAN, Z. A., STUDENIKINA, E. A., VOLOVIK, S. P., SIOKOU-FRANGOU, I., ZERVOUDAKI, S., CHRISTOU, E. D., SKIRTA, A. Y. and H. J. DUMONT 2001 — Population development of the invader ctenophore, *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. *Mar. Biol.* **139**: 431–445.
- STOECKER, D. K., VERITY, P. G., MICHAELS, A. E. and L. H. DAVIS 1987 — Feeding by larval and post-larval ctenophores on microzooplankton. *J. Plankt. Res.* **9**(4): 667–683.
- SULLIVAN, B. K. and M. A. REEVE 1982 — Comparison of estimates of the predatory impact of ctenophores by two independent techniques. *Mar. Biol.* **68**: 61–65.
- TRAVIS, J. 1993 — Invader threatens Black, Azov Seas. *Science* **262**: 1366–1367.
- VAN DER VEER, H. W. and C. F. M. SADÉE 1984 — Seasonal occurrence of the ctenophore *Pleurobrachia pileus* in the western Dutch Wadden Sea. *Mar. Biol.* **79**(3): 219–227.
- VINOGRADOV, M. E., FLINT, M. V. and E. A. SHUSHKINA 1985 — Vertical distribution of mesozooplankton in the open area of the Black Sea. *Mar. Biol.* **89**: 95–107.
- WANG, Z., THIÉBAUT, E. and J. C. DAUVIN 1995 — Spring abundance and distribution of the ctenophore *Pleurobrachia pileus* in the Seine estuary: advective transport and diel vertical migration. *Mar. Biol.* **124**: 313–324.
- WILLIAMS, R. and N. R. COLLINS 1985 — Chaetognaths and ctenophores in the holoplankton of the Bristol Channel. *Mar. Biol.* **85**(1): 97–107.
- YIP, S. Y. 1982 — A note on the effect of preserving ctenophores in formaldehyde-seawater. *Ir. Nat. J.* **20**: 416–419.