Comparative ecology of the copepods *Calanoides carinatus* and *Calanus agulhensis* in the southern Benguela and Agulhas Bank ecosystems

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DECLARATION

This thesis reports the results of original research carried out at Marine and Coastal Management (MCM, formerly the Sea Fisheries Research Institute), within the Department of Environmental Affairs and Tourism. The ideas presented in this thesis are largely my own, although the idea for the study originated with Dr William T. Peterson., currently at NMFS, Newport, Oregon, USA.

The data on copepod abundance and distribution (both horizontal and vertical), as well as copepod egg production, were collected on numerous surveys conducted by MCM between 1988 and 2000. I participated in many of these cruises, but sampling was a team effort by many colleagues at MCM. Samples were largely analyzed by the technical staff of the Plankton Section (now Biological Oceanography). Shipboard experiments to measure copepod feeding rates (including gut pigment contents) were conducted by myself, with assistance from colleagues, including Dr Mark Gibbons from the University of the Western Cape. All laboratory experiments were conducted by myself.

Data on chlorophyll abundance were provided by Dr Betty Mitchell-Innes of MCM. Phytoplankton cell counts were made by Dr Betty Mitchell-Innes and Mr Marius Weilbach. GIS maps of copepod abundance were provided by Mr Laurent Drapeau, of IDYLE and MCM. Ms Janet Coetzee provided data on pelagic fish abundance. Dr Anthony Richardson, SAHFOS, UK, provided advice on interpreting Generalised Additive Models.

This work has not been submitted for a degree at any other university, and any assistance I received is fully acknowledged.

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ACKNOWLEDGEMENTS

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Vive le copépod sportif!

ABSTRACT

Calanoides carinatus and *Calanus agulhensis* are large calanoid copepods that comprise a major component of the diet of commercially important pelagic fish off South Africa. The aim of this study was to investigate the niche separation between these two species, using zooplankton net samples collected during biannual hydroacoustic surveys of pelagic fish between 1988 and 2000, as well as results from ship- and laboratory-based egg production and feeding experiments. C. *carinatus* is most abundant on the productive central West Coast, but also occurs at relatively low abundance on the Agulhas Bank, mainly on the outer shelf. It is probably transported here from upwelling centres on the East Coast, along the narrow shelf inshore of the Agulhas Current. Abundance of *C. agulhensis* is closely associated with the cool ridge of upwelled water, the Agulhas Ridge, on the central Agulhas Bank, which is characterized by enhanced primary production and a quasi-permanent retention mechanism. Convergent northwest flow on the western Agulhas Bank results in considerable advection of *C. agulhensis* by the shelf-edge jet current to the West Coast outer shelf region. *C. carinatus* and *C. agulhensis* have similar functional responses to temperature and food concentration in terms of egg production and ingestion rate. Although both species select the larger particles that dominate the food biomass, *C. carinatus* may feed less efficiently on small (<10 μm) food particles. The two copepods also have different preferences in terms of food species, with *C. carinatus* preferring chains of small diatoms, whereas *C. agulhensis* shows greater omnivorous tendencies. *C. agulhensis* recovers faster than *C. carinatus* from short periods of starvation, whereas *C. carinatus* recovers more rapidly than *C. agulhensis* from long periods of starvation. This is because *C. carinatus* is able to accumulate greater wax-ester-rich lipid reserves than *C. agulhensis*, and can withstand longer periods without feeding. Both species display similar patterns of ontogenetically-based diel vertical migration under the same environmental conditions on the Agulhas Bank, delaying their daytime descent when food abundance is relatively poor. However, *C. carinatus* has a significantly greater amplitude of diel vertical migration compared to *C. agulhensis*, which may be related to its faster swimming ability. The abundance of *C. carinatus* on the West Coast is enhanced by seeding from resting stages, local retention through ontogenetically-based vertical migration, and adaptation to the variable food environment, including rapid development, and the accumulation of lipid reserves. The abundance of *C. agulhensis* on the Agulhas Bank is enhanced by elevated growth rates, production and retention associated with the Agulhas Ridge, and adaptation to low but consistent food availability. The two copepod species are thus at a competitive disadvantage in their non-core areas. They also tend to occur at the margins of these regions, where food conditions are relatively poor, and the risk of predation and offshore advection are relatively high. These factors result in the perennial occurrence of high abundances of *C. carinatus* off the West Coast, and of *C. agulhensis* on the Agulhas Bank.

CHAPTER 1

Introduction and literature review

Calanoides carinatus and *Calanus agulhensis* are large, predominantly herbivorous, calanoid copepods that constitute important components of the zooplankton biomass of the southern Benguela upwelling region and the Agulhas Bank ecosystem off the west and south coasts of South Africa (Fig. 1.1). They have been relatively well studied compared to other copepod species in the region because of their dominance, ease of handling and importance to fisheries. *C. carinatus* is a characteristic species of all upwelling areas off the west coast of Africa (Thiriot 1978; Arashkevich *et al.* 1996), and is also found off Somalia on the east coast of Africa (Smith 1982) and off Brazil (Valentin 1984). In the southern Benguela upwelling region it may comprise up to 67% of the copepod biomass (Verheye 1991), but usually considerably less. *C. agulhensis* has its centre of distribution on the Agulhas Bank (De Decker *et al.* 1991), a roughly triangular extension of the continental shelf off southernmost Africa, and accounts for approximately 50-80% of copepod biomass in this region (Verheye *et al.* 1994).

Copepods, including *C. carinatus* and *C. agulhensis,* comprise an important component in the diet of species fished commercially off South Africa, particularly anchovy *Engraulis encrasicolis* (James 1987), sardine *Sardinops sagax* (van der Lingen 1994; Louw *et al.* 1998), round herring *Etrumeus whiteheadi* (Wallace-Fincham 1987) and Cape horse mackerel *Trachurus trachurus capensis* (Kerstan and Leslie 1994; Pillar and Barange 1998). Adult and immature copepodites are eaten by adult and juvenile fish, whereas copepod eggs and nauplii are important food items for larval fish. Detailed studies of the ecology and life history of dominant copepod species can thus help to improve overall understanding of the complex foodweb dynamics in the southern Benguela/Agulhas Bank ecosystem.

C. carinatus and *C. agulhensis* are found throughout the year in South African shelf waters, and their distribution ranges often overlap. The most common regions of co-occurrence are between Cape Point and Cape Columbine, when *C. agulhensis* is associated with the intrusion of Agulhas Bank water up the West Coast, and near the shelf edge in both regions. Despite these overlaps in distribution, abundance of *C. carinatus* on the Agulhas Bank is always much lower than that of *C. agulhensis,* while numbers of *C. carinatus* on the West Coast shelf always exceed those of *C. agulhensis*. This suggests that each species is better adapted to its "home range" in one or more

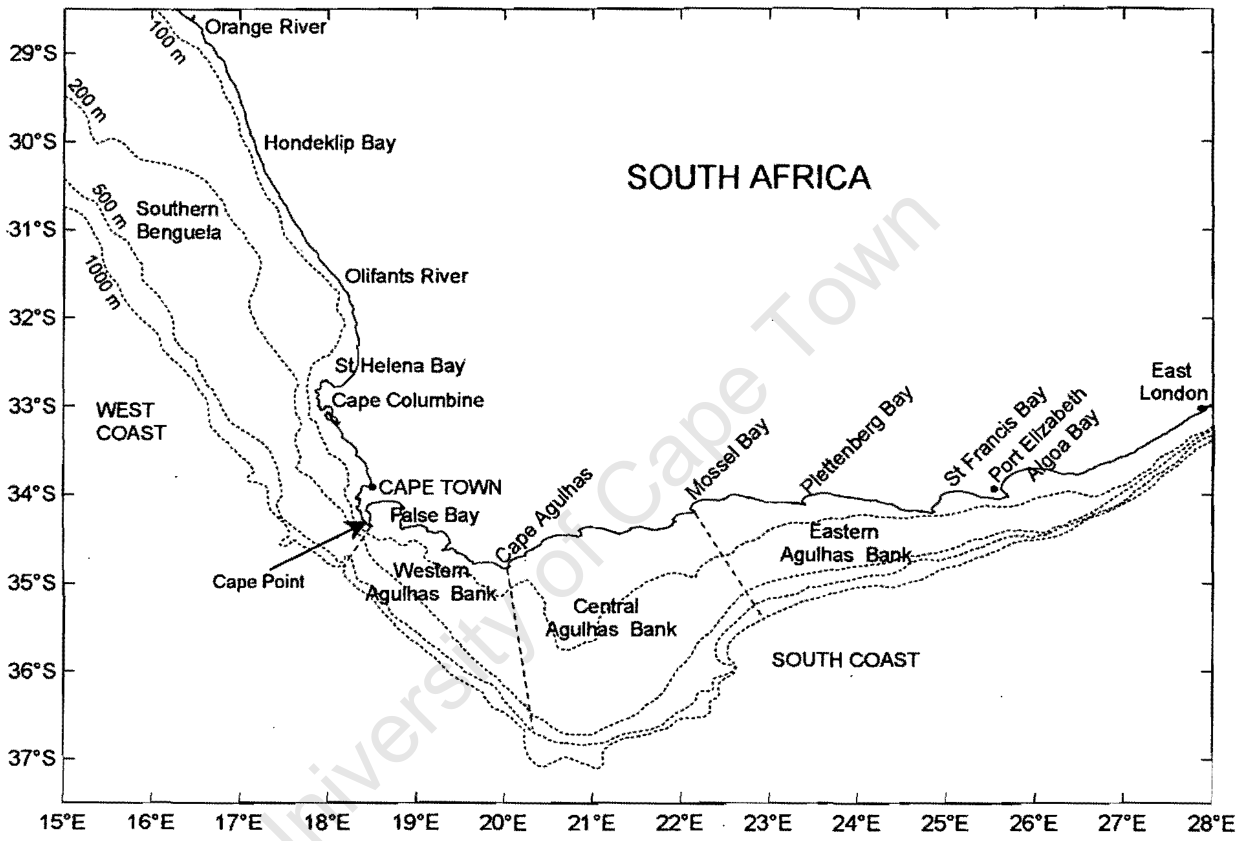


Figure 1.1. Map of the west and south coasts of South Africa, where most of the work on *C. carinatus* (in the southern Benguela) and *C. agulhensis* has been conducted. Places mentioned in the text and the bathymetry are shown.

ways, allowing it to out-compete the other on a long-term basis. This thesis explores a number of hypotheses as to why this may be the case.

This chapter provides a brief overview of the oceanography of the study area, but is primarily a review of literature referring to *Calanoides carinatus* and *Calanus agulhensis*, with emphasis on the southern Benguela and Agulhas Bank regions (Fig. 1.1), although research on *C. carinatus* in other upwelling systems is also discussed. Knowledge of both species off South Africa has developed in tandem with biological oceanography in the region (reviewed by Hutchings and Field 1997), beginning with early descriptive and distributional studies, such as those of Cleve (1904), De Decker (1964, 1973) and Carter (1977). Later studies focussed on the mechanisms and processes underlying upwelling in the southern Benguela. Verheye (1989) investigated the distribution, dynamics and production of *C. carinatus*, the dominant copepod, and suggested how it is able to maintain itself within this dynamic upwelling system (Verheye *et al.* 1991; Verheye and Field 1992). In laboratory studies around this time, the development rates of both *C. carinatus* and *C. agulhensis* were measured (Peterson and Painting 1990), and the feeding rates of *C. carinatus* were investigated (Peterson *et al.* 1990a). Information from all these studies was later used to construct a population dynamics model simulating temporal variability in *C. carinatus* biomass off the west coast (Plagányi *et al.* 1999).

In the late 1980s, research effort shifted towards the role of copepods as food for pelagic fish, in particular that of *C. agulhensis* on the Agulhas Bank (Peterson *et al.* 1992; Peterson and Hutchings 1995), where it forms an important food source for spawning anchovy. Extensive information on growth and production rates of this species were obtained from annual monitoring surveys off the west and south coasts (Hutchings *et al.* 1995b), as well as from two years of monthly sampling during spring and summer as part of the South African Sardine and Anchovy Recruitment Programme (SA-SARP; Painting 1993). This formed the basis for Richardson's (1998) thesis on the variability of copepod abundance and growth in the southern Benguela, which led to new insights regarding the relative importance of temperature and food to copepod growth rates (Richardson and Verheye 1998, 1999). A comparison of *C. agulhensis* with other species in its genus can be found in Huggett and Richardson (2000).

1.1. OVERVIEW OF THE OCEANOGRAPHY OF THE REGION

This overview is condensed from papers by Shannon (1989), Boyd *et al.* (1992), Boyd and Shillington (1994), Shannon and Nelson (1996) and Hutchings *et al.* (2000). A conceptual picture of some aspects of the oceanography is shown in Fig. 1.2a, and typical values of near-surface currents are shown in Fig. 1.2b.

The oceanography off South Africa is dominated by the warm western boundary Agulhas Current on the East Coast, and the cool eastern boundary Benguela system with its coastal upwelling off the West Coast (Fig. 1.2a). These two regimes are separated by the broad, roughly triangular coastal plain off the South Coast, the Agulhas Bank. Along the eastern seaboard, the Agulhas Current flows polewards along the narrow shelf at an average speed of 1-2 m s^{-1}, before diverging from the coast towards the tip of the Agulhas Bank and retroflecting eastwards into the South Indian Current along the subtropical convergence. Near Port Elizabeth, large seaward meanders in the Agulhas Current may sometimes develop and move slowly downstream. Eddies and filaments that shear off these meanders move parcels of Agulhas Current water onto the shelf. Large rings or eddies may also be shed from the current in the retroflection zone; these drift slowly into the South Atlantic Ocean, eventually dissipating.

Strong easterly winds during summer result in upwelling at promontories along the South Coast, particularly on the western Agulhas Bank between Cape Point and Cape Agulhas, and on the eastern Agulhas Bank between Mossel Bay and Port Elizabeth (Fig. 1.1). Westerly winds dominate during winter. The oceanography of the eastern Bank is dominated by wind forcing and the position and orientation of the inshore margin of the Agulhas Current. Water upwelled at capes on the eastern Bank appears to feed a subsurface ridge of cold water extending southwestward from the coast over the eastern and central Bank; this is described in more detail in Chapter 2.

The interior region of the Agulhas Bank is characterized by strong stratification and a deep mixed layer in summer, when subtropical surface water overlies cool bottom water drawn onto the shelf by dynamic processes linked to the divergence of the Agulhas Current from the coast. In winter, the thermocline is eroded by wind-induced mixing due to westerly gales, and reduced solar heating, resulting in a uniformly well-mixed, deep upper layer (80-90 m). Currents tend to be weak and prone to west-east flow reversals, particularly on the eastern Bank (Fig. 1.2b). Flow tends to be cyclonic around the southern and western margins of the cool ridge, but variable inshore of the ridge. Dynamic upwelling is common along the outer shelf edge, particularly on the

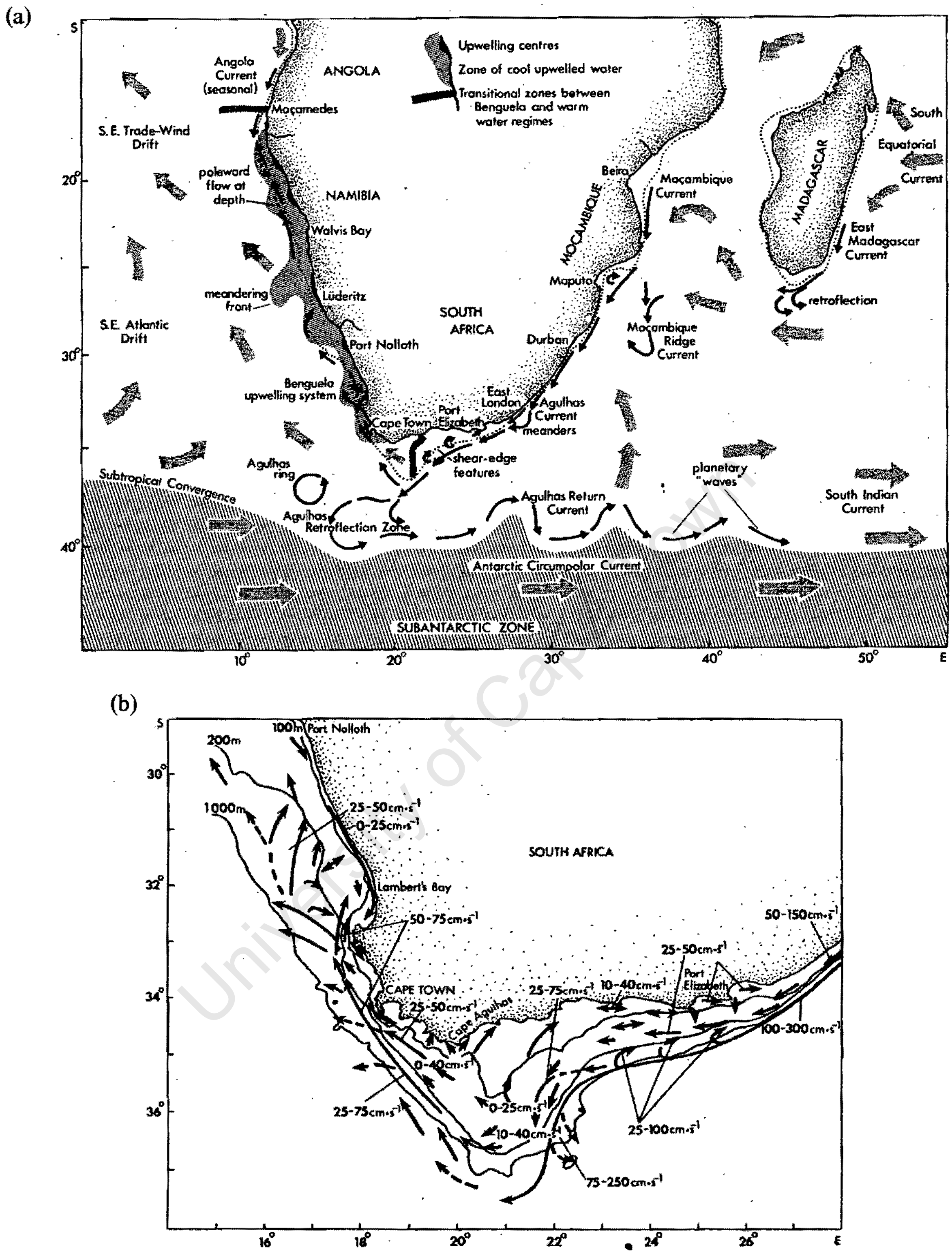


Figure 1.2. (a) Conceptual picture of some aspects of the physical oceanography around southern Africa (from Shannon 1989) and (b) schematic flowfield of near-surface currents based on data collected between November 1989 and January 1992. Velocity values reflect typical values, not extremes (from Boyd *et al.* 1992).

eastern margin, where shear-edge eddies may result in a north-eastward counterflow (Fig. 1.2b). The western Agulhas Bank is characterized by convergent north-west flow (Fig. 1.2b); this develops into a strong shelf-edge jet current (typically 0.25-0.75 $m\,s^{-1}$) that accelerates past Cape Point towards the West Coast.

Off the west coast of South Africa, south-easterly, upwelling-favourable winds reach a maximum during spring and summer, with the upwelling season extending from September to March. Modulation of upwelling with periods of 3-10 days occurs under wind relaxation or reversal associated with the passage of cyclones south of the continent during the upwelling season. Principal upwelling cells are located off the Cape Peninsula (34°S), Cape Columbine (33°S) and Hondeklip Bay (30°S), with the latter also referred to as the Namaqua cell. A well-developed longshore system of fronts demarcates the seaward extent of upwelled water. Cool-water filaments are also associated with the oceanic front, with typical lifespans of several days to several weeks. Near-surface flow is equatorward over much of the west coast shelf, but poleward at depth over the shelf and continental slope. At Cape Columbine the jet current appears to bifurcate into offshore and alongshore northward components, the latter including partial flow into St Helena Bay (Fig. 1.1), an important retention area.

1.2. LITERATURE REVIEW FOR *CALANOIDES CARINATUS*

1.2. 1. Distribution and abundance

General distribution

Calanoides carinatus (Figs 1.3a and b) is a characteristic and often dominant species of many tropical and temperate upwelling systems, particularly those around the African continent (Thiriot 1978; Peterson 1998). Diapause is a key feature of its life-history, enabling it to overwinter in deep waters and reseed the coastal environment at the onset of the upwelling season. A comparison of its abundance in coastal upwelling regions off Africa is provided by Verheye (1989; 1991, his Table 7) and Verheye *et al.* (1992, their Table 2). *C. carinatus* occurs over and beyond the continental shelf in the North-West African upwelling area (Schnack 1982; Schulz 1982), off equatorial West Africa, including Ivory Coast (Binet and Suisse de Sainte Claire 1975), Ghana (Mensah 1974; Houghton and Mensah 1978), the Gulf of Guinea (Bainbridge 1960; Binet and Marchal 1993) and Congo (Petit and Courties 1976; Petit 1982), in the Bay of Biscay and off the coast of Portugal (Williams

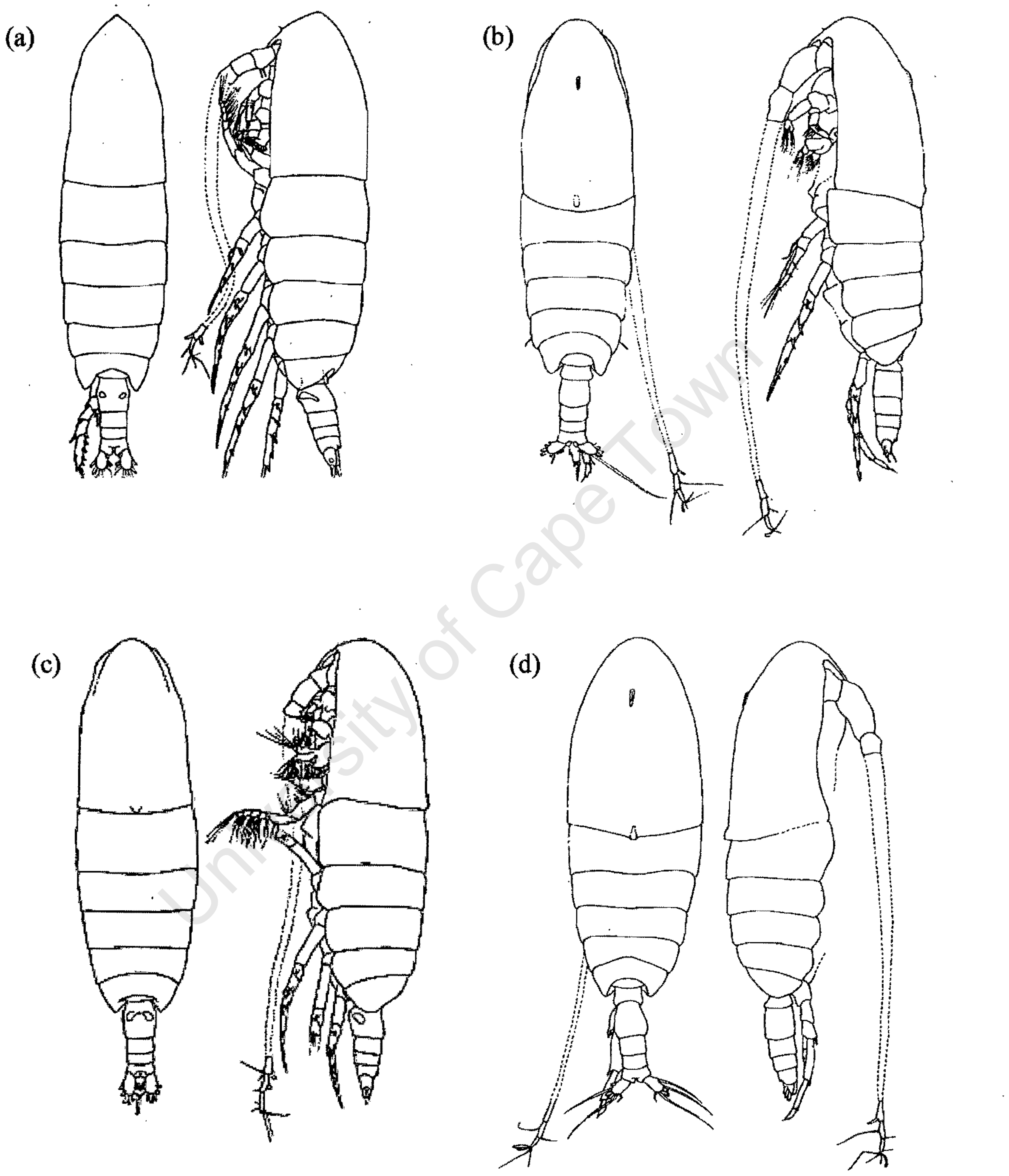


Figure 1.3. Dorsal and lateral views of (a) female (*TL* = 2.74 mm) and (b) male (*TL* = 2.16 mm) *C. carinatus* (Figs from Brodskii 1972; mean lengths from this study), and (c) female (*TL* = 2.83 mm) and (b) male (*TL* = 2.86 mm) *C. agulhensis* (from De Decker *et al.* 1991). *TL* = total length.

and Conway 1988; John *et al.* 1998), off Somalia and in the Gulf of Aden (Smith 1984; Baars *et al.* 1998), and in the nearshore upwelling zone off Brazil (Valentin 1984) and Argentina (Hoffmeyer 1994; Ramirez and Sabatini 2000). *C. carinatus* has also been found in samples collected with the Longhurst Hardy Plankton Recorder in deep oceanic water, off the continental shelf, to the southwest of the British Isles (Williams and Conway 1988), where it is thought to have drifted in deep Mediterranean outflow water (>600 m) from the Iberian Peninsula (John *et al.* 1998; Stohr *et al.* 1997).

De Decker (1964) regularly found *C. carinatus* south of Madagascar in waters between the 700 and 3000-m isobaths. He also noted that it occurred along the south and east coast of Australia, and in the Indo-Malayan area. Tranter (1977) found *C. carinatus* in a narrow tropical belt to the south of Java, but only during the south-east monsoon of the "Java dome" upwelling system. Unterüberbacher (1964) noted that *C. carinatus* has also been found in the Mediterranean, the Philippines, the China Sea and the Izu region of Japan. Off southern Africa, *C. carinatus* is abundant in both the northern and southern Benguela upwelling regions, occurring off the coasts of Angola (Marques 1953, 1956, 1958, cited in De Decker 1984; H. Verheye, pers. comm.), Namibia (Unterüberbacher 1964; Timonin *et al.* 1992), and South Africa (De Decker 1964; Verheye *et al.* 1992). De Decker (1964, p. 17) found this species "in gigantic swarms over the whole length of the Benguela Current as far as Angola" during summer. The surface distribution of *C. carinatus* during a number of cruises in the South-Western Indian and South-Eastern Atlantic oceans in the 1960s is shown in Fig. 1.4a (De Decker 1984), indicating the presence of this species off Namibia, around the entire coastline of South Africa, and in the Indian Ocean south of Madagascar. In Chapter 2, the distribution and abundance of all copepodite stages of *C. carinatus* off the west and south coasts of South Africa is investigated, using samples collected from biannual cruises (May/June and November/December) between 1988 and 2000.

Benguela upwelling system

In contrast to most upwelling areas in other eastern boundary current systems, upwelling may occur all year round in the Benguela ecosystem (Shannon 1985). Accordingly, *C. carinatus* may be found close to the coast throughout the year, although less abundantly in the southern Benguela during winter when upwelling is minimal (Verheye *et al.* 1991). These authors suggested that the existence of both an inshore active component and an offshore resting component allows *C. carinatus* to maintain a perennial presence in the region. True diapause is therefore not essential for local populations to bridge long periods of unfavourable conditions, as it is in lower latitudes, although

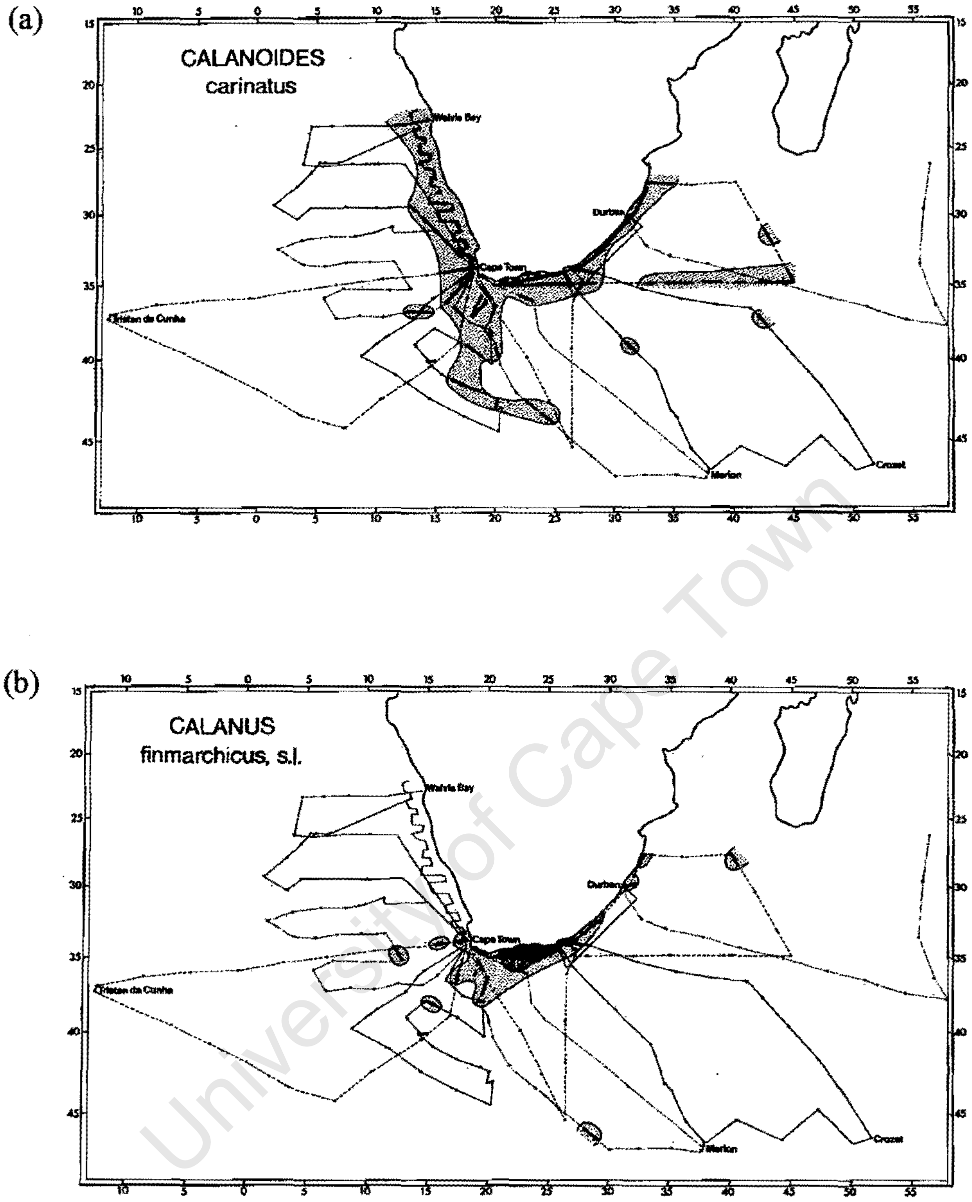


Figure 1.4. Distribution of (a) *C. carinatus* and (b) *C. agulhensis* from continuous sampling of near-surface plankton during various cruises between 1961 and 1968 in the South-Western Indian and South-Eastern Atlantic oceans. Thickened lines on the ship's routes indicate stretches where the species was found in the continuous pump samples. Shaded areas are suggested distribution patterns; darker shading indicates areas of higher abundance (from De Decker 1984).

stage C5s have been found in deep (600 m) water offshore during summer (Borchers and Hutchings 1986). Seasonal fluctuations in the abundance of *C. carinatus* in the southern Benguela, ranging from 4 700 ind. m^{-2} in winter to 11 200 ind. m^{-2} during peak upwelling, are consequently less striking than those in tropical upwelling regions (Verheye *et al.* 1991). Studies have shown *C. carinatus* to comprise between 13 and 23% of the mesozooplankton biomass in the southern Benguela (Verheye *et al.* 1991), and up to 67% of the copepod biomass, equivalent to 36% of copepod abundance (Painting 1989).

C. carinatus has also been reported to be commonly found off the south coast of South Africa, and was present in all but two sections of a continuous, near-surface survey from Durban to Cape Town during July 1961 (Fig. 1.5; De Decker 1964). This survey was not quantitative, but instead indicated whether species were common or rare. Adults predominated between Cape Town and Port Elizabeth, whereas juveniles were more abundant from the eastern side of Algoa Bay to south of Durban. No individuals were found in section VIII, between Mossel Bay and the Tsitsikamma River (~24.4°E), or in Algoa Bay (section VI). *C. carinatus* was rarer towards the east, at least near the surface, and was never found "in any quantities worth mentioning" in 100-0 m vertical hauls off the coast of Kwa-Zulu Natal (De Decker 1964, p. 17, in reference to unpublished work by what was then known as the Division of Sea Fisheries). In a later paper, De Decker (1973) listed *C. carinatus* as one of the three most important calanoids of the Agulhas Bank, being both abundant and widely dispersed. He found the youngest copepodite stages (C1-C2) to be concentrated in relatively small areas, mostly around centres of upwelling, from where the later stages dispersed further afield as they matured.

Carter (1977) investigated the seasonal abundance of copepods on the east coast, using samples collected from cross-shelf transects off Port Edward, Durban and Cape St Lucia (Fig. 1.6). He found *C. carinatus* to attain high relative abundances in the inshore/Agulhas Current boundary region off Durban, with the juveniles being restricted to this zone, but with very low densities of adults in both the core region of the Agulhas Current and farther offshore. Greatest abundance was in late spring. Juveniles attained high densities (4 000-10 000 individuals per standard 200–0 m net haul), especially in the winter/spring period. Cyclonic eddies were observed to be relatively common in the continental shelf region off Durban, and juvenile *C. carinatus* appeared to be associated with the enhanced primary productivity or "upwelling" characteristic of these eddies. Carter (1977) proposed that the frequent occurrence of these cyclonic eddies off Durban would provide the *C. carinatus* population with ample opportunity for recruitment. *C. carinatus* was less abundant off Port Edward compared to Durban, but again the juveniles were restricted to the inshore/Agulhas

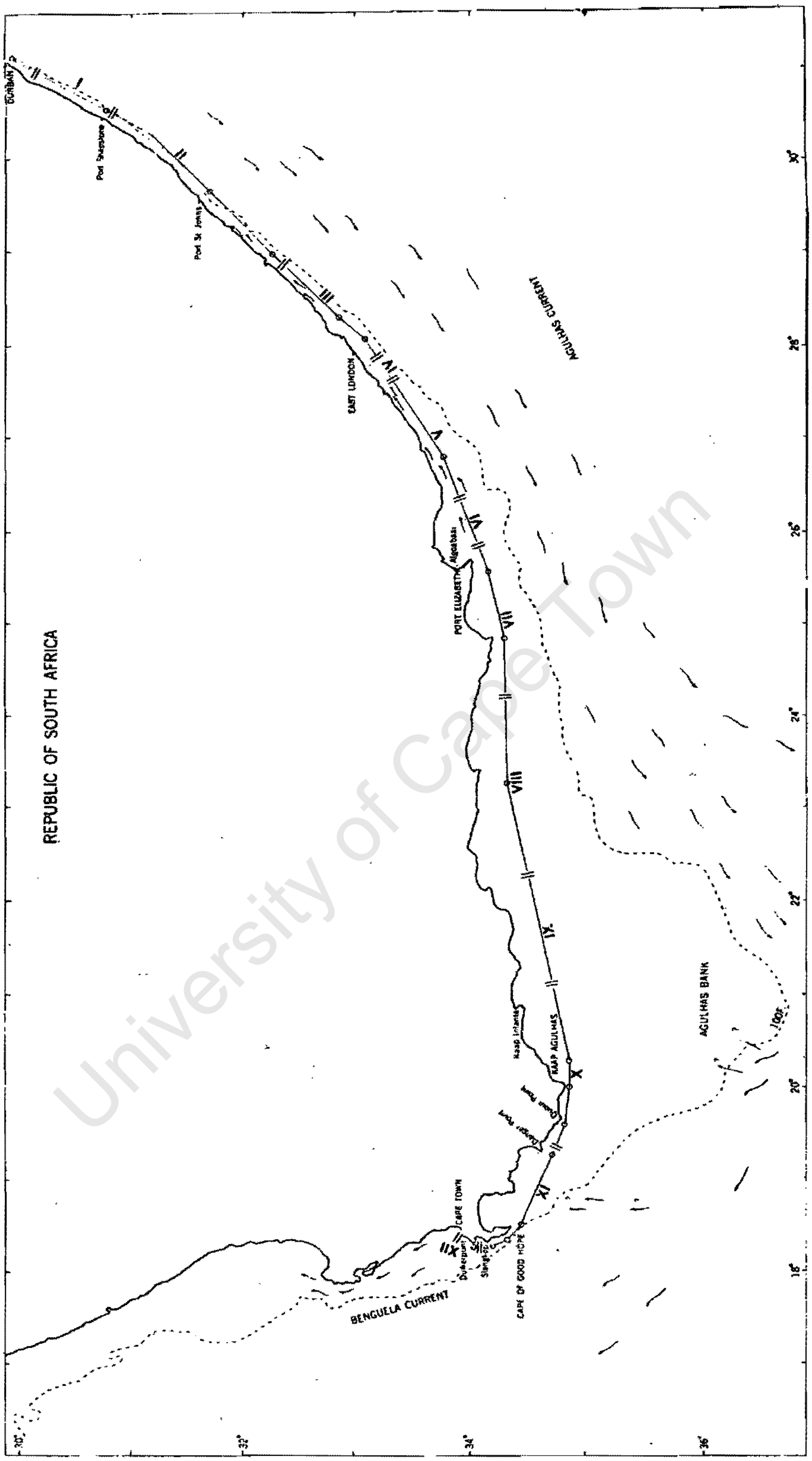


Figure 1.5. Route of *Africana* II (legs I-XII) during a continuous survey from Durban to Cape Town in July 1961 (from De Decker 1964).

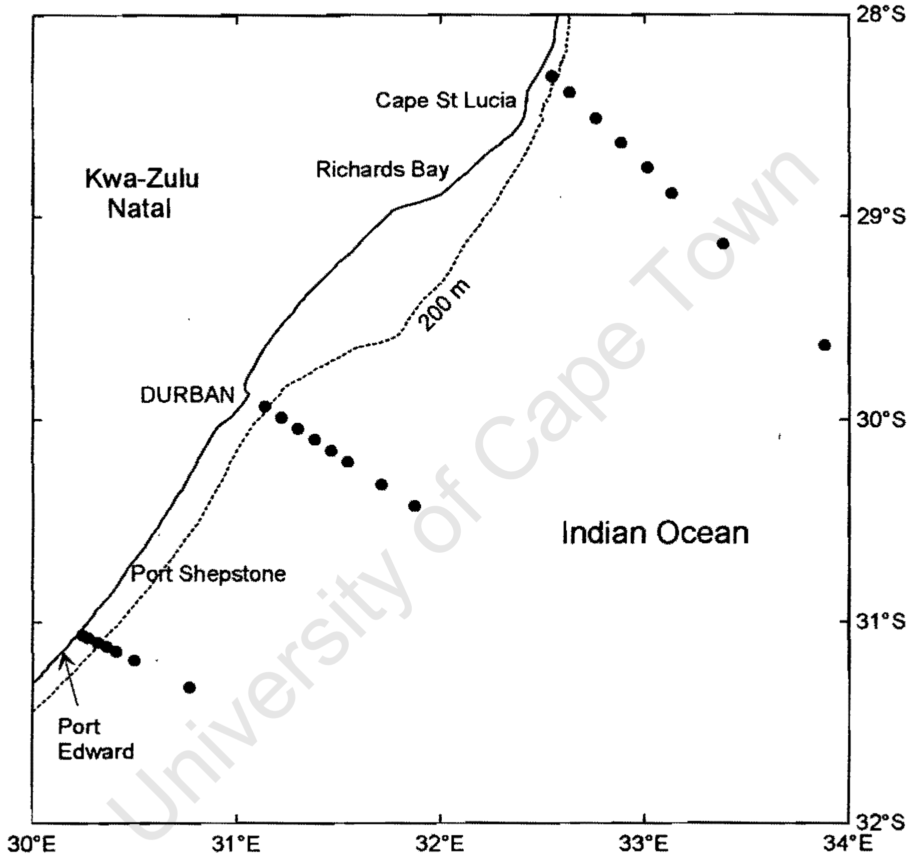


Figure 1.6. Map showing the location of plankton stations along three transects sampled off the east coast of South Africa between October 1972 and March 1976 (redrawn from Carter 1977).

Current boundary region whereas the adults were not, suggesting that the copepodite stages were better indicators of upwelling than were the adults.

Off Namibia, *C. carinatus* is found throughout the year in the upper water column (Unterüberbacher 1964; Timonin *et al.* 1992), comprising 15% or more of the total copepod population in the vicinity of Walvis Bay (Unterüberbacher 1964). Abundance of *C. carinatus* over the shelf varies considerably according to upwelling phase, from 4 000 ind. m^{-2} during non-upwelling, to 93 000 ind. m^{-2} during active upwelling, and up to 370 000 ind. m^{-2} during relaxation (Arashkevich *et al.* 1996). In addition to this active component of the population, comprising all developmental stages, there is a resting component dominated by diapausal C5s (90-95%) in deep (300-1 000 m) water offshore (Timonin *et al.* 1992; Arashkevich *et al.* 1996; Timonin 1997). The abundance of deep-living animals near the slope in different seasons is relatively constant, from 4 000-9 000 ind. m^{-2} (Timonin 1990, cited in Arashkevich *et al.* 1996).

Equatorial West Africa

Off equatorial West Africa, the presence of *C. carinatus* in surface waters is limited to the short (~3 month) upwelling season, when 4-6 generations are produced (Binet and Suisse de Sainte Claire 1975). At the end of the upwelling season, lipid-rich C5 copepodites descend to deep (>500 m) water, where they remain in a state of arrested development, or diapause, until upwelling resumes (Binet and Suisse de Sainte Claire 1975; Petit and Courties 1976; Arashkevich *et al.* 1996; Peterson 1998). During the upwelling season, *C. carinatus* may exceed densities of 1 000 ind. m^{-2}, and comprise 40-90% of total copepod abundance (Binet and Suisse de Sainte Claire 1975).

Somalia

Off Somalia, *C. carinatus* is only found in surface (0-200 m) waters during the summer southwest monsoon (SWM), with mean densities of over 100 ind. m^{-3} (>8 500 ind. m^{-2}); maximum densities of 621 ind. m^{-3} (123 000 ind. m^{-2}) were recorded in 1964 (Smith 1984). During the winter northeast monsoon (NEM), fairly uniform but low densities (>1 ind. m^{-3}) of subadults have been found between depths of 300 and 1 500 m (Baars *et al.* 1998), when the population is entrained in the "Great Whirl", a gyre-like feature that probably retains the copepods within 1 000 km of the coast for most of this season.

South-west Atlantic

In their review of the occurrence of Calanidae off Argentina, Ramirez and Sabatini (2000) found what they refer to as *Calanoides* cf. *carinatus* (due to some uncertainty about the taxonomy) to be one of the three most abundant calanids in the region. It was present year round from ~35 to 46°S, not having been recorded in higher latitudes. Abundance was "frequent" (up to 1000 ind. m^{-3}) to "abundant" (1001-10 000 ind. m^{-3}) in the inner and middle shelf waters during all four seasons, with greatest densities usually in summer (sometimes exceeding 10 000 ind. m^{-3}) between 42 and 45°S. This species has also been recorded farther north, in the Cabo Frio region off Brazil (Valentin 1984), where it is common in the coastal upwelling region during spring and summer, and off Uruguay (Goberna 1986, cited in Ramirez and Sabatini 2000).

1.2.2. Development, growth and production

Development rates of *C. carinatus* in the laboratory under conditions of abundant food have been well documented for the southern Benguela (Borchers and Hutchings 1986; Peterson and Painting 1990), and have also been investigated for animals collected off the coast of North-West Africa (Hirche 1980). Egg production in relation to the food environment has been relatively well-studied, both in the field and the laboratory, and is explored further in Chapters 3 and 4. However, relatively little information is available on somatic growth and moulting rates of the juvenile stages in the field, principally due to the greater effort that has been directed towards measuring growth rates of *C. agulhensis* on the Agulhas Bank during annual surveys in November. Estimates of secondary production for *C. carinatus* to date have hence relied to some extent on the assumption that growth rate (d^{-1}) is linearly related to the log of body mass (μg dry wt; Walker and Peterson 1991). Richardson *et al.* 2001 suggest that a non-linear model of growth rate in relation to body mass may be more precise over a broad size-range of copepods.

Development rates

Maximum egg-to-adult development times of *C. carinatus* continuously fed excess quantities of the flagellate *Pseudoisochrysis paradoxa* declined from 75 days at 7°C to 12 days at 18°C (Borchers and Hutchings 1986). Development time at 7°C was extremely prolonged, and rapidly declined to only 41 days at 8°C. Intermittent feeding increased development time, which was approximately twice as long for animals that were starved for half of their development time. Eggs took one day to hatch at 18°C. Whereas Hirche (1980) found that females do not start producing eggs until 5-7 days after moulting, Borchers and Hutchings (1986) frequently observed females to lay eggs within 3 days of moulting.

Peterson and Painting (1990) recorded slightly slower development of *C. carinatus* at 15°C (18.3 compared to the 17 days reported by Borchers and Hutchings (1986); Fig. 1.7a) for animals fed excess quantities of a mixture of the diatom *Thalassiosira weissflogii* and the flagellate *Tetraselmis suecica*, but suggested that Borchers and Hutchings (1986) may have reported times from egg hatching, and not egg laying, to adult. Verheye (1991) fitted the following power curve to the Borchers and Hutchings (1986) data, which was corrected to include egg development time:

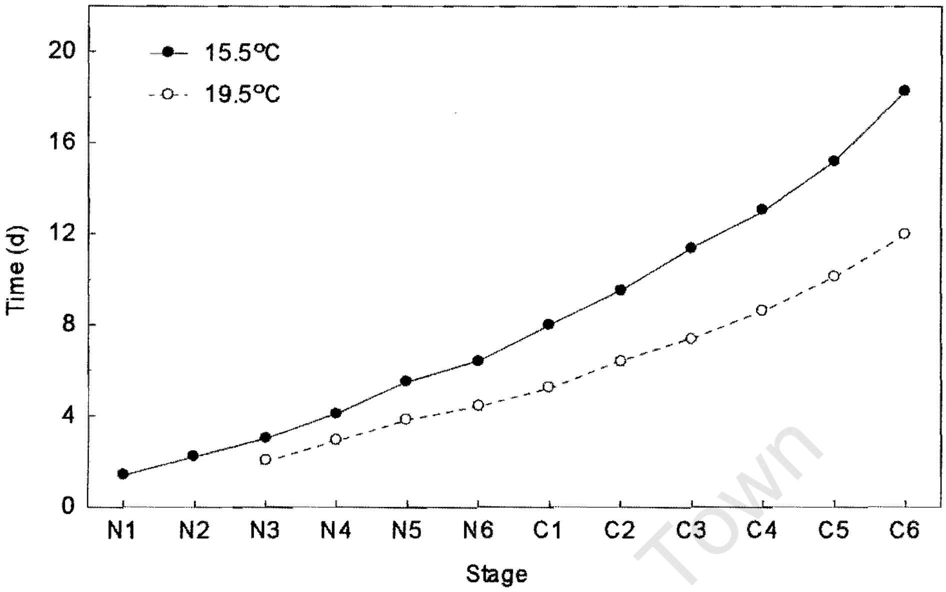
$$D_t = 1469.2 \times (T-1.5)^{-1.665}$$

where D_t is the total development time (d) at ambient temperature T (°C).

Hirche (1980) recorded an even slower minimum development time of 21 days at 15°C for animals collected off North-West Africa and reared on *Gymnodinium* or a mixed algal diet in Germany. The reason for this discrepancy is unknown, but may be related to diet or some other experimental condition. Hirche (1980) also provides a useful description of the morphology and distinguishing features of *C. carinatus* eggs and nauplii (Fig. 1.8) reared in the laboratory, and Binet and Suisse de Sainte Claire (1975) provide information on lengths (Table 1.1) and segmentation of the copepodite stages (C1-adult) collected off Ivory Coast.

C. carinatus development is equiproportional (Corkett 1984), and approximately isochronal (Miller *et al.* 1977) from N3 to C3 (Peterson and Painting 1990). Egg hatching time is 25% longer than for *C. agulhensis* (27 h compared to 21 h), but the N3 stage duration is much shorter, 1.1 days compared to 3.0 days, at 15°C. Development time of the first-feeding naupliar stage of most copepods, usually N2 or N3, is prolonged (Landry 1983), probably due to development of the mouthparts. Rapid development through to N4 in *C. carinatus*, however, combined with a slightly longer egg hatching time, suggests that the first two naupliar stages may be capable of feeding (Peterson and Painting 1990). This possibility was also raised by Borchers and Hutchings (1986), who found newly-hatched and 2-day old nauplii able to survive starvation for the same length of time. They argued that, if newly hatched larvae do not feed for the first 2 days, then the survival time of these (starved) 2-day old nauplii should be shorter than that of (starved) newly hatched nauplii, since the 2-day old nauplii will have used their food reserves without replenishment.

(a) *Calanoides carinatus*



(b) *Calanus agulhensis*

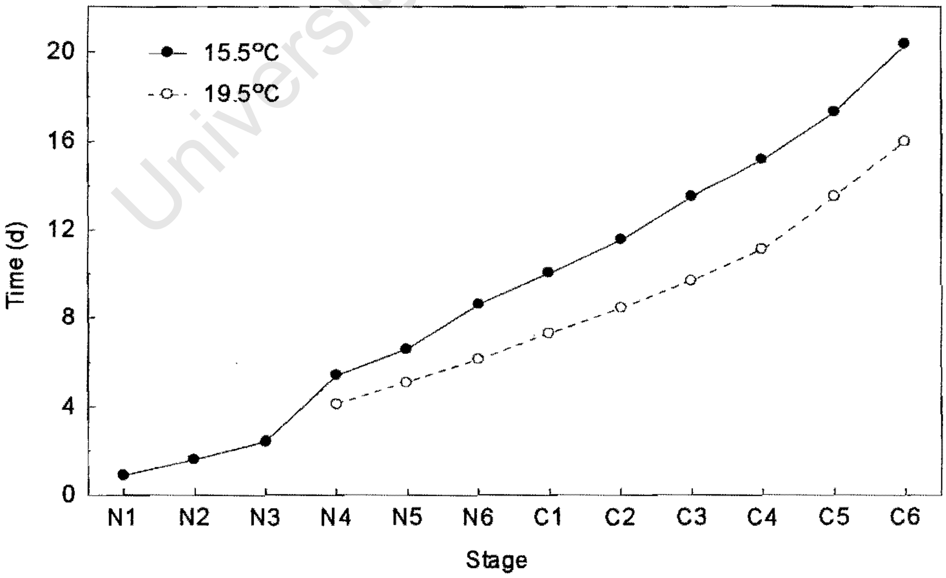


Figure 1.7. Median development time of (a) *C. carinatus* and (b) *C. agulhensis* (from Peterson and Painting 1990).

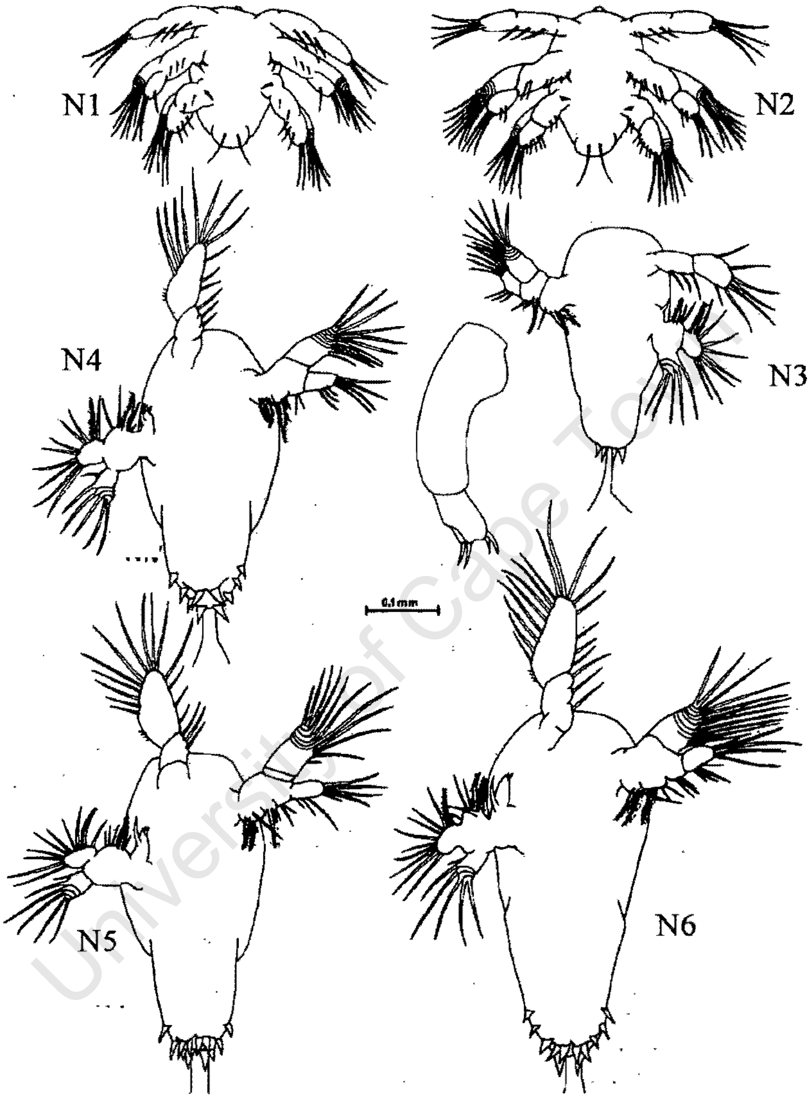


Figure 1.8. The six nauplius stages of *C. carinatus*, seen from the ventral side. Stages N1 and N2 are shown with legs in their natural position. For N3 a lateral view is also given to show dorso-ventral flexure. In N3-4 each limb is shown on one side only. The appendages are brought into a position to show the full outline. Fine setules, present on many of the setae, are only drawn on "remarkable spines". Scale = 0.1 mm (from Hirche 1980, p.119).

Table 1.1. Average mass, total length, prosome length, stage duration and lipid content of *C. carinatus* and *C. agulhensis* copepodites, adults and eggs.

C. carinatus	C1	C2	C3	C4	C5	Male	Female	Egg
Mass (µg dry weight)	3.3[1], 4[2]	5.7[1], 7[2]	12.8[1], 18[2]	28.1[1], 30[2]	61.9[1], 60[2], 58[3]	72.9[1]	123.5[1]	0.75[2], 0.8[3]
Total length (µm)	788[13]	1020[4]	1385[4]	1794[4]	2311[4]	2163[4]	2735[4]	160[5], 151[13]
	700 (600-820)[6]	940 (820-1020)[6]	1310 (1160-1520)[6]	1850 (1520-2200)[6]	2280 (1760-2520)[6]	2420 (2080-2600)[6]	2640 (2280-3000)[6]	
Prosome length (µm)	614[1]	799[1], 820[4]	1002[1], 1137[4]	1336[1], 1465[4]	1705[1], 1887[4]	1780[1], 1781[4]	2041[1], 2233[4]	
	540-680[6]	780-840[6]	1040-1200[6]	1240-1500[6]	1440-1900[6]	1800-2060[6]	1600-2520[6]	
Stage duration in laboratory (d)[7] at 15.5°C	1.5	1.9	1.6	2.2	3.1	-	-	
Stage duration in laboratory (d)[7] at 19.5°C	1.2	1.0	1.2	1.5	1.9	-	-	
Lipid content (% dry weight)	-	-	-	-	57-72[3], 36.1[8]	-	14.5[8]	75[3]

C. agulhensis	C1	C2	C3	C4	C5	Male	Female	Egg
Mass (µg dry weight)	4[2]	9[2]	22[2]	46[2]	97[2]	110[9]	202[2], 184/199[10]	0.6[5]
Total length (µm)	785[11], 825[4]	939[11], 1027[4]	1350[11], 1376[4]	1700[11], 1788[4]	2309[11], 2215[4]	2724[11], 2547[4]	2763[11], 2730[12], 2602[4]	166[13]
Prosome length (µm)	650[11], 667[4]	800[11], 822[4]	1090[11], 1100[4]	1398[11], 1409[4]	1781[11], 1738[4]	1986[11], 1947[4]	2132[11], 2056[4]	
Stage duration in laboratory (d)[7] at 15.5°C	1.5	2.0	1.7	2.1	3.0	-	-	0.9
Stage duration in laboratory (d)[7] at 19.5°C	1.1	1.3	1.4	2.4	2.5	-	-	
Lipid content (% dry weight)	-	-	-	-	17.1[8]	-	16.7[10], 8.3[8]	

[1] Verheye (1991)
[2] Peterson *et al.* (1990b)
[3] Borchers and Hutchings (1986)
[4] this study, animals collected on the Agulhas Bank, January 1992
[5] Peterson *et al.* (1990a)
[6] mean (range), animals collected off Ivory Coast (Binet and Suisse de Sainte Claire 1975)
[7] food-satiated stage duration (Peterson and Painting 1990)
[8] preliminary results, W. Hagen and H. Verheye, pers comm.
[9] Marine and Coastal Management, unpublished data
[10] freeze-dried/oven-dried, Attwood and Peterson (1989)
[11] Stuart and Huggett (1992)
[12] De Decker *et al.* (1991)
[13] Richardson *et al.* (2001); egg diameter excludes perivitelline space

Comparative stage durations for C1-C5 (from Peterson and Painting 1990) are shown in Table 1.1. *C. carinatus* develops from egg to adult 2 days faster than *C. agulhensis* at 15.5°C, and 4 days faster at 19.5°C (Fig. 1.7). Furthermore, *C. carinatus* has the most rapid development of the majority of calanoids studied to date (15-36 d at 15°C, with *Pseudocalanus elongatus* the fastest at 15 days), and of most other copepod species as well (10-50 d at 15°C), faster development being recorded for *Acartia*, *Eurytemora* and *Temora* spp. (Mauchline 1998; his Table 47). This characteristic aids retention in the highly advective environment of an upwelling system, by accelerating swimming ability and thus vertical migratory behaviour linked to population maintenance strategies (see section 1.4).

The effect of temperature on somatic growth and egg production

There are insufficient data to investigate relationships between temperature and growth rate of juvenile *C. carinatus*. However, field measurements of egg production show no clear relationship with temperature (Armstrong *et al.* 1991; Richardson and Verheye 1998). Data collected during the summer hydro-acoustic pelagic fish stock assessment surveys and monthly SARP cruises indicate that *C. carinatus* egg production is generally <120 eggs ♀$^{-1}$ d^{-1} between 11 and 18°C, and <85 eggs ♀$^{-1}$ d^{-1} above 18°C (Richardson and Verheye 1998), although data from the latter temperature category were more scarce. No females were found in water warmer than 20°C.

The effect of food concentration and particle size on somatic growth and egg production

As with temperature, there are insufficient measurements of *C. carinatus* somatic growth rates off South Africa to explore fully possible relationships with food abundance and particle size. However, Walker and Peterson (1991) calculated growth rates of *C. carinatus* C1-♀ by measuring moulting rates of some of the stages and assuming a linear relationship between growth rate and body size. Except for C1s, which showed the same growth rate (0.37 d^{-1}) at both large (diatom) and small (microflagellate) cell-dominated stations, growth rates were faster in water dominated by large (>10 μm) cells. Stages C3 and larger were growing slower than maximum observed rates, suggesting food-limitation of these larger stages, as has also been indicated for *C. agulhensis* (Richardson and Verheye 1999).

Maximum egg production rates of 120 and 154 eggs ♀$^{-1}$ d^{-1} were recorded for continuously and intermittently fed females respectively at 18°C (Borchers and Hutchings 1986), whereas mean satiated rates of egg production were 70 eggs ♀$^{-1}$ d^{-1}. This is similar to the asymptotic rate of egg production (73.7 eggs ♀$^{-1}$ d^{-1}) determined for field-caught animals by Richardson and Verheye (1998), who found that *C. carinatus* egg production was correlated with both total chlorophyll *a* concentration and the proportion of cells >10 µm; they fitted an Ivlev curve to the former and a linear regression to the latter. These results confirm those of earlier work in the southern Benguela system. Egg production by female *C. carinatus* downstream of the Cape Columbine upwelling centre in March/April 1987 was closely coupled to hydrologically-mediated fluctuations in food availability (Armstrong *et al.* 1991), and egg production was significantly reduced when ambient chlorophyll *a* concentrations of 12 and 6 mg Chl *a* m^{-3} were diluted to 25% and 0%. Egg production was positively related to the mean concentration of chlorophyll *a* in the euphotic zone, although the large variance in the data precluded the accurate identification of an asymptotic level of egg production. Faster rates of egg production were observed during a bloom of the large (250 µm) diatom *Coscinodiscus gigas* than when the community was dominated by microflagellates (<6 µm). Similarly, along a cross-shelf transect off the Olifants River, Walker and Peterson (1991) observed a 5-fold increase in *C. carinatus* egg production at stations dominated by large cells.

The effect of starvation on egg production, and starvation tolerance

Shipboard experiments by Armstrong *et al.* (1991) revealed that egg production by freshly captured females was significantly lower (20.1 vs. 34.7 eggs ♀$^{-1}$ d^{-1}) when they were incubated in filtered seawater compared to ambient sea water of 6-12 mg Chl *a* m^{-3}, indicating a rapid response to altered food conditions. In a laboratory study by Borchers and Hutchings (1986), previously well-fed *C. carinatus* also responded immediately to starvation, with no eggs being laid once the female was placed in filtered seawater. When food was reintroduced 5 days later, no eggs were laid for the first 24 h, but egg production subsequently reached food-saturated levels of 70 eggs ♀$^{-1}$ d^{-1} after just 3 days when fed excess quantities of the flagellate *Pseudoisochrysis paradoxa*, and reached a record level of 154 eggs ♀$^{-1}$ d^{-1} after 5 days.

Starvation tolerance increased linearly with age, from 2-day old nauplii onwards (Borchers and Hutchings 1986). Tolerance was inversely related to temperature, with females surviving for 12 to 21 days without food at 15°C. Wild-caught adults had shorter survival times than females reared under excess food conditions in the laboratory, suggesting smaller lipid reserves (probably a result of food-limitation) and thus lower starvation tolerance in the field. This may either be representative of field conditions in general, or else pertain specifically to the feeding history of animals captured for the above experiment.

Borchers and Hutchings (1986) measured the lipid content of *C. carinatus* C5s to be 57-72% of dry body weight, which is higher than that reported for most calanoid copepod species (Lee *et al.* 1971a, b; Båmstedt 1986). Once mature, females appear unable to replenish their lipid reserves (Borchers and Hutchings 1986). This is probably because assimilated food is used to produce eggs rather than to restore food reserves. Accumulation of lipid reserves seems to be primarily a female survival strategy to ensure longevity and survive adverse feeding conditions in an unpredictable environment (Armstrong *et al.* 1991). Females can then become reproductively active when feeding conditions are more favourable and the probability of survival of their offspring is enhanced.

Measurements of production

During a 27-day time series in St Helena Bay, mean daily production of juvenile (C1-C5) *C. carinatus* (taking diel vertical migration into consideration) was estimated to be 29.2 mg C m^{-2} d^{-1}, varying between 5.6 and 213.8 mg C m^{-2} d^{-1} (Verheye 1991). Specific production rates (P/B) varied between 0.11 and 0.23 d^{-1} (mean = 0.17 d^{-1}). Mean total production by adult (1.0 mg C m^{-3} d^{-1}) and juvenile (0.7 mg C m^{-3} d^{-1}) *C. carinatus* was estimated to be 1.7 mg C m^{-3} d^{-1}, equivalent to 2% of the mean daily primary production. Assuming an assimilation efficiency of 70-80%, *C. carinatus* would require a mean daily ration of 5.5 mg C m^{-3} d^{-1} or 8% of the daily primary production to maintain their mean daily production.

By comparison, slower production rates of 0.84 and 0.59 mg C m^{-3} d^{-1} were calculated for *C. carinatus* (C1-♀) in diatom- (large cell-) and microflagellate- (small cell-) dominated water respectively along a cross-shelf transect off the Olifants River (Walker and Peterson 1991). Although production rates for the two water types were fairly similar, biomass was three times higher in the microflagellate-dominated water, resulting in much slower daily P/B values of 0.04 d^{-1} for this water type, compared to 0.19 d^{-1} for diatom-dominated water.

1.2.3. Feeding studies

Several studies have measured ingestion rates by mainly female *C. carinatus* in relation to food abundance and size in the southern Benguela, but no work appears to have been done on actual food type selection. This is in contrast to the more detailed food selection studies, including feeding by males, off North-West Africa (Mensah 1974; Schnack 1982). In Chapter 5, size selection, species selection and diel feeding patterns are explored in the southern Benguela and Agulhas Bank ecosystems.

Individual ingestion rates in relation to cell size and concentration

Peterson *et al.* (1990a) used four different methods to determine ingestion rate by female *C. carinatus* on the diatom *Thalassiosira weissflogii* in the laboratory at 15°C. Mean ingestion rate increased with cell concentration, from 0.84 µg Chl ♀$^{-1}$ d^{-1} at 1 500 cells ml^{-1}, to 1.5 µg Chl ♀$^{-1}$ d^{-1} at 3 000 cells ml^{-1}, and to 2.7 µg Chl ♀$^{-1}$ d^{-1} at the highest concentration of 8 000 cells ml^{-1}. Mean gut passage time was 10.2 min. There was little evidence of diel variation in gut pigment content in this laboratory experiment.

Field studies in the southern Benguela upwelling region have shown ingestion rates of *C. carinatus* to be related to cell size as well as cell concentration. Ingestion rates of 64 and 344 ng Chl ind^{-1} d^{-1} were measured for female *C. carinatus* feeding on small- and large-cell-dominated assemblages respectively (Peterson 1989). Mean ingestion rates were low (10-13 ng Chl ind^{-1} d^{-1}) when chlorophyll levels were low (<3 mg Chl m^{-3}), but much higher (~427 ng Chl ind^{-1} d^{-1}) when chlorophyll levels were >3 mg Chl m^{-3}. Maximum ingestion rates of 1 124 ng Chl ind^{-1} d^{-1} were measured for female *C. carinatus* in the southern Benguela during summer (Verheye *et al.* 1992). Daily ingestion rates of *C. carinatus* in the northern Benguela were also linked to chlorophyll concentration (Timonin *et al.* 1992), with maximum rates of 460 ng Chl ind^{-1} d^{-1} measured for female *C. carinatus* over the inner shelf. Ingestion rates were 1.5 to 3 times higher during nighttime than during the day, and were linked to body size and stage, with highest rates measured for females (Timonin *et al.* 1992).

Most studies have assumed *C. carinatus* to be principally herbivorous, and it remains unclear to what extent, if at all, this species may exercise omnivory. In the upwelling area off North-West Africa, food organisms identified from gut contents consisted principally of small centric diatoms (Schnack 1982). During shipboard feeding experiments, grazing rates by female *C. carinatus* were 10 times higher on the weak-linked chains of *Thalassiosira rotula* (cell size: 40x15 µm; cell volume: 19 000 µm^3) with an average chain length of 2-4 cells, than on the strong-linked chains of the larger *Stephanopyxis palmeriana* (cell size: 700x35 µm; cell volume: 67 000 µm^3) with an average length of 8 cells per chain. In further experiments, females were incubated in a culture containing 3 different size-classes (15, 20 and 30 µm diameter) of the dinoflagellate *Scripsiella faroense*. The largest size-class was always least abundant in this culture, but highest in total biomass. In 6 out of 10 experiments, the largest cells were removed at a higher grazing rate than the smaller cells, although the difference was not significant. There was, however, a positive electivity index for the largest cells in 8 of the experiments (Schnack 1982). Off Somalia, the cells comprising the largest proportion eaten by female *C. carinatus* were generally large (the diatoms *Rhizosolenia delicatula*, *Nitzschia delicatissima*, *Eucampia cornuta* and *Thalassionema nitzschoides*), between 35 and 85 µm (Smith 1982). Off Ghana, gut contents of C4, C5 and female *C. carinatus* included diatoms (e.g. *Nitzschia*, *Anabaena*, *Asterionella*, *Skeletonema*, *Thalassiothrix*, *Bacteriastrum*, *Thalassiosira*, *Chaetoceros* and *Navicula* spp.) and dinoflagellates (e.g. *Peridinium* and *Ceratium* spp.) commonly found in coastal waters during the upwelling season (Mensah 1974). During phytoplankton blooms, the diatom species responsible for the bloom was found to be the most abundant organism in the guts of the copepods, although Mensah (1974) concluded that C1-C3s and the deep-living C5s feed mainly on bacteria, and the males on bacteria alone. This has not been confirmed by any other studies, however.

The extent of feeding by male *C. carinatus* seems to be limited. In the upwelling area off North-West Africa, whereas 95% of females had food in their guts, food was not usually found in the guts of males, which were stated as having reduced mouthparts (Schnack 1982). Mensah (1974) described the mouthpart morphology of copepodite, female and male *C. carinatus* as essentially similar, and typical of herbivorous copepods, possessing abundant fine setae and setules, particularly the maxillae. However, whereas the copepodites and females possessed blunt mandibular teeth, indicating a grinding function, the mandibles of the males lacked a mandibulatory component (Fig. 1.9a; Schnack 1982), suggesting that they were able to filter food organisms, but unable to grind their food prior to ingestion. Off Somalia, males were capable of feeding, although invariably at lower rates than females (Smith 1984). The largest grazing impact by males was 185 mg C m^{-2} d^{-1}, compared to 780 mg C m^{-2} d^{-1} for females.

Community ingestion rates

The few studies conducted on grazing by the copepod community in both the southern and northern Benguela have indicated a fairly limited impact on the phytoplankton (Peterson *et al.* 1990b; Verheye *et al.* 1992; Timonin *et al.* 1992). For example, Peterson *et al.* (1990b) estimated that the entire copepod community ingested only 1-5% of the phytoplankton standing stock per day over the shelf off the Olifants River during spring. *C. carinatus* ingestion rates in St Helena Bay during autumn ranged between 0.5 and 15.9 mg C m^{-3} d^{-1}, which was equivalent to 4.4% of the primary production (Verheye 1989); no information is provided in terms of the phytoplankton standing stock. Painting *et al.* (1993) calculated that a maximum of 4.6% of the phytoplankton standing crop was removed by the *C. carinatus* population off Cape Columbine during late summer, in maturing upwelled water. Similar results were obtained in the northern Benguela, where *C. carinatus*

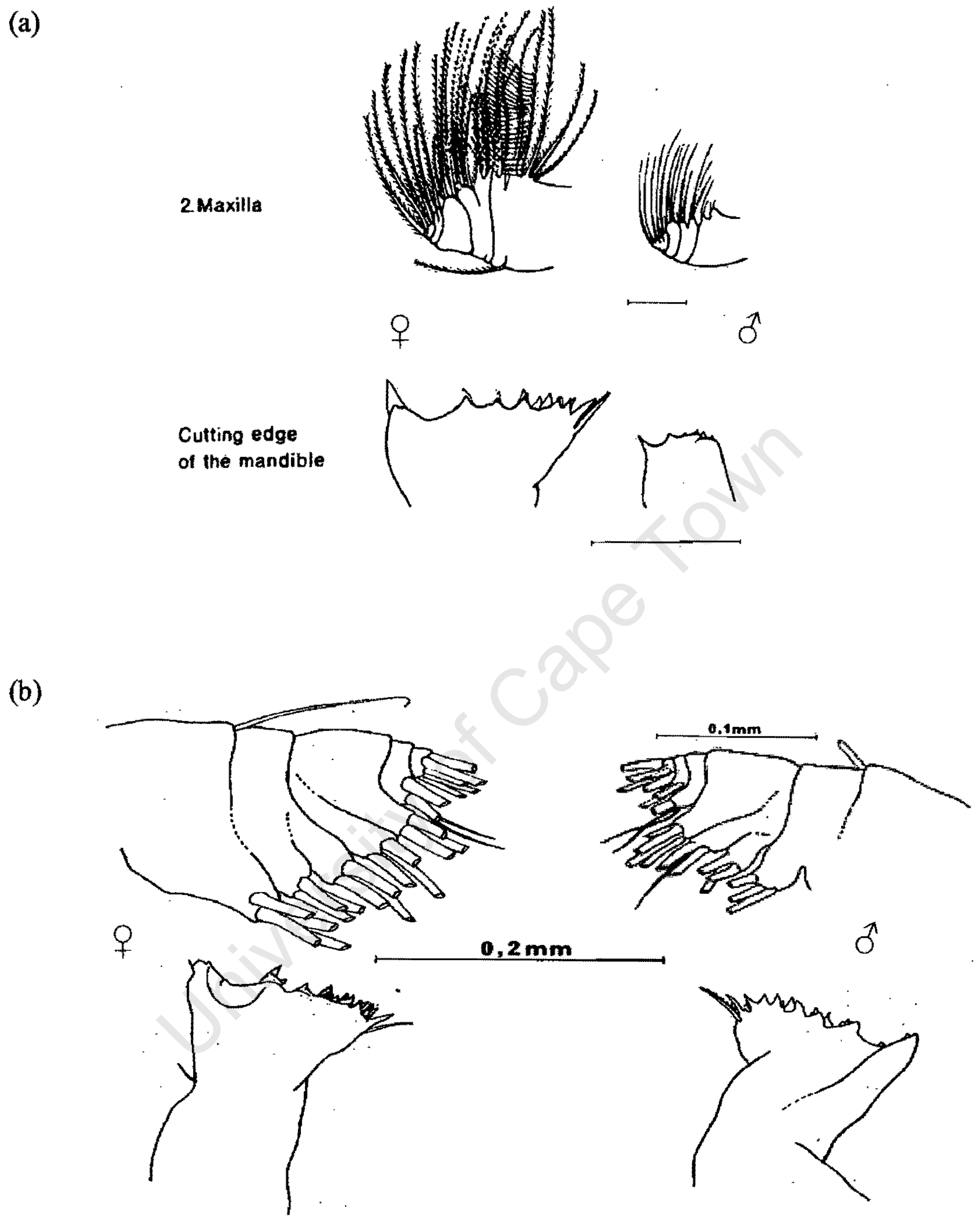


Figure. 1.9. (a) The structure of the second maxilla and the cutting edge of the mandible of female (left) and male (right) *C. carinatus* from the North-West African upwelling area. Scales are 0.1 mm. ♀ 2.3 mm, ♂ 1.9 mm (from Schnack 1982); (b) the second maxilla and mandible gnathobasis of female (left) and male (right) *C. agulhensis* from the Agulhas Bank (from De Decker *et al.* 1991).

populations removed up to 5% per day of the phytoplankton standing stock over the inner shelf area during spring (Timonin *et al.* 1992). The offshore populations, which mainly comprised C5s in water depths of more than 200 m, were not feeding and appeared to be in a state of diapause. In contrast to the Benguela upwelling region, grazing by the *C. carinatus* community in the upwelling area off Somalia can have a much greater impact on the phytoplankton, reaching up to 45% of the daily primary production in the nearshore area, near the centre of upwelling (Smith 1984). Grazing farther offshore at the same latitude (5°N) was only 6% of the daily primary production.

1.2.4. Life history strategies: vertical migration, population maintenance and diapause

The life history strategy of *C. carinatus* is thought to be relatively well-understood in several upwelling areas, including the southern Benguela, the northern Benguela, Equatorial West Africa and Somalia. Studies pertaining to vertical distribution, ontogenetic and diel vertical migration, population maintenance, lipid physiology and diapause have all contributed towards our knowledge of what Peterson (1998) suggests is the only copepod species to be truly adapted to upwelling systems.

The southern Benguela upwelling system

The diel vertical migratory behaviour of copepodite and adult *C. carinatus* in the southern Benguela upwelling system was investigated by Verheye (1991) and Verheye and Field (1992) at an anchor station in St Helena Bay. Ontogenetic layering was evident both day and night, with deeper distributions during the latter, and increasing amplitude of diel vertical migration (DVM) with increasing age (Fig 1.10; Verheye *et al.* 1992). The extent of DVM, as indicated by diel differences in weighted mean depth (WMD), was also linked to food availability, which varied according to the phase of upwelling. DVM was extensive when food was plentiful near the surface (following the advection of newly upwelled water), but suppressed when surface chlorophyll levels were low (during relaxation of upwelling). These results support suggestions of a trade-off between food intake and predation risk, as has been suggested by Huntley and Brooks (1982) amongst others, whereby animals spend more time in the surface layer at low food densities in order to reach satiation.

The migratory behaviour of *C. carinatus* was sexually differentiated, with females migrating more extensively than males, which remained at depth (Fig. 1.10; Verheye and Field 1992). Females were also segregated with depth according to their reproductive state, with ripe females tending to migrate

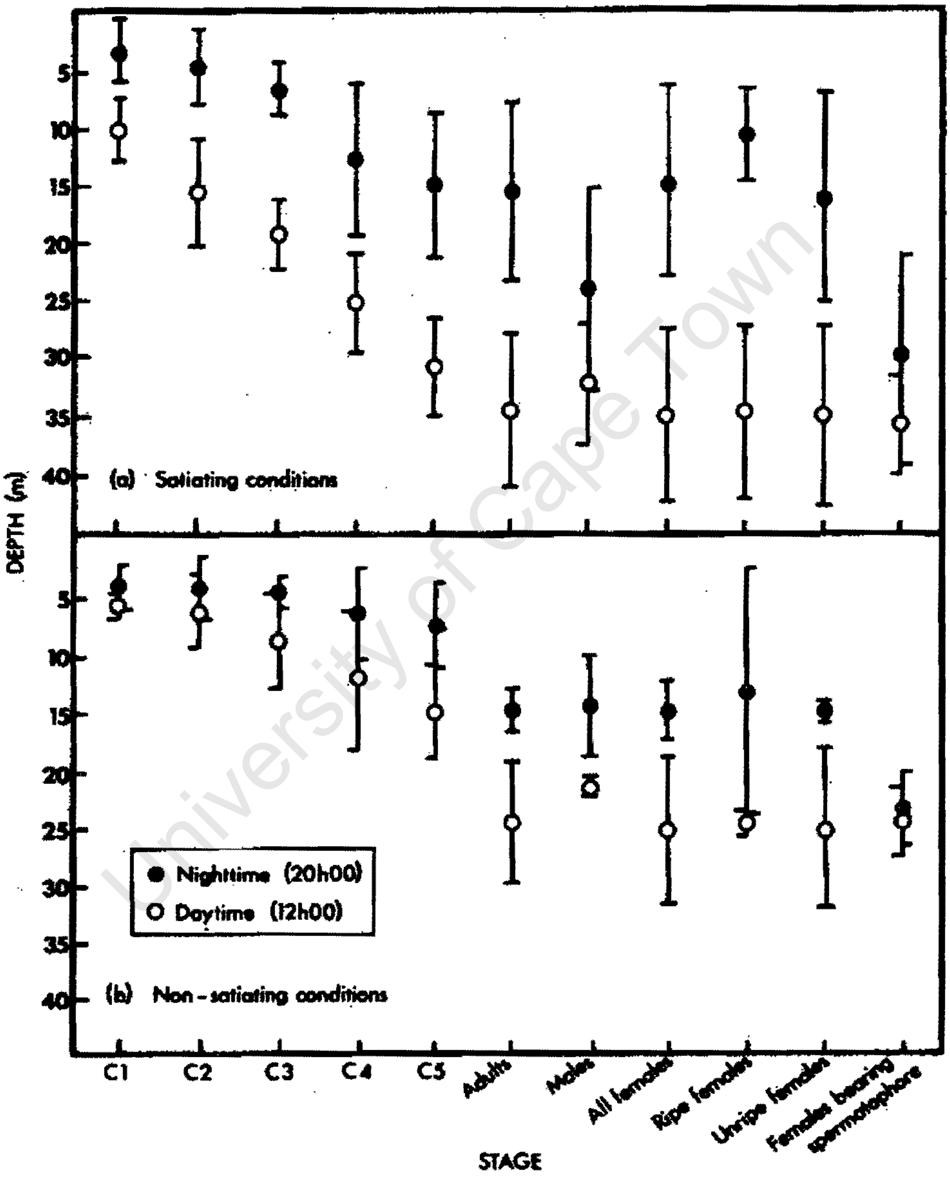


Figure 1.10. Diel variation in ontogenetic layering of *C. carinatus* under (a) satiating and (b) non-satiating feeding conditions. Data points are weighted mean depths. Error bars are 95% confidence limits (from Verheye *et al.* 1992).

more extensively into shallower water at night (WMD ≈10-15 m) than immature and spent females (WMD ≈17 m), particularly under conditions of abundant food. Spermatophore-bearing females, indicating recent mating, displayed limited DVM, remaining at depth (WMD ≈ 24-31 m) during nighttime. This behaviour led Verheye and Field (1992) to suggest that copulation occurs at depth during nighttime, which would render copulating pairs less conspicuous to visual predators. WMDs of *C. carinatus* eggs at night, when peak spawning occurs (Armstrong *et al.* 1991), varied between 3.0 and 7.1 m, with the eggs sinking to between 5.2 and 17.5 m during daytime.

Quarterly cross-shelf distribution patterns of juvenile and adult *C. carinatus* off Cape Columbine during 1974 were analysed by Verheye *et al.* (1991). All stages were found throughout the year, without the strong seasonal fluctuations in abundance usually encountered for that species at lower latitudes. Overall abundance was lowest (4 700 m^{-2}) in June, during winter, and greatest (11 200 m^{-2}) in December, concurrent with active upwelling. Older stages (C4 to adult) were most abundant in March (>2 000 m^{-2}) and least abundant in June (<1 000 m^{-2}), whereas younger stages (C1-C3) were most abundant in December (1 800-3 000 m^{-2}), with lower densities (<1 500 m^{-2}) in the other months sampled. Under quiescent conditions, such as in June, early juveniles were concentrated near the coast, whereas older stages were farther offshore (Fig. 1.11a; Verheye *et al.* 1992). During active upwelling, however, as was observed during October, the centre of abundance of young stages shifted offshore, whereas older stages tended to be most abundant near the coast (Fig. 1.11b).

Seasonal variations in cross-shelf distribution of the developmental stages are a function of ontogenetic layering and differential vertical migration (Verheye *et al.* 1991; 1992). These behavioural traits result in the developmental stages having different probabilities of exploiting the alongshore and onshore/offshore components of the water circulation system under different upwelling phases. During active upwelling, wind-driven Ekman transport advects surface-dwelling young stages northwards and offshore, where they may eventually accumulate and sink at the upwelling front (see Fig. 1.12; Verheye *et. al.* 1992). Those that sink may either be returned shoreward in an onshore subsurface compensation current, or transported northwards in the subsurface Columbine jet current or southwards in the bottom counter-current. Animals may also be transported into St Helena Bay. Strong offshore winds may transport young surface-dwelling copepodite stages farther offshore, where they may be transported northwards into the northern Benguela by the main shelf-edge jet. Older stages appear to be less affected by surface transport, as indicated by their predominance inshore during upwelling phases. As these stages migrate more extensively, they spend proportionally less time in the Ekman surface layer. Daytime residence at

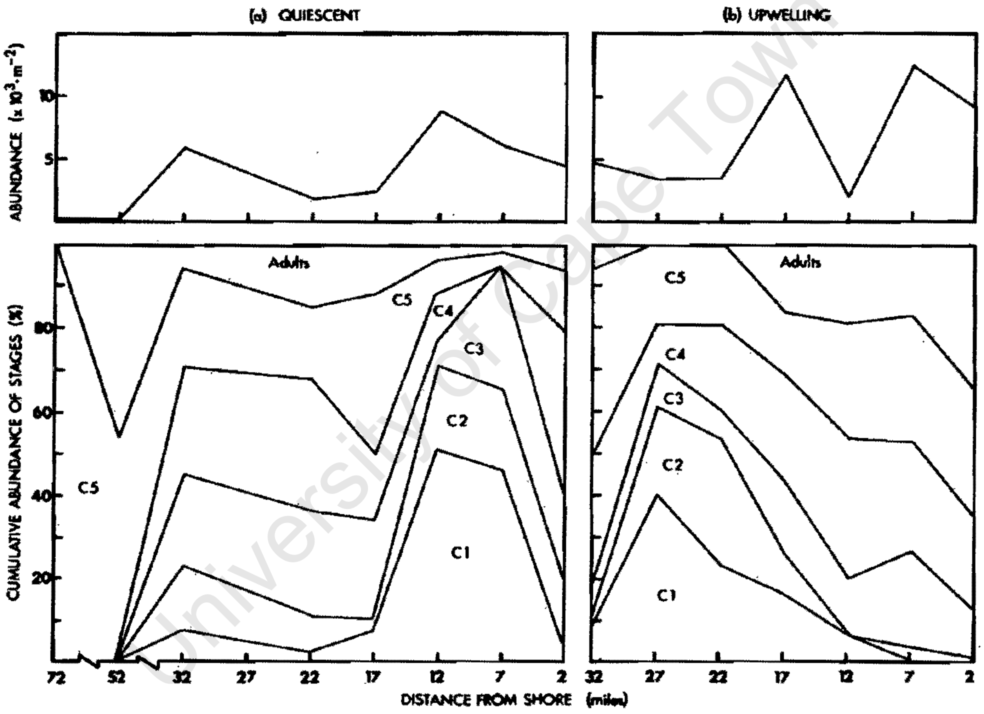


Figure 1.11. Cross-shelf distribution of *C. carinatus* life-cycle stages during (a) quiescent and (b) upwelling conditions off the Cape Columbine upwelling centre in 1974. Data are expressed as percentage occurrence of each stage per station (from Verheye *et al.* 1992).

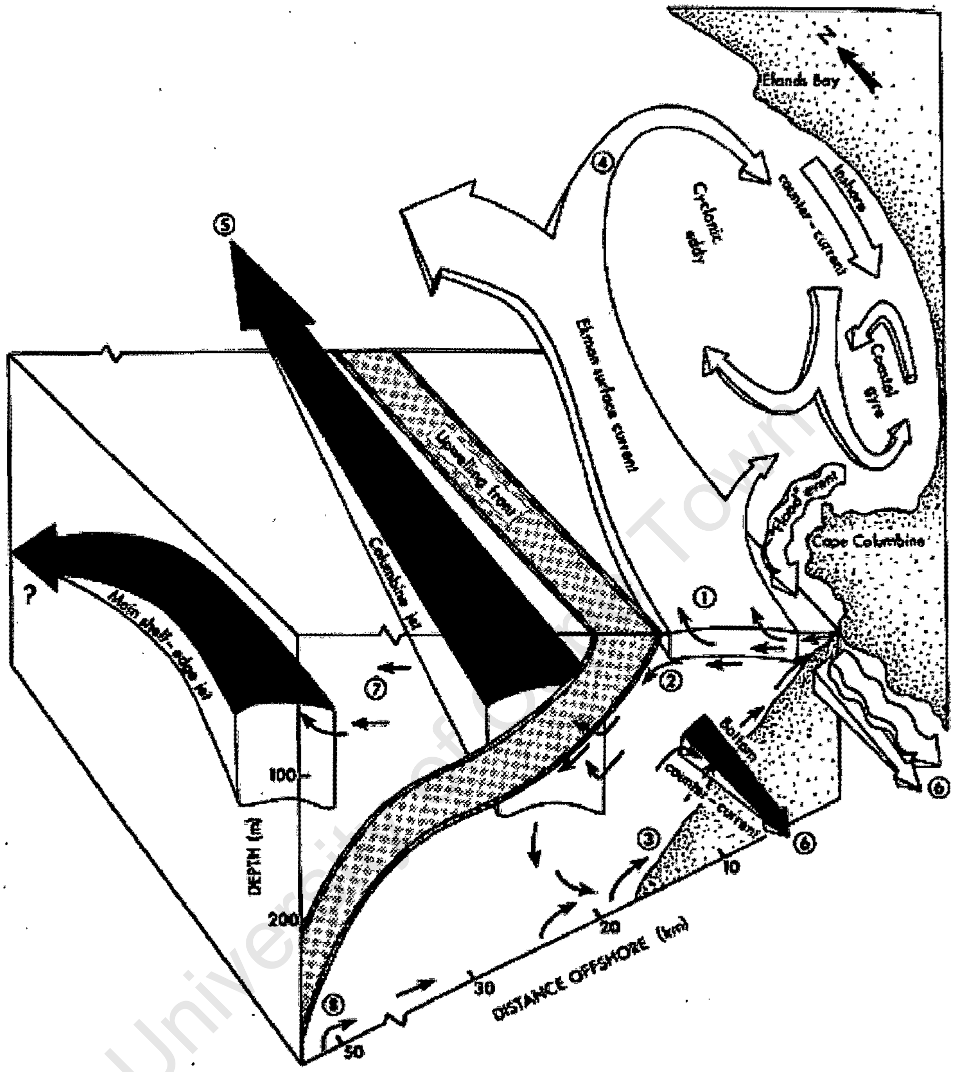


Figure 1.12. Conceptual model of the circulation system in the Cape Columbine - St Helena Bay region illustrating population maintenance and reseeding mechanisms of migrant copepods during coastal upwelling. The major components are (1) wind-driven Ekman transport of surface-dwelling young stages, (2) accumulation and sinking at the upwelling front, (3) onshore subsurface return flow of older stages, (4) entrainment into St Helena Bay, (5) northward transport, (6) surface and subsurface southward replenishment, (7) offshore advection under strong winds and northward transport, (8) reseeding of coastal populations with deep resting stages. Dark arrows represent subsurface currents, clear arrows indicate near-surface current features (from Verheye *et al.* 1992).

depth would also allow animals transported offshore to be returned with the onshore subsurface return flow during upwelling.

Verheye *et al.* (1991) suggested three life-history strategies that contribute to the perennial occurrence of *C. carinatus* in the southern Benguela upwelling region. The first is a permanently "active" component in the nearshore zone, where feeding and spawning continue. This includes retention areas such as St Helena Bay. The second strategy is a short-term "resting" phase, as C5s and adult females, on the outer shelf in 100-300 m of water (9-12°C), between upwelling bouts in winter. The third strategy is true diapause of pre-adults (C5) at great depth (>500 m, 4-6°C), which is supported by the observation of C5s in deep (>600 m) water by De Decker and Mombeck (1964) and Borchers and Hutchings (1986). With the onset of upwelling, these "overwintering" individuals are advected to the coast, where they mature and mix with the active nearshore component to start new generations. During March 1995, not one of >100 *C. carinatus* C5s collected near the surface at the end of a transect off the Olifants River in ~500 m water moulted during a 24 hr-incubation (A. Richardson, pers. comm.). These animals were very sluggish and easy to pick, suggestive of a lowered metabolic state. Whether they could have been either pre- or post-diapausal, or in some intermediate resting state, must remain speculative in the absence of supplementary information such as size, lipid content and respiration rate.

The northern Benguela upwelling system

In the northern Benguela ecosystem, as in the southern Benguela, *C. carinatus* is found throughout the year in the upper water column over the continental shelf and slope (Unterüberbacher 1964; Timonin *et al.* 1992). In addition to this active component of the population, comprising all developmental stages, there is a resting component dominated by diapausal C5s (90-95%) in deep (300-1 000 m) water offshore (Timonin *et al.* 1992; Arashkevich *et al.* 1996; Timonin 1997). Abundance of *C. carinatus* over the shelf varies considerably according to upwelling phase, from 4 000 m^{-2} during non-upwelling, to 93 000 m^{-2} during active upwelling, and up to 370 000 m^{-2} during relaxation (Arashkevich *et al.* 1996). The abundance of deep-living individuals near the slope in different seasons is relatively constant, from 4 000-9 000 m^{-2} (Timonin 1990, cited in Arashkevich *et al.* 1996). This suggests that there may be a permanent pool of diapausing animals throughout the year off the northern Benguela, in contrast to North-West Africa, where formation of diapausal stock is thought to occur once a year at the end of the upwelling season (Binet and Suisse de Sainte Claire 1975; Petit and Courties 1976).

During active upwelling, two pathways of assimilated energy have been distinguished amongst the surface population (Timonin *et al.* 1992; Arashkevich *et al.* 1996). The first is allocation of energy to structural growth and rapid gonad development, whereas the second is accumulation of lipid reserves. The first pathway is characteristic of C5s with low lipid content and advanced gonad development; these animals are anticipated to moult into adults and to produce the next generation. The second pathway is characteristic of C5s with high lipid content and small, under-developed gonads; these "fat" animals are thought to become the diapausal component of the population, descending into deeper layers at the end of the upwelling season. Diapausal C5s that descend into deep waters are characterized by considerably lower respiration rates, empty guts and low mobility (Arashkevich *et al.* 1996). High lipid contents and low respiration rates enable these copepods to survive extended periods without feeding. Kosobokova *et al.* (1988) calculated that C5s with a maximum lipid content of 50 µg following descent would be able to survive for 88-106 days, approximately three months.

Some C5s collected in deep waters (300-500 m) had low lipid contents and advanced gonads, as well as respiration rates double those of recently descended copepods, and similar to those of females from the same layer (Arashkevich *et al.* 1996). The biochemical composition, oil sac volume and gonad size of these C5s were also similar to those of the deep adults. This suggests that termination of diapause, and moulting of deep-living C5s into adults, takes place at depth, as demonstrated for *Calanus finmarchicus* (Miller *et al.* 1991) and several *Neocalanus* spp. (Conover 1988; Ohman 1987). Arashkevich *et al.* (1996) also suggest that there is an endogenous mechanism for the termination of diapause, with adults actively ascending from deep (>400 m) to upper layers (200-300 m), where they are upwelled towards the coast and join the active part of the population. This hypothesis is supported by the presence of recently moulted adults in the 100-300 m layer (Arashkevich *et al.* 1996) and many exuviae in the 300-500 m layer (Timonin *et al.* 1992).

Equatorial West Africa/Gulf of Guinea

The vertical distribution and population maintenance of *C. carinatus* copepodites at a coastal station (60 m) off Ivory Coast during the upwelling season is described by Binet and Suisse de Sainte Claire (1975). Stages were found progressively deeper with age, with maximum abundance of stages C1-C3 at 5 m, C4 at 18 m, and C5 at 31 m. Females were most abundant at 18 m and males at 31 m. There was a differential horizontal movement of the stages, with early stages advected alongshore from west to east by the surface (0-15 m) Guinea Current, and late stages and adults returned by the westward-flowing Ivorian undercurrent (Binet and Marchal 1993). The shallowness of the undercurrent and this pattern of vertical distribution are likely to account for the fact that phytoplankton and zooplankton seasonal cycles are in phase in the Guinea Current Large Marine Ecosystem, an observation not common to all eastern boundary current ecosystems. When the upwelling season has ended, and the surface waters become warmer, the relatively abundant and lipid-rich C5s descend to deep (>500 m) water where they overwinter in a diapausal state until the following upwelling season in June (Binet and Suisse de Sainte Claire 1975).

Somalia

The surface circulation in the north-western Indian Ocean is unique, because it reverses direction twice a year under the monsoonal wind regime (Baars *et al.* 1998). In summer, during the South-West Monsoon (SWM) from June to October, the circulation is clockwise, whereas in winter, during the North-East Monsoon (NEM) from November to March, it is counter-clockwise. During the SWM, strong upwelling occurs off Somalia and off the Arabian Peninsula. The upwelling zone off the east coast of Somalia is dominated by the fast (>300 cm s^{-1}; Smith 1982) Somali Current, which turns offshore at two sites, about 3-5°N and 7-9°N, causing upwelling at the northern sides of these locations. Between these two centres of upwelling is a large clockwise gyre known as the Great Whirl.

Separation of the Somali Current from the coast induces upwelling of deep water that is cold (17-22°C) and nutrient rich, resulting in blooms of large diatom species (Smith 1982). *C. carinatus* females and copepodites are abundant in areas of upwelling during the SWM, suggesting active reproduction, but are not found in surface waters (0-200 m) during the winter NEM. During onset of the SWM, there is a strong westward equatorial flow towards the Somali coast at depths that are occupied by overwintering stages (C5) off West Africa (500 and 700 m). Baars *et al.* (1998) found adults and sub-adults in all depth strata sampled, down to 600 m, although densities were much lower below 100 m. *C. carinatus* is found in surface samples only after upwelling is well established and are most abundant in the areas where the coldest, deepest water surfaces (Smith 1982). Females were rare or absent in water warmer than 20°C (Smith 1984). As currents bordering the areas of upwelling are swift, *C. carinatus* is forced out of the surface layer quickly, in a period of time less than one generation. Copepods are entrained in the Great Whirl, with an estimated transit time of 81 days (approximately 4 generations) at the surface, increasing with depth. The Great Whirl, which is probably the physical mechanism that maintains *C. carinatus* in the Somali area of the north-western Indian Ocean, covers thousands of kilometres and persists year round.

This gyre-like circulation is thought to remain at depth during the NEM, with a transit time of ~47 days at its core (600 m), and 235 days at 200 m. The circulation during both monsoons and the hydrographic structure are such that *C. carinatus* should not be lost to the interior of the north-western Indian Ocean, but rather should be maintained within 1000 km of the Somali coast most of the time. *C. carinatus* was absent from the upper 300 m during the NEM in 1993, in agreement with previous findings, but sub-adults were found in fairly uniform densities between 300 and 1000 m, and were also found between 1000 and 1500 m (Baars *et al.*1998). Stored lipid is thought to allow the C5s to survive at depth when the surface temperature warms, with the gyre eventually returning them to the coast (Smith 1982). Upwelling combined with ontogenetic migration brings the copepods to the surface in a region of blooming phytoplankton. The ontogenetic migration of *C. carinatus* in this region is thus essentially an annual life-history strategy and on the same temporal scale as the reversals in the monsoonal winds, and associated upwelling.

South-west Atlantic

Ramirez and Sabatini (2000) suggest that the life-cycle of *Calanoides* cf. *carinatus* in Argentinian waters involves strategies related to local upwelling events, although they have no evidence either to support or to rule out ontogenetic vertical migration or diapause in their region. This remains a topic for further research.

1.2.5. Modelling studies

Only one detailed modelling study of *C. carinatus* has been conducted to date. Plagányi *et al.* (1999) constructed a simple, one-dimensional population dynamics model to simulate temporal variability in *C. carinatus* biomass off the west coast of South Africa. Satellite-derived estimates of sea surface temperature and chlorophyll *a* concentration were used as primary inputs. A list of variables, initial values, parameters and model assumptions is shown in Table 1.2. The model simulates the way in which the effects of a pulse of primary production are successively damped as it passes through the various developmental stages (Figs 1.13a and b). There was close coupling between peaks in chlorophyll *a* and the abundance of the young stages, but a 6-8 day lag before any effect on the biomass of the older stages was apparent. If adverse food conditions lasted for more than ~16 days following an upwelling cycle, there was no peak in biomass of copepodites or adults. The model was robust with respect to most of its parameters, but showed greatest sensitivity to parameters that are difficult to determine empirically, such as predator-induced mortality rates.

Table 1.2. Summary of (a) variable names and their associated units, (b) base-case parameter values and (c) model assumptions (from Plagányi *et al.* 1999)

(a)

Description of variables	Notation	Units
Stage classes NI–NVI	*NAUP*	no. m^{-3}
CI–CIV	*COP1*	no. m^{-3}
CV	*COP2*	no. m^{-3}
Adults	*AD*	no. m^{-3}
Ripe females	F_r	no. m^{-3}
Unripe females	F_u	no. m^{-3}
Biomass of copepodite stages CI–CVI	T_{biom}	µg C m^{-3}
Sea surface temperature	*SST* (*T*)	°C
Average temperature over starvation period	T_{ave}	°C
Chlorophyll *a* concentration	*CHL*	mg m^{-3}
Net-chlorophyll (>10 µm)	$B_{>10}$	mg m^{-3}
... lagged net-chlorophyll concentration	$B_{>10(-1)}$	mg m^{-3}
Recent feeding history (days fed)	*FH*	days
Starvation index (days starved)	*SI*	days
Total development time	D_t	days

(b)

Parameter/model function	Notation	Units	Base-case value
Initial values			
Initial abundance estimate	N_1	no. m^{-3}	402
Population sex ratio	F:M ratio		9:1
Population age composition:	Prop. NI–NVI		0.30
	CI–CVI		0.42
	CV		0.13
	ADULTS		0.15
Model parameters/functions			
Grazing threshold	F_{crit}	mg Chl *a* m^{-3}	3
Net-chlorophyll fraction	$B_{>10}$	mg (Chl *a* > 10 µm) m^{-3}	*f*(Chl *a*)^a
Egg mortality rate	M_{egg}	day^{-1}	0.9
Predator-induced mortality rate	M_{pred}	day^{-1}	0.1
Starvation mortality (NI–NVI, CI–CIV)	M_{food}	day^{-1}	$f(\text{age}, T, FH, SI)^a$
Adult and CV starvation tolerance	M_{50}	days	$f(T)^a$
Fecundity	F_t	eggs female^{-1} day^{-1}	$f(B_{>10(1,-1)}, SI)^a$
Total development time	D_t	days	$f(T, SI)^a$
Proportion of individuals moulting per time step	$dev_{i,t}$	day^{-1}	$f(D_t, \text{age})^a$

^{a}Calculated as a function of the variables in parentheses, as described in the text.

(c) Major assumptions. The evidence in support of the various assumptions is indicated by the symbols in parentheses as follows: (–) poor; (+) fair and (++) good

1. Horizontal losses = horizontal gains (+)
2. The use of single depth-independent estimates of Chl *a* and *SST* provides an adequate description of ambient conditions experienced by copepods (+)
3. Development rates are food limited (++)
4. Individual egg production is independent of copepod numerical density (–)
5. The same grazing threshold operates for all ages (+)

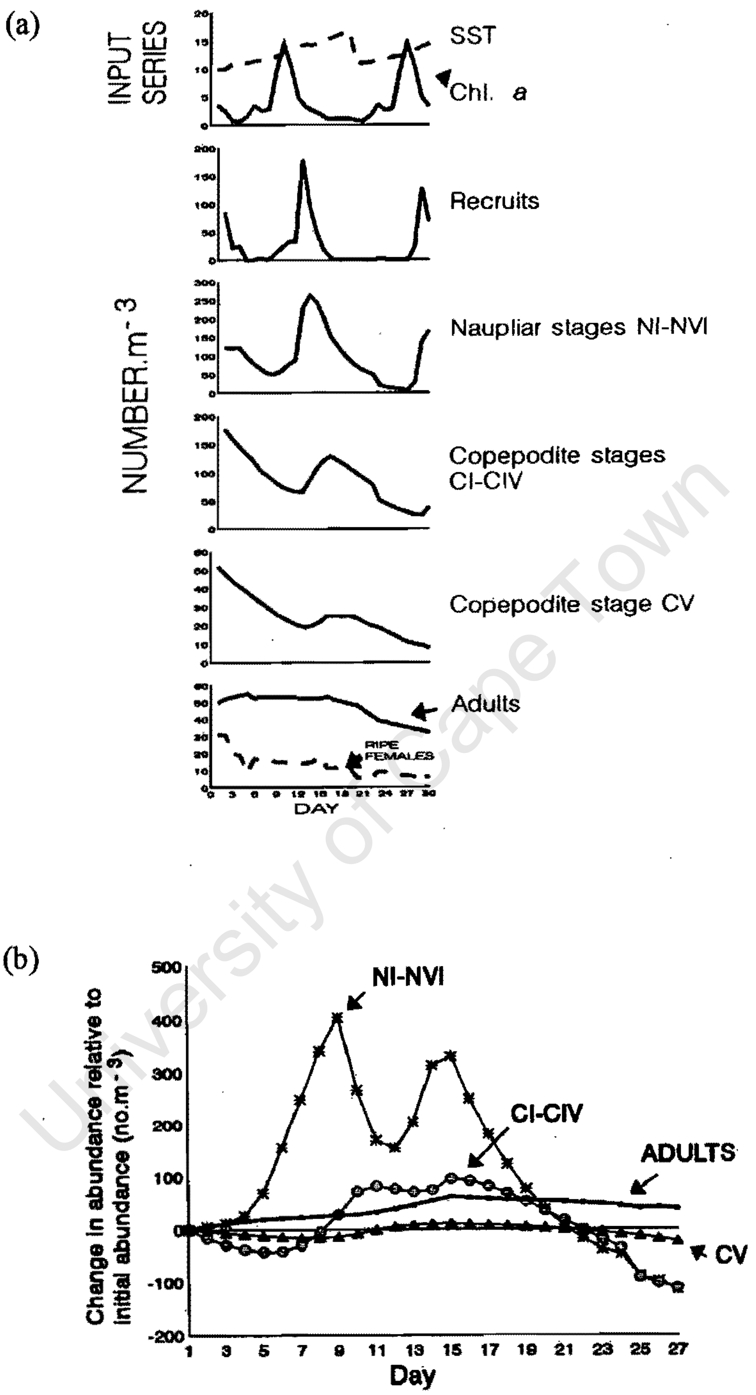


Figure 1.13. (a) Temporal changes in abundance of the various developmental stages of *C. carinatus* following a characteristic 12-day upwelling cycle; (b) Plots of model-predicted changes in abundance of the various developmental stages relative to their initial value (from Plagányi *et al.* 1999).

1.3. LITERATURE REVIEW FOR *CALANUS AGULHENSIS*

1.3.1. Taxonomy

The species known today as *Calanus agulhensis* was first recorded in South African waters by Cleve (1904), who identified it as *C. finmarchicus*. This nomenclature persisted for many years, and was used by De Decker (1964) in his comprehensive report on the marine Copepoda of South Africa. In later work, De Decker (1973, 1984) referred to this copepod as *C. finmarchicus sensu lato*, using this terminology to designate a form of uncertain taxonomic status, although showing morphological resemblance with both *C. australis* (Brodskii 1959) and *C. pacificus v. pacificus* (Brodskii 1959). The various sibling species in the Southern Hemisphere that derived from the original *C. finmarchicus* stock appeared to be concentrated on and near shelf areas (e.g. Australia, Tasmania, New Zealand, Chile, Argentina and Tristan de Cunha) but were rare in the open ocean. De Decker (1984) further suggested that it might represent a separate taxon (sic), different from the varieties of *C. australis* recorded in similar latitudes off Australia, New Zealand and South America, but also belonging to the *C. helgolandicus* species-group. Hutchings (1985) referred to the species as *C. finmarchicus v. australis*, whereas other workers used the name *C. australis* (Attwood and Peterson 1989; Peterson and Painting 1990; Peterson *et al.* 1990b). *Calanus agulhensis sp. nov.* (Figs 1.3c and d) was finally described in 1991 (De Decker *et al.* 1991), and this name shall be used throughout this thesis, even when referring to studies published before 1991.

1.3.2. Distribution and abundance

Cleve (1904) found *Calanus agulhensis* to be common south of the Cape Colony (extending eastwards from Cape Town to the Fish River at ~27°E), but rare to the west and east. This was later confirmed by De Decker (1964), who found a fairly abundant population consistently present over the Agulhas Bank, occurring only at certain times and in small numbers off the West Coast and KwaZulu-Natal. During a continuous survey of near-surface plankton from Durban to Cape Town in July 1961 (Fig. 1.5), *C. agulhensis* was collected from most areas along the cruise-track between the Bashee River (~29°E) and Cape Point, with adult females dominating the samples. Although found in adjoining regions, *C. agulhensis* showed a notable increase in abundance over the Agulhas Bank, and De Decker (1984) therefore considered the Agulhas Bank to be the centre of dispersal for this species (see Fig. 1.4b).

When Carter (1977) investigated the distribution of calanoid copepods in the Agulhas Current system off KwaZulu-Natal in the early 1970s (Fig. 1.6), he found *C. agulhensis* within the neritic community inhabiting the region inshore of the western boundary of the Agulhas Current. The species was rare off Durban, but occurred fairly frequently off Port Edward (~30.2°E) farther south, suggesting that it was transported eastward from the Agulhas Bank area into the KwaZulu-Natal region along the coast, counter to the Agulhas Current. De Decker (1984) also recorded an isolated occurrence of *C. agulhensis* southwest of Madagascar (Fig. 1.4a), confirming his suspicion that the Madagascar shelf could harbour this species. He suggested that its presence in this region would be due to advection by the East Madagascar Current, or by migrating eddies generated at its retroflection.

Extensive information on the distribution and abundance of *C. agulhensis* has been collected by Marine and Coastal Management (formerly the Sea Fisheries Research Institute) during biannual, hydro-acoustic pelagic fish stock assessment surveys since 1988. Data from the Spawner Biomass Surveys conducted in November/December each year have received the most attention so far. *C. agulhensis* accounted for 53-82% of the copepod biomass on the Agulhas Bank during November 1988, 1989 and 1990 (Verheye *et al.* 1994), with largest biomass in the midshelf region on the central Agulhas Bank, declining towards the east and west (Fig. 1.14). Biomass during 1988 and 1989 averaged ~1 g dry wt m^{-2} on the western Agulhas Bank, and ~5 g dry wt m^{-2} east of Cape Agulhas (Peterson and Hutchings 1995). Interannual variability of *C. agulhensis* abundance, standing stock and demographic structure on the Agulhas Bank between 1988 and 1993 is discussed by Hutchings *et al.* (1995b). Information on the distribution and abundance of all copepodite stages of *C. agulhensis* off the west and south coasts of South Africa during May/June and November/December from 1988 to 2000 is presented in Chapter 2.

Greatest densities of *C. agulhensis* during austral summer are often associated with a quasi-permanent ridge of cool, upwelled water south of Mossel Bay (Fig. 1.15a; Peterson *et al.* 1992; Boyd and Shillington 1994; Peterson and Hutchings 1995). Peterson and Hutchings (1995) suggested that at least four factors contribute to this pattern of distribution: (i) cyclonic circulation associated with the ridge, which probably enhances retention of copepod nauplii and juveniles; (ii) fast egg recruitment rates in the nearshore zone and downstream of the upwelling ridge; (iii) fast naupliar and juvenile growth rates due to enhanced food concentration within and around the upwelling ridge; and (iv) lower planktivorous fish density in this region compared to farther west. The generally smaller biomass of *C. agulhensis* on the western Agulhas Bank is thought to be a

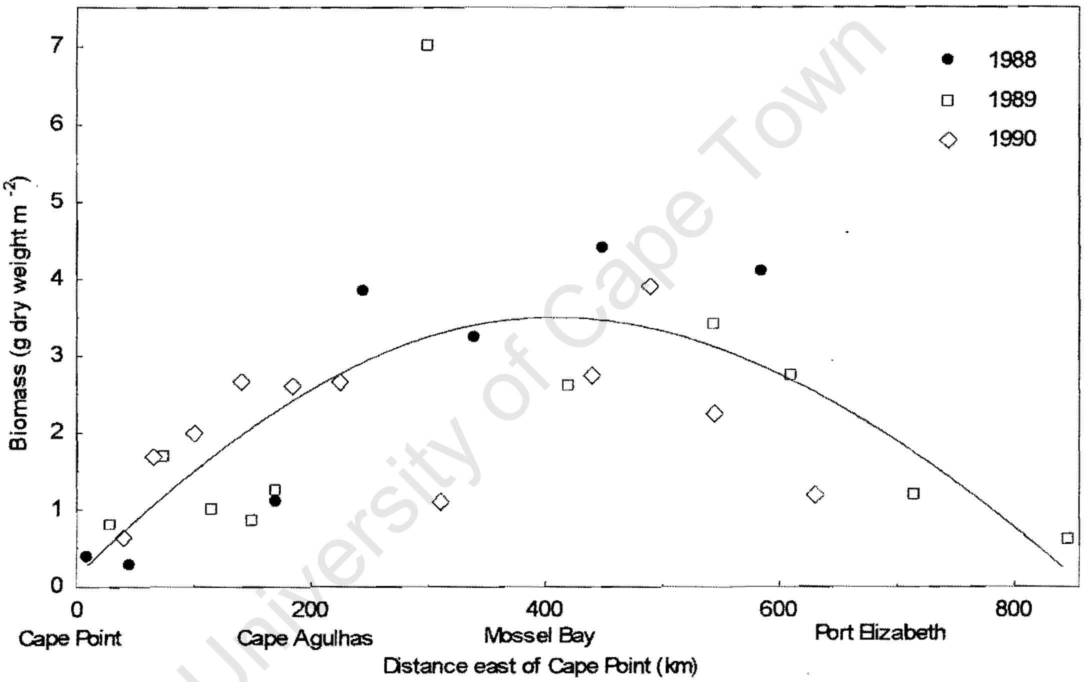


Figure 1.14. Longshore gradient in biomass (g dry wt m $^{-2}$) of *C. agulhensis* across the Agulhas Bank from November 1988 to 1990. Each data point is the mean biomass along a line of stations (from Verheye *et al.* 1994).

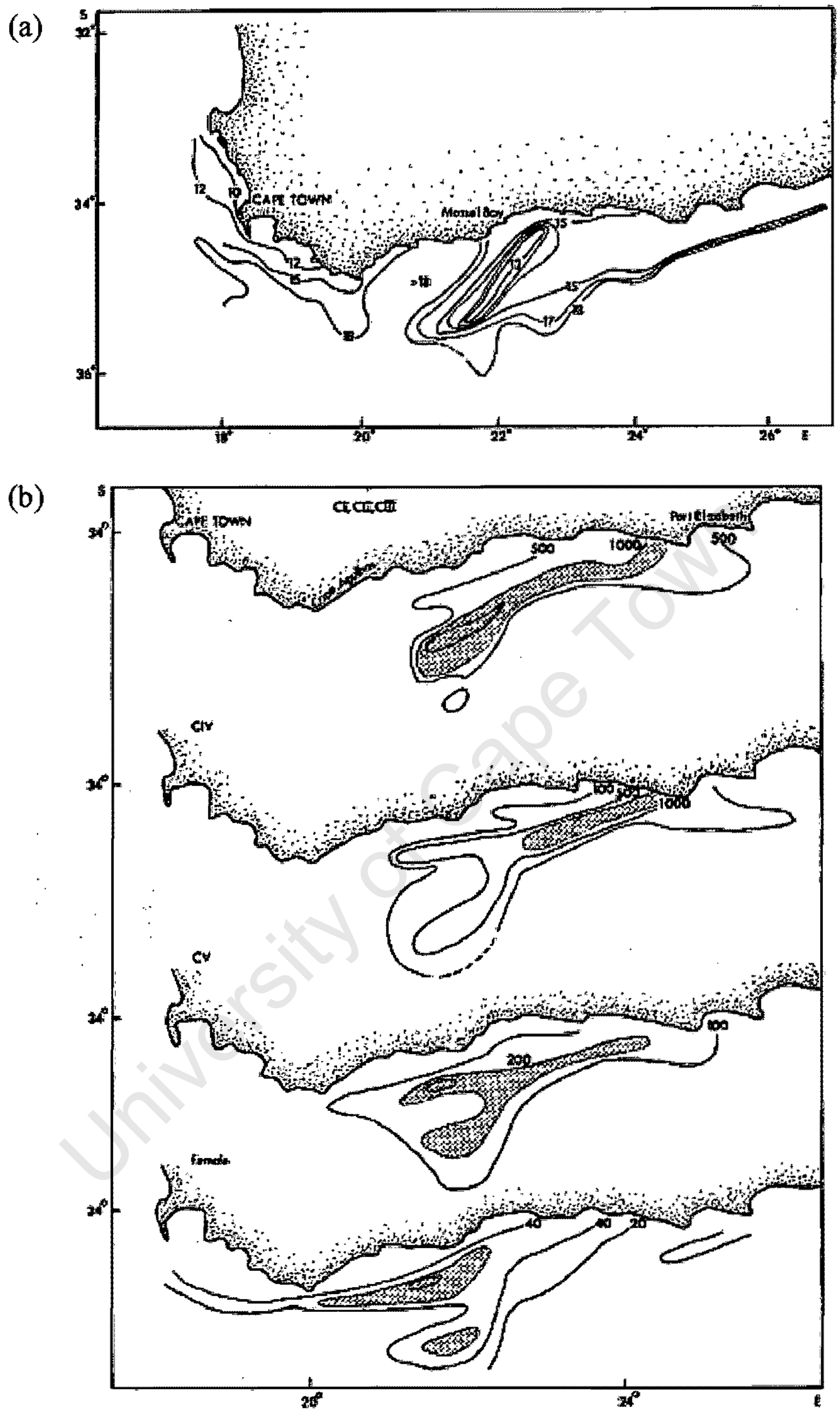


Figure 1.15.: (a) Temperature (°C) at 30 m over the Agulhas Bank during November 1989, indicating the "ridge" of cool upwelled water south of Mossel Bay (from Peterson *et al.* 1992); (b) Distribution (No.m^{-2}) of *C. agulhensis* developmental stages over the Agulhas Bank during November 1989 (from Largier *et al.* 1992).

result of predation by spawning anchovy (Peterson *et al.* 1992; Peterson and Hutchings 1995), which abound in this region during summer (Hampton 1987; Barange *et al.* 1999).

Although cyclonic circulation around the ridge is thought to enhance the local retention of *C. agulhensis*, it has been hypothesised that there is a net westward advection of *C. agulhensis* developmental stages across the Agulhas Bank, along the thermocline (Largier *et al.* 1992). Several observations support this hypothesis. First, there is a general movement of planktonic biota such as fish eggs and larvae westwards across the Agulhas Bank (Shelton and Hutchings 1982; Fowler and Boyd 1998). This advection continues north around Cape Point and onto the West Coast, where *C. agulhensis* is found in warm water along the shelf break (see Chapter 2). Second, largest densities of copepods on the western Agulhas Bank are generally found midshelf (Pillar 1986; Richardson *et al.* 1998), spatially dissociated from the inshore Chl *a* maximum (Brown 1992; Mitchell-Innes *et al.* 1999). This is thought to be a consequence of advective input of copepods from the adjacent central and eastern Agulhas Bank region, rather than *in situ* growth (Largier *et al.* 1992; Peterson *et al.* 1992). Last, the distribution of stages C1-C3 is usually centred on the cool upwelling ridge (Fig. 1.15b), whereas that of older stages C4-C6 is offset towards the west (Fig 1.15b; Largier *et al.* 1992; Peterson and Hutchings 1995). Moreover, when the ridge is absent, as in November 1990, the centre of distribution of *C. agulhensis* is displaced further westward (Hutchings *et al.* 1995b). This advection towards the west is thought to be a mechanism for replenishing the deficit in copepod stocks caused by anchovy predation on the western Agulhas Bank (Peterson *et al.* 1992).

1.3.3. Development, growth and production

The development of *C. agulhensis* in the laboratory has been well documented (Peterson and Painting 1990), and considerable effort has been directed towards understanding the effects of temperature and food availability on rates of somatic growth and egg production (Attwood and Peterson 1989; Hutchings *et al.* 1995b; Peterson and Hutchings 1995; Richardson and Verheye 1998, 1999). The effect of different periods of starvation on egg production of *C. agulhensis* and *C. carinatus* is compared in Chapter 4.

Development rates

The development rate of *C. agulhensis* in the laboratory was investigated by Peterson and Painting (1990). Animals were fed excess amounts of a mixture of the diatom *Thalassiosira weissflogii* and the flagellate *Tetraselmis suecica*. *C. agulhensis* developed from egg to adult in 20.3 days at

15.5°C and 16.0 days at 19.5°C (Fig. 1.7b). Egg hatching time was 21h. Stages N1 and N2 moulted quickly to N2 and N3 respectively (<1d per moult), but the N3s had a long stage duration (~3d at 15.5°C) before moulting to N4, which is thought to be due to the development of mouthparts. The range between first and last appearance of a stage was 4-7 days from N3 to C5. Most of the variability was evident at the N3 stage, with some added variability at the C5 stage. All adults produced were female. Isochronal development (Miller *et al.* 1977) was approximated from N4 to C4 at 15.5°C and from N4 to C5 at 19.5°C.

In general, *C. agulhensis* conforms to the common developmental pattern summarised by Landry (1983), whereby: (i) the first (non-feeding) naupliar stages (N1 and N2) have a short duration; (ii) the first-feeding naupliar stage (N3) is prolonged; (iii) the remaining naupliar stages and most of the copepodite stages (N4-N6, C1-C4) develop at the same rate; and (iv) the fifth copepodite stage is prolonged. However, growth of *C. agulhensis* does not adhere strictly to either the isochronal or the equiproportional rule (Corkett 1984).

The effect of temperature on somatic growth and egg production

A large number of moulting rate (~700) and egg production (~3000) experiments for *C. agulhensis* have been conducted during the biannual pelagic fish stock assessment surveys (1988 onwards), and during monthly South African SARP (Sardine and Anchovy Recruitment Programme) cruises between September and March 1993-1994 and 1994-1995 (Richardson and Verheye 1998, 1999). This represents one of the largest data sets of copepod growth rates from the field in the world, and has provided new perspectives on the debate about the relative importance of food and temperature to copepod growth rates (see Huntley and Lopez 1992; Kleppel *et al.* 1996).

Female growth rate, measured by egg production, suggests a dome-shaped relationship with (incubation) temperature in the field (Fig. 1.16a), with growth rates of ≤0.2 d^{-1} (≤60 eggs $♀^{-1}$ d^{-1}) for temperatures <13°C and >18°C, and up to 0.4 d^{-1} (120 eggs $♀^{-1}$ d^{-1}) between 13 and 18°C (Richardson and Verheye 1998). A similar relationship was found between somatic growth and temperature for the larger copepodite stages (C3-C5), with slower growth rates for temperatures <13°C and >18°C, and faster growth between 13 and 18°C. These relationships are probably a consequence of the dome-shaped relationship between chlorophyll *a* and temperature (Mitchell-Innes and Pitcher 1992; Pitcher *et al.* 1996; Richardson and Verheye 1998), whereby low chlorophyll *a* concentrations (and thus slow rates of copepod egg production – see below) are associated with both cool (<13°C) and warm (>18°C) temperatures, whereas water of temperatures between 13 and 18°C has higher chlorophyll *a* concentrations (Fig. 1.16b; Richardson and Verheye 1998), leading to faster rates of egg production. Growth rates of smaller stages do not show this dome-shaped relationship with temperature, probably because they are rarely food-limited (see next section).

The effect of food concentration and particle size on somatic growth and egg production

Peterson and Hutchings (1995) found that *C. agulhensis* growth rate, measured by moulting rates of stages N6-C5 and egg production rates of females, is correlated with the concentration of chlorophyll *a*. Similarly, Richardson *et al.* (2003) found a significant relationship between the daily weight specific growth rate of all copepodite stages (including females) and chlorophyll *a*. There is considerable evidence, however, to suggest that the larger stages are increasingly food-limited (Hutchings *et al.* 1995b; Peterson and Hutchings 1995; Richardson and Verheye 1999; Richardson *et al.* 2003). First, mean growth rate decreases by an order of magnitude from 0.55 d^{-1} for N6 to 0.05 d^{-1} for females, whereas maximum growth rate shows only a two-fold decrease, from 0.69 d^{-1} for N6 to 0.33 d^{-1} for females (Richardson and Verheye 1999). The small decrease in maximum growth rate is probably a consequence of allometry, whereas the more substantial decrease in mean growth rate implies that an environmental factor may be acting differentially on the growth rate of different stages. Second, large stages require more food to reach food-saturated growth rates compared with smaller stages (Fig. 1.17; Peterson and Hutchings 1995; Richardson and Verheye 1999). Third, large copepods only rarely grow at maximal rates, whereas small stages frequently grow at near-maximal rates (Peterson and Hutchings 1995; Richardson and Verheye 1999). Last, the optimal size of food particles is related to copepod size (Berggreen *et al.* 1988; Mauchline 1998), with larger copepods preferring larger phytoplankton cells. Large cells, such as diatoms, are only periodically abundant (usually at times of relaxation in upwelling), whereas small cells, such as flagellates, are omnipresent and ubiquitous (Richardson and Verheye 1999). Collectively, these findings suggest that the ambient food environment limits the growth rate of large *C. agulhensis* stages, with stage duration in the field increasing significantly for older stages. In contrast, small *C. agulhensis* stages are always growing at near-maximal rates. Vidal (1980) found that sub-optimal food concentration only slightly retarded the growth of young copepod stages, whereas older stages were more seriously affected. A consequence of progressive food limitation of *C. agulhensis* with increasing age is that juvenile growth is unrelated to female growth (Hutchings *et al.* 1995b; Richardson and Verheye 1999).

Field studies have also shown that *C. agulhensis* egg production and somatic growth rates are related to phytoplankton cell size. The somatic growth rates of all copepodites are positively related

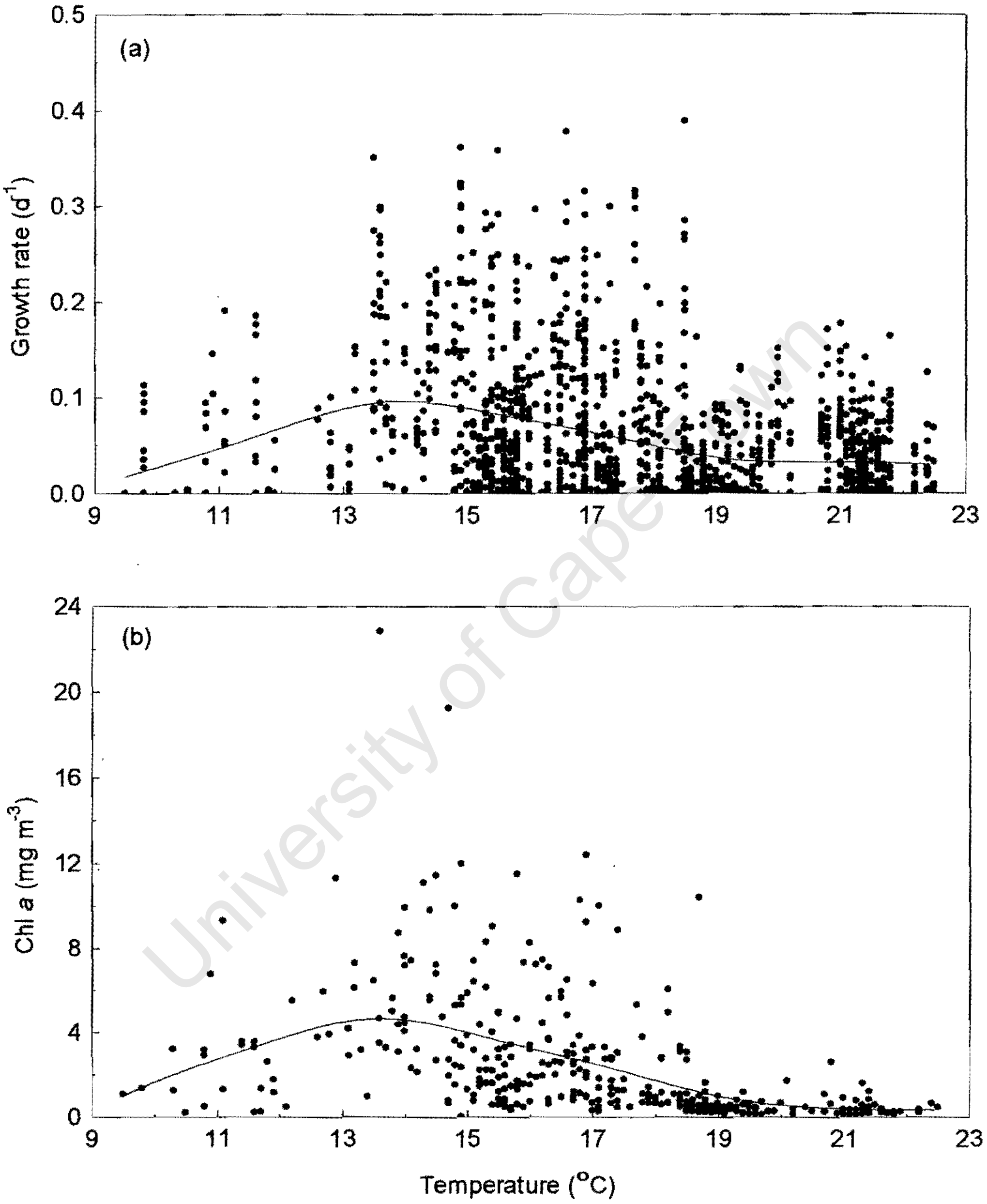


Figure 1.16. The dome-shaped relationship between (a) growth rate of female *C. agulhensis* and temperature, and (b) Chl *a* concentration and temperature. The curves were fitted using the distance-weighted least squares procedure (after Richardson and Verheye 1998).

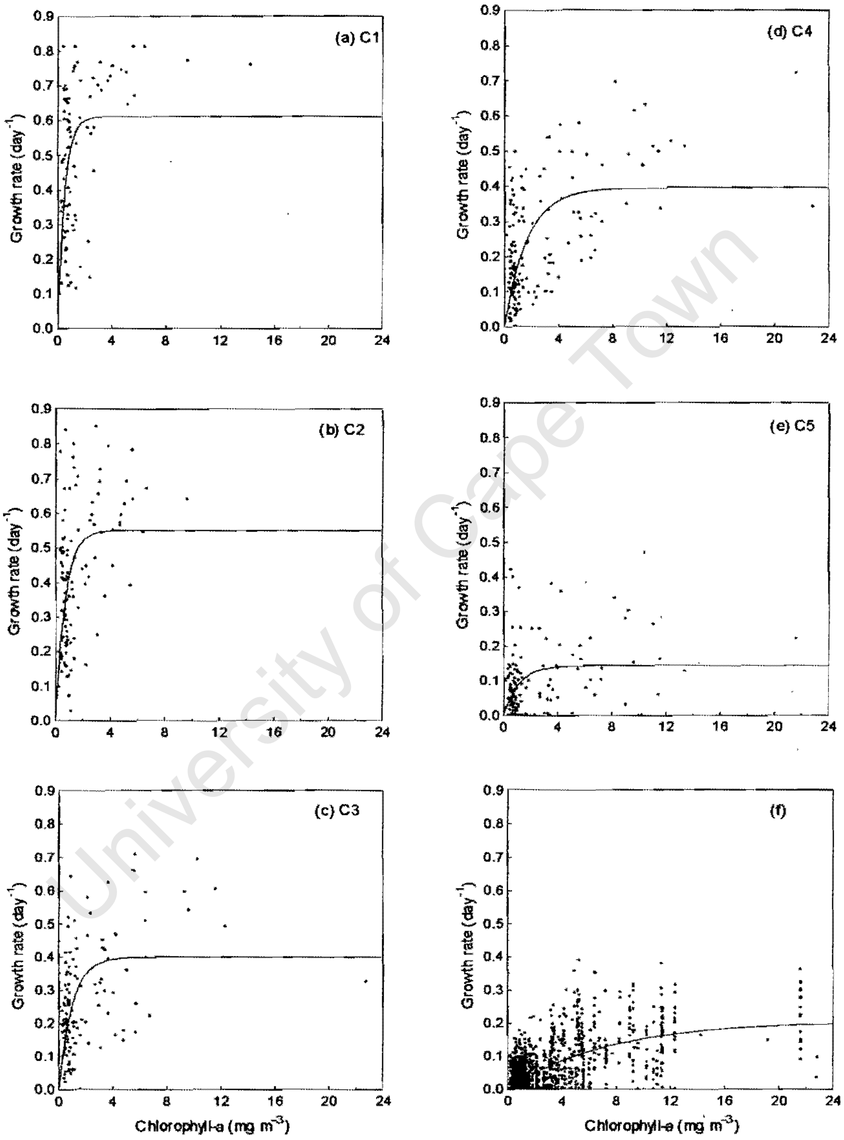


Figure 1.17. Growth rates of C1 to ♀ *C. agulhensis* in relation to chlorophyll *a*. Ivlev curves were fitted to the data (from Richardson and Verheye 1999)

to the proportion of cells >10 μm estimated spherical diameter (ESD) in size (Richardson and Verheye 1998). Moreover, Walker and Peterson (1991) observed an almost 7-fold improvement in daily egg production in areas dominated by large cells compared with areas dominated by small cells. Off the west coast of South Africa, chlorophyll *a* concentration is positively related to cell size (Mitchell-Innes and Pitcher, 1992), so that the effect of cell size on growth is confounded with the effect of cell concentration. Richardson and Verheye (1998) concluded that when small phytoplankton cells dominate the phytoplankton assemblage, growth of *C. agulhensis* in the field might not be limited by cell size *per se*, but by the typical concentrations of these cells (≤2 mg Chl *a* m^{-3}).

The effect of starvation on egg production

Attwood and Peterson (1989) investigated the effect of starvation on the egg production and lipid content of previously fed *C. agulhensis* females. Unstarved females had a lipid content of 16.7% dry weight. This declined exponentially during starvation, with 6.4 μg lipid (~20% of the lipid reserves) used during the first day without food. Egg production was inhibited within 24 h of starvation, terminating thereafter. Following starvation periods of 1-5 days, a recovery period of ~5 days of exposure to *ad libitum* food was required for egg production to return to normal. Following longer starvation periods of 7 and 9 days, extrapolation of the results indicated that egg production was likely to recover only after 7.7 and 16 days of excess food. These results, which are discussed further in Chapter 4, emphasise the important influence of feeding history on *C. agulhensis* egg production in a strongly pulsed food regime such as the southern Benguela upwelling region.

Measurements of production

Production rates of *C. agulhensis* on the Agulhas Bank during November are generally greater east of Cape Agulhas compared to the western Agulhas Bank (WAB), which is also the case for biomass (Hutchings *et al.* 1995b; Peterson and Hutchings 1995). Specific production rates (P/B) of *C. agulhensis* during November 1988 and 1989 ranged from 0.05 to 0.10 on the WAB, and from 0.15 to 0.23 on the central and eastern Agulhas Banks (CAB/EAB; Peterson and Hutchings 1995). Juvenile growth rates were slightly higher from 1990 to 1993, and mean daily P/B over the whole Agulhas Bank from November 1988 to 1993 ranged from 0.09 to 0.27 (Hutchings *et al.* 1995b); these showed no relationship with egg production, indicating that it is not possible to predict *C. agulhensis* population growth from egg production rates alone.

During November 1988 and 1989, *C. agulhensis* accounted for ~25% of copepod production on the WAB and 60% on the CAB/EAB, which is equivalent to 10 and 240 mg C m^{-2} d^{-1} respectively (Peterson and Hutchings 1995). Similar results for the WAB are given by Richardson (1989), who estimated production by *C. agulhensis* to comprise 11-25% of total copepod production during SARP 1 and 2 (1993/1994 and 1994/1995). Production by *C. agulhensis* on the WAB was considerably higher during the SARP study, however, ranging from 21.1 to 35.9 mg C m^{-2} d^{-1} during SARP 1, and from 30.6 to 44.4 mg C m^{-2} d^{-1} during SARP 2 (Richardson 1989). Production varied seasonally, but was always greater during November/December compared to September/October or January/February. Interannual variability of production appears to be due to shifts in the distribution of biomass and demography of *C. agulhensis* more than to variability of growth rates (Hutchings *et al.* 1995b); this is supported by Huntley and Lopez (1992), who also suggested that biomass is more variable than growth.

1.3.4. Feeding studies

A limited amount of work has been done on the feeding behaviour of *C. agulhensis*, and has mainly originated from field measurements off the west coast of South Africa. Additional feeding studies from both the West Coast and the Agulhas Bank, in which the effect of food abundance and food size as well as diel feeding rhythm are explored, can be found in Chapter 5.

Ingestion rates in relation to cell size and concentration

Field studies have shown that ingestion rates of *C. agulhensis* are related to both phytoplankton cell size and concentration. Individual ingestion rates by female *C. agulhensis* on the West Coast were four times faster on large cell-dominated food assemblages (373 ng Chl $♀^{-1}$ d^{-1}) compared to those dominated by small cells (93 ng Chl $♀^{-1}$ d^{-1}; Peterson 1989). Mean ingestion rate was also substantially slower (21 and 60 ng Chl $♀^{-1}$ d^{-1}) under low food conditions (<3 mg Chl m^{-3}) compared to high food conditions (347 and 432 ng Chl $♀^{-1}$ d^{-1}; >3 mg Chl m^{-3}) on both the West Coast and the Agulhas Bank respectively (Verheye *et al.* 1994). A maximum ingestion rate of 878 ng Chl $♀^{-1}$ d^{-1} was measured for *C. agulhensis* during summer (Verheye *et al.* 1992). Ingestion rate tends to increase ontogenetically, ranging from 95 ng Chl ind^{-1} d^{-1} for C3s to 324 ng Chl ind^{-1} d^{-1} for female *C. agulhensis* in the inshore region during autumn (Peterson *et al.* 1990b). No information has been published on feeding by males, but the similar size and structure of the male and female mandibles (Fig. 1.9b), and only slightly smaller male 2nd maxilla, suggests that they are likely to feed at greater intensities than *C. carinatus* males, and on a similar size-range to *C. agulhensis* females.

Feeding and vertical migration

Peterson *et al.* (1990b) investigated vertical migration and ingestion rates of C3, C4, C5 and female *C. agulhensis* at two anchor stations along a 100 nm transect off the Olifants River. All stages migrated vertically at the offshore station (190 m deep, 3.8 mg Chl *a* m^{-3} in the upper 20 m), but some remained in the upper water column throughout the day at the inshore station (80 m deep, 17.2 mg Chl *a* m^{-3} in the upper 20 m). A diel feeding rhythm was observed, with low gut pigment content during daylight hours, remaining fairly constant from the morning through to the afternoon, but increasing rapidly approximately one hour before sunset, as a result of high feeding rates by supposedly starved individuals. Gut fullness declined 2-3 hours after sunset, levelling off at up to 6 times higher than mean daytime values. *C. agulhensis* C3s, C4s and C5s ingested 20% of their ration during the daytime, while females ingested approximately 15% during the day. At the inshore station only 35% of the energy required for egg production was met by the ingestion of phytoplankton, suggesting omnivory.

In comparison to *C. carinatus*, very little is known about the vertical migratory behaviour of *C. agulhensis*, with only the one study described above from the West Coast. In Chapter 6 the diel and ontogenetically-based vertical migration of *C. agulhensis*, and to a lesser extent *C. carinatus*, is explored in relation to food conditions on the Agulhas Bank. No modelling studies have yet been conducted on *C. agulhensis,* except as a component of a simple mass-balance model of copepod biomass on the western Agulhas Bank (Richardson 1998), a development of earlier work by Peterson *et al.* (1992). A worthy prospect for the future would be to develop an individual-based model (IBM) of *C. agulhensis* population dynamics on the whole Agulhas Bank, linked to a regional three-dimensional hydrographic model of circualtion. Such a model, known as Plume, has already been developed for the southern Benguela (Penven *et al.* 2001), but its application to the Agulhas Bank is limited by the present eastern boundary of the model at 24°E. It is hoped that Plume will be extended farther east in the near future.

1.4 SUMMARY AND HYPOTHESES TO BE TESTED

C. carinatus has been relatively well studied in a number of upwelling regions, in particular the southern and northern Benguela, North-West Africa and Somalia, whereas *Calanus* is arguably the best studied, large calanoid genus in the world. Research conducted to date suggests that *C. carinatus* and *C. agulhensis* have a number of ecological similarities. Although diapause is a key feature in the life cycle of *C. carinatus* in areas where upwelling is seasonal (e.g. North-West Africa, Somalia), it does not appear to be as important (if at all) in the southern Benguela, where upwelling is perennial, although reduced in winter. Whereas diapause is common in *Calanus* congeners at higher latitudes, it has not been documented for *C. agulhensis*. Although seasonal studies such as those conducted on *C. carinatus* in the S. Benguela are lacking for *C. agulhensis*, both species seem to be relatively abundant during winter as well as during summer. Both species are regarded as predominantly herbivorous, with faster rates of egg production and growth when phytoplankton food is abundant and dominated by large cells. However, both species are often food limited, as demonstrated by slow growth rates of larger stages.

Some key differences between the two species include the faster development rate of *C. carinatus*, and its apparent ability to begin feeding at N1, in contrast to *C. agulhensis* which begins feeding at N3, in common with most other calanoid species. *C. carinatus* is able to accumulate greater lipid reserves, apparently double that of *C. agulhensis* under similar feeding conditions, and has greater maximum weight-specific rates of egg production when food is plentiful.

Off South Africa, *C. carinatus* is most abundant off the West Coast, in the southern Benguela upwelling regime, whereas *C. agulhensis* dominates the Agulhas Bank off the South Coast. Despite having separate areas of dominance, there appears to be considerable overlap in distribution of the two species. The fact that both species are commonly present in both regions but only abundant in one, suggests that each species is better adapted to the particular conditions characteristic of its core area, and is able to maintain life-cycle closure in this region. Key physical differences between the regions may pertain to temperature, stability or circulation, whereas critical biological characteristics may include food abundance (quantity) or suitable size or species composition (quality), as well as predation risk. The critical factor/s could manifest on either a spatial or temporal level, or possibly both, such as the abundance, frequency and persistence of phytoplankton blooms. These factors are likely to be either limiting or favourable to each species in terms of its characteristic physiology or behaviour, such as growth and egg production or vertical migration and population retention, and may result in competition for shared food resources.

The southern Benguela provides a cool and relatively food-rich environment in terms of phytoplankton. However, the pulsed nature of wind-driven upwelling is likely to result in considerable variability in food abundance, as well as the potential for advective losses from the system. There is also a high risk of predation by recruiting pelagic fish during winter. In contrast, the Agulhas Bank provides a warm, retentive environment, relatively stable in summer, but characterized by wind mixing in winter. The abundance of phytoplankton is relatively low but consistent compared to the West Coast; a consequence of this low phytoplankton abundance is a greater proportion of small cells. Predation risk by pelagic fish is greatest during the summer spawning season, but invertebrate predation is considered to be a lower risk compared to the West Coast.

The differences in the core habitats occupied by the two copepod species present a number of hypotheses to be tested in order to explain the differences in their relative abundance. From a broad perspective, these hypotheses are that *C. carinatus* and *C. agulhensis* (1) have different thermal preferences or tolerances, (2) have different dietary requirements in terms of food abundance, size and/or type, (3) are adapted to different scales of temporal variability of food availability, and (4) have different vertical migratory behaviour and/or population retention mechanisms. More specifically, the hypotheses are as follows:

Hypothesis 1: *C. carinatus* egg production is inhibited by warm temperatures typical of the Agulhas Bank; conversely, *C. agulhensis* egg production is reduced at cooler temperatures characteristic of the Benguela upwelling region.

Effect: Egg production by *C. carinatus* is greater than that by *C. agulhensis* at cool temperatures; conversely, egg production by *C. agulhensis* is greater than that by *C. carinatus* at warm temperatures.

Test: Measure egg production at different temperatures (9-21°C) in the laboratory under non-limiting food conditions.

Hypothesis 2: *C. agulhensis* can attain satiation at a lower food concentration than *C. carinatus*.

Effect: *C. agulhensis* requires less food than *C. carinatus* to achieve maximum rates of egg production, thus *C. carinatus* will be at a competitive disadvantage on the Agulhas Bank.

Test: Compare food concentrations in the ocean required for both species to achieve satiation (and maximum rates of egg production).

Hypothesis 3: *C. carinatus* feeds less efficiently than *C. agulhensis* on small cells typical of low food concentrations associated with the Agulhas Bank.

Effect: *C. carinatus* ingestion and egg production rates are low compared to *C. agulhensis* when the phytoplankton food is dominated by small cells, thus *C. carinatus* is energetically disadvantaged on the Agulhas Bank.

Test: Measure ingestion and egg production rates over a range of food sizes in the ocean, including small- (<10 μm) cell-dominated food types.

Hypothesis 4: *C. carinatus* is better adapted to the pulsed food environment characteristic of the southern Benguela upwelling region; conversely, *C. agulhensis* is better adapted to more consistent food availability typical of the Agulhas Bank.

Effect: Egg production by *C. agulhensis* recovers more slowly, or does not recover, from intermittent food availability characteristic of a pulsed upwelling system, thus *C. agulhensis* is energetically disadvantaged on the West Coast.

Test: Measure recovery of egg production by both species in the laboratory following different periods of starvation (1-9 days).

Hypothesis 5: *C. agulhensis* does not display ontogenetically-based diel vertical migratory (DVM) behaviour on the Agulhas Bank.

Effect: *C. agulhensis* may be unable to use DVM as a retention mechanism on the West Coast, as has been demonstrated for *C. carinatus*, and thus would be prone to substantial advective loss from the Benguela upwelling system.

Test: Explore DVM of *C. agulhensis* on the Agulhas Bank, and explore DVM of both species under the same conditions. This hypothesis is also relevant to potential differences in diel feeding behaviour.

The hypotheses regarding the effect of temperature (Hypothesis 1) and consistency of food availability on egg production (Hypothesis 4) were tested in the laboratory. The advantage of laboratory studies is that other variables likely to affect egg production are controlled as far as possible, such as the provision of non-limiting food in the temperature experiments and constant temperature in the starvation experiments, as well as recent feeding history through acclimation of copepods to laboratory conditions. Drawbacks of such laboratory experiments include the use of algal monocultures that are not representative of natural food assemblages in the ocean, repeated handling of animals during acclimation, and extended confinement in containers. Hypotheses 2 and 3 (effects of food concentration and food size) were tested in the field, which has the advantages of providing realistic feeding conditions on natural food assemblages, and less handling of the animals. The main disadvantage is that variables other than those being tested can rarely be controlled, in particular feeding history. However, generalized additive models are a useful and novel technique for exploring the relative importance of multiple variables in these situations, particularly for non-linear relationships.

CHAPTER 2

Distribution and abundance of *Calanoides carinatus* and *Calanus agulhensis* off South Africa

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2.1 INTRODUCTION

To date, relatively little information has been published on the large-scale distribution and abundance of the two dominant, large copepod species, *Calanoides carinatus* and *Calanus agulhensis*, off the coast of South Africa. De Decker (1964, p. 17) described *C. carinatus* as being present "in gigantic swarms over the whole length of the Benguela Current as far as Angola" during summer. Verheye *et al.* (1991) noted that *C. carinatus* may be found close to the South African west coast throughout the year, although less abundantly during winter when upwelling is minimal. Greatest densities of 2 600 ind. m^{-3} were recorded off the Cape Peninsula during the upwelling season, and 1 565 ind. m^{-3} in St Helena Bay during autumn (Verheye *et al.* 1992). *C. carinatus* has also been reported to be common off the South Coast (De Decker 1964), attaining high relative abundance in the inshore/Agulhas Current boundary region off Durban (Carter 1977), particularly during late spring.

Early investigations by Cleve (1904) and De Decker (1964) indicated that *C. agulhensis* was common off the South Coast, and rare off the West and East Coasts. De Decker (1984) considered the Agulhas Bank to be this species' centre of dispersal. This was confirmed by later surveys conducted by Marine and Coastal Management (formerly Sea Fisheries Research Institute) from 1988 onwards. *C. agulhensis* was found to account for 53-82% of the copepod biomass captured with a 200-µm mesh net on the Agulhas Bank during three November surveys (1988-1990; Verheye *et al.* 1994), with largest biomass in the midshelf region on the central Agulhas Bank, declining towards the east and west. Greatest densities of *C. agulhensis* during summer have been associated with a quasi-permanent ridge of cool, upwelled water south of Mossel Bay (Peterson *et al.* 1992; Boyd and Shillington 1994; Peterson and Hutchings 1995; see also Fig. 1.15 in Chapter 1). Cyclonic circulation associated with the ridge is thought to enhance the local retention of *C. agulhensis*, in particular the nauplii and juveniles (Peterson and Hutchings 1995).

This chapter describes the distribution and abundance of *C. carinatus* and *C. agulhensis* off the west and south coasts of South Africa during 28 summer and winter surveys conducted by Marine and Coastal Management between 1988 and 2000. The distributions of the various stages of *C. agulhensis* on the Agulhas Bank in November 1988 and November 1989 were previously described in Peterson and Hutchings (1995) and Largier *et al.* (1992) respectively. Additional samples collected on the West Coast during November 1988 were analyzed for the present study, and data collected from the South Coast were re-analyzed to be consistent with subsequent years' analyses.

2.2 MATERIAL AND METHODS

2.2.1 Data collection

Sample material and environmental data were collected on 28 cruises conducted by Marine and Coastal Management off the west and south coasts of South Africa between 1988 and 2000 (Table 2.1). Most of the data were collected during routine hydro-acoustic stock-assessment surveys of pelagic fish (anchovy, sardine and round herring) during November/December (late spring/early summer, referred to henceforth as the "summer surveys") and May/June (late autumn/early winter, referred to henceforth as the "winter surveys"). Additional data were collected in January 1992 (mid-summer) during the Agulhas Bank Boundary Processes (ABBP) cruise. The position of all stations sampled is indicated in Fig. 2.1. The summer surveys (shown in red), which are scheduled to coincide with peak spawning by anchovy, usually extend from Hondeklipbaai on the West Coast to Port Alfred on the South Coast. The winter surveys (shown in blue), which are used to estimate the biomass of recruiting fish, usually include the entire west coast shelf south of the Orange River mouth, and extend as far as Cape Agulhas on the South Coast, although in 1994 the survey extended as far eastward as Port Alfred. The ABBP cruise (shown in green) comprised a number of transects crossing the Agulhas Bank and continental shelf edge between Cape Town and 29°E on the East Coast.

At each station, fluorescence profiles were obtained using a Chelsea Instruments Aquatracka MkIII attached to a Magnum rosette sampler fitted with six 18-l bottles. Discrete water samples for chlorophyll analyses were collected from the surface and the depth of maximum fluorescence; these were used to calibrate the *in situ* water column fluorescence profiles after each cruise (B. Mitchell-Innes, Marine and Coastal Management, unpublished data). Chl *a* concentration was measured fluorometrically using a Turner Designs Model 10-000R fluorometer (Parsons *et al.* 1984). Water samples were concentrated onto Whatman GF/F filters, which were extracted in 90% acetone for 24 h at -20°C in the dark, and then centrifuged for 12 minutes at 1 000 r.p.m. Fluorescence was measured before and after acidification with 10% HCl to correct for phaeopigments. High fluorescence values were adjusted for quenching (B. Mitchell-Innes, Marine and Coastal Management, pers. comm.).

Table 2.1. List of cruises on which data were collected.

Month	Vessel & Voyage No.	Cruise Dates (dd/mm/yy)	Cruise Name
June 1988	Africana 065	27/06/88 - 18/07/88	Anchovy & Sardine Recruitment Survey
November 1988	Africana 068	18/11/88 - 15/12/88	Pelagic Fish Spawner Biomass Survey
June 1989	Africana 073	08/06/89 - 22/06/89	Anchovy & Sardine Recruitment Survey
November 1989	Africana 078	07/11/89 - 30/11/89	Pelagic Fish Spawner Biomass Survey
May 1990	Africana 081	02/05/90 - 11/05/90	Anchovy Early Recruitment Survey
June 1990	Africana 083	21/06/90 - 04/07/90	Anchovy & Sardine Recruitment Survey
November 1990	Africana 087	06/11/90 - 30/11/90	Pelagic Fish Spawner Biomass Survey
May 1991	Africana 092	07/05/91 - 24/05/91	Anchovy & Sardine Recruitment Survey
November 1991	Africana 097	07/11/91 - 03/12/91	Pelagic Fish Spawner Biomass Survey
January 1992	Africana 099	07/01/92 - 28/01/92	Agulhas Bank Boundary Processes Cruise
May 1992	Africana 103	12/05/92 - 20/05/92	Anchovy & Sardine Recruitment Survey
November 1992	Africana 108	05/11/92 - 02/12/92	Pelagic Fish Spawner Biomass Survey
May 1993	Africana 112	21/05/93 – 06/06/93	Anchovy & Sardine Recruitment Survey
November 1993	Africana 117	09/11/93 - 03/12/93	Pelagic Fish Spawner Biomass Survey
May 1994	Africana 121	03/05/94 – 26/05/94	Anchovy & Sardine Recruitment Survey
November 1994	Africana 126	14/11/94 - 07/12/94	Pelagic Fish Spawner Biomass Survey
June 1995	Algoa 023	10/06/95 – 26/06/95	Anchovy & Sardine Recruitment Survey
October/	Algoa 030	20/10/95 - 29/10/95	Pre-Spawner Biomass Survey
November 1995	Africana 132	13/11/95 - 04/12/95	Spawner Biomass Survey
June 1996	Algoa 039	03/06/96 - 25/06/96	Anchovy & Sardine Recruitment Survey
November 1996	Africana 137 Algoa 045	21/10/96 - 03/11/96 05/11/96 - 16/11/96	Pelagic Fish Spawner Biomass Survey
May 1997	Africana 145	15/05/97 – 31/05/97	Anchovy & Sardine Recruitment Survey
November 1997	Africana 148 Algoa 051	28/10/97 - 07/11/97 14/11/97 - 09/12/97	Pelagic Fish Spawner Biomass Survey
June 1998	Algoa 056	18/5/98 – 8/6/98	Anchovy & Sardine Recruitment Survey
November 1998	Algoa 059	03/11/98 – 07/12/98	Pelagic Fish Spawner Biomass Survey
May 1999	Africana 153	10/05/99 – 31/05/99	Anchovy & Sardine Recruitment Survey
November 1999	Algoa 068	01/11/99 – 06/12/99	Pelagic Fish Spawner Biomass Survey
May 2000	Algoa 074	17/05/00 – 01/06/00	Anchovy & Sardine Recruitment Survey
November 2000	Algoa 087	01/11/00 – 06/12/00	Pelagic Fish Spawner Biomass Survey

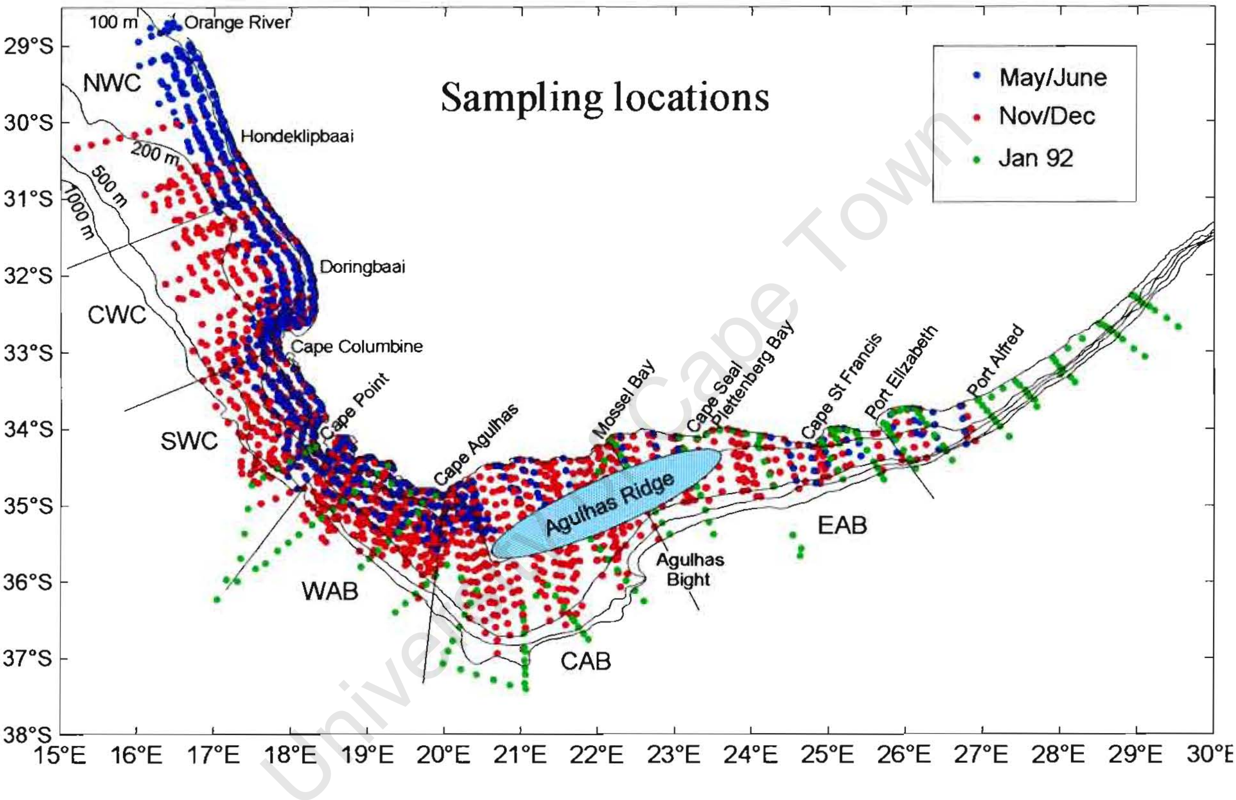


Figure 2.1. Map showing station positions from all 28 surveys between July 1988 and November 2000, as well as areas and locations mentioned in the text, and the approximate position of the Agulhas Ridge.

Copepods were collected from the upper 200 m using a vertically hauled Bongo net (0.57-m diameter, 200-µm mesh) equipped with a General Oceanics flowmeter and pressure and temperature sensors. Samples were preserved in 5% buffered formalin. In the laboratory, samples were allowed to settle in a graduated measuring cylinder for 24 h and then diluted to 10 times the settled volume of copepods. Two 2-ml sub-samples were removed using a modified Stempel pipette, and all *C. carinatus* and *C. agulhensis* were counted and identified to stage. A 200-µm mesh is adequate to collect quantitatively all copepodite stages of *C. carinatus* (Verheye 1991), and thus also the larger and more robust copepodite stages of *C. agulhensis* (see Table 1.1 in Chapter 1 for length measurements and dry weights of both species). For the first 5 years of the time-series (1988-1992), stages C1-C3 of both species were not differentiated, but were pooled into single categories called "juvenile *C. carinatus*" and "juvenile *C. agulhensis*". Although stages C1-C3 were differentiated in the samples collected during subsequent years (1993 onwards), as well as those from November 1988, they were combined for the data analyses.

Geographical Information System (GIS) maps of mean abundance (No.m^{-2}) of all stages of both species were provided by L. Drapeau (Institut de Recherche pour le Développement and Marine and Coastal Management) using ArcView Version 3.1. These were based on abundance data from all but two (January 1992 and May 2000) of the cruises listed in Table 2.1. Contour maps of temperature, Chl *a* concentration and copepod abundance as well as current vector maps (when data were available) were plotted using Surfer Version 7.00. Interpolation was performed using Kriging, and contour levels used in the maps of copepod abundance were selected to highlight the greatest concentrations of each stage; relatively low densities may not be indicated. Contour maps of the temperature at 30 m were used to detect the semi-permanent cool-water feature south of Mossel Bay, referred to as the Agulhas Ridge, which can be roughly identified by the 17°C isotherm occurring within 30 m of the surface (Boyd and Shillington 1994).

2.2.2 Definition of geographical areas

Cape Point is commonly used to separate the South African coastline into the West and South coasts, and each coast has been further divided into 3 regions based primarily on convention, but also according to physical and/or biological characteristics (Fig. 2.1 and Table 2.2). The three regions on the West Coast correspond to separate upwelling cells as defined by Shannon and Nelson (1996): the Cape Peninsula cell in the south, referred to here as the South West Coast (SWC), extending from Cape Point to Cape Columbine; the Columbine cell farther north, designated the Central West Coast (CWC), extending from Cape Columbine to 31°S; and the Namaqua cell in the extreme north, designated the North West Coast (NWC), extending from 31°S to the mouth of the Orange River. The South Coast is divided into three areas referred to as the Western Agulhas Bank (WAB), extending

Table 2.2. Definition of sampling areas

Coast	Geographical Area	Limits of area	Acronym	Recoded GAM Area	Pelagic Stratum
West	North West Coast	Orange River – 31°S	NWC	A	A
	Central West Coast	31°S - Cape Columbine	CWC	B	A
	South West Coast	Cape Columbine – Cape Point	SWC	C	B
South	Western Agulhas Bank	Cape Point – Cape Agulhas	WAB	D	C
	Central Agulhas Bank	Cape Agulhas – Mossel Bay	CAB	E	D
	Eastern Agulhas Bank	Mossel Bay – Port Alfred	EAB	F	E

from Cape Point to Cape Agulhas; the Central Agulhas Bank (CAB), extending from Cape Agulhas to the Agulhas Bight, near Mossel Bay; and the Eastern Agulhas Bank (EAB), extending eastwards from Mossel Bay to Port Alfred. These geographical areas, or strata, are also used in the stratified random sampling design (Jolly and Hampton 1990) followed during the acoustic pelagic surveys (Barange *et al.* 1999), although the NWC and CWC are usually combined into one stratum. The number of stations sampled in each area during each cruise is indicated in Table 2.3.

2.2.3 Generalized additive models

Generalized additive models (GAMs; Hastie and Tibshirani 1990) were used to explore relationships between copepod abundance and environmental variables using S-Plus software (Insightful Corp. 2001). As such relationships may be non-linear, and may also be confounded by interactions between the variables, a non-linear modelling approach is considered to be preferable to a linear approach. GAMs extend linear models by flexibly modelling additive non-linear (non-parametric) relationships between predictor (x) and response (y) variables. Whereas linear models assume that the response is linear in each predictor, additive models assume only that each predictor affects the response in a smooth way. The smoother used was the locally weighted least-squares regression loess (lo). Visual assessment of the model residuals suggested that a Gaussian distribution was appropriate to describe the error structure, so this was used in all models. To construct the GAMs, a forward and backward stepwise model fitting procedure was used, based on the AIC (Akaike's Information Criterion) statistic (Chambers and Hastie 1992), with each predictor included as both smoothed and linear terms. For this procedure, a list of formulae is supplied for each term, which indicate the different forms in which the term may appear in the model. For example, the expression

```
"sst" = ~ 1 + sst + lo(sst)
```

means that sst could (1) be excluded from the model entirely (indicated by a constant of "1"), (2) appear as a linear function ("sst"), or (3) appear as a smooth function estimated non-parametrically ("lo(sst)"). A series of models is fitted, each comprising one term from each of the term formulae, until all possible combinations have been used. The model with the best fit in terms of the AIC statistic is then selected. All terms in the final model are significant according to the AIC. The range of the smoothed response function (y-axis) is proportional to the importance of the predictor in explaining the variability of the response.

The response variable used in the GAMs was copepod abundance, which was log-transformed using (log y+1, m^{-3}) because of the large number of zeroes in the dataset. Separate models were derived for the different life history stages of both species (C1-C3, C4, C5, male and female) as well as for total abundance (all stages combined). Numbers per m^3 were used instead of numbers per m^2, as the latter is the product of numbers per m^3 and depth, and would thus confound the effect of water-column depth (one of the predictors) in the models. A number of predictors were included in the initial GAMs to find the optimal combination that explained the most variability in abundance. Categorical variables included *year* (1988 to 2000), *season* (winter or summer), *area* (NWC, CWC, SWC, WAB, CAB or EAB), *coast* (West or South) and *shelf* (inner, <100 m; mid-, 100-200 m; or outer, >200 m). Continuous variables included *sounding* (water-column depth, m), *sst* (sea surface temperature, °C), *t30* (temperature at 30 m, °C), *Chl* (extracted total Chl concentration from the fluorescence maximum, mg m^{-3}) and *Chla* (extracted Chl *a* concentration from the fluorescence maximum, mg m^{-3}). For the summer cruises, some additional predictors were considered, namely *MLD* (mixed layer depth – depth where temperature is 0.5 °C lower than SST, m), *BSI50* (50 m bulk stability index – temperature change per meter between surface and 50 m, °C m^{-1}), *IntChlm3* (total Chl concentration integrated over the upper 30 m, mg m^{-3}) and *IntChlam3* (Chl *a* concentration integrated over the upper 30 m, mg m^{-3}). The geographical areas listed above were recoded using alphabetic characters to yield a more logical geographical sequence in the GAM graphic output, from north to south on the West Coast (A-C) and from west to east on the South Coast (D-F), as indicated in Table 2.2.

GAMs were also used to investigate the hypothesis that the centre of distribution of *C. agulhensis* is displaced further westward when the ridge is absent, as was apparent during November 1990 (Hutchings *et al.* 1995). Simple models were used to relate the abundance of the different copepodite stages of *C. agulhensis* on the South Coast during the November surveys to the continuous variable *longitude* (longitude, °E). Models were used to compare results for four November surveys when the Agulhas Ridge was clearly present (1988, 1989, 1993 and 2000), and four when it was absent (1990, 1992, 1994, 1998).

Relationships between copepod biomass and pelagic fish biomass were explored using data on anchovy, sardine and round herring biomass (tons) from the summer and winter surveys, which were provided by J. Coetzee, Marine and Coastal Management. Mean annual biomass (mg dry wt m^{-2}) of *C. agulhensis* on the South Coast during summer, and of *C. carinatus* on the West Coast during winter, were used to investigate possible density-dependent interactions beween these copepod and fish species.

2.3 RESULTS

Firstly, a generalized view of the distribution of *C. agulhensis* and *C. carinatus* is presented, followed by a summary of some of the environmental features of the region (e.g. SST and Chl *a*). Secondly, more specific features characterizing the distribution of these two copepod species in relation to their environment are described. Thirdly, these relationships are explored further by relating the abundance of these species to temporal, spatial and environmental variables using GAMs. Finally, possible density-dependent interactions between these copepods and pelagic fish are explored.

2.3.1 Horizontal distribution of *C. carinatus* and *C. agulhensis*

GIS maps of mean abundance (No.m^{-2}) of all stages of both species from 28 cruises between 1988 and 2000 provide a good indication of the core abundance areas of *C. carinatus* (Fig. 2.2a) and *C. agulhensis* (Fig. 2.2b) off the coast of South Africa. *C. carinatus* was most abundant off the West Coast, but was also found on the Agulhas Bank, mainly on the outer shelf region between the 100- and 200-m depth contours. *C. agulhensis* was most abundant over the Agulhas Bank, although it also occurred off the West Coast, particularly farther offshore. There was a marked geographical change in dominance of the two species at Cape Point, with abundance of *C. carinatus* comparatively low east of Cape Point, and abundance of *C. agulhensis* comparatively low north of Cape Point.

Regions of overlap are indicated in Fig. 2.3, by stations where females of both species were found simultaneously during the surveys. Females co-occurred over much of the survey range, but more commonly over the SWC shelf, mainly during winter, and along the WAB shelf edge. Co-occurrence was also common on the outer Agulhas Bank east of Cape Agulhas, between the 100- and 200-m depth contours. The proportion of the stations where females of both species were found ranged from 4.3% in May 1999 and 2000 to 40% in June 1990, with 14.4% co-occurrence on average (Table 2.3). Co-occurrence was slightly more common in summer, at 16.3% compared to 11.5% in winter.

Areas of greatest abundance of all copepodite stages of both species can be observed in contour plots of abundance (No.m^{-2}) from each cruise, which are provided in Appendix 1. These are supplemented by contour plots of SST, the temperature at 30 m, integrated Chl *a* concentration in the upper 30 m (where data were available, otherwise of maximum Chl *a* concentration in the euphotic zone) and current vectors (where data were available). The summer pelagic surveys are presented first, followed by the January 1992 ABBP survey, and then the winter pelagic surveys.

<u>Overview of the physical and biotic environment</u>

Summer:

SST over the Agulhas Bank in summer was typically 17-20°C, but cooler (<17°C) in areas characterized by coastal upwelling, particularly the inshore WAB. Warmer water (>20°C) was more

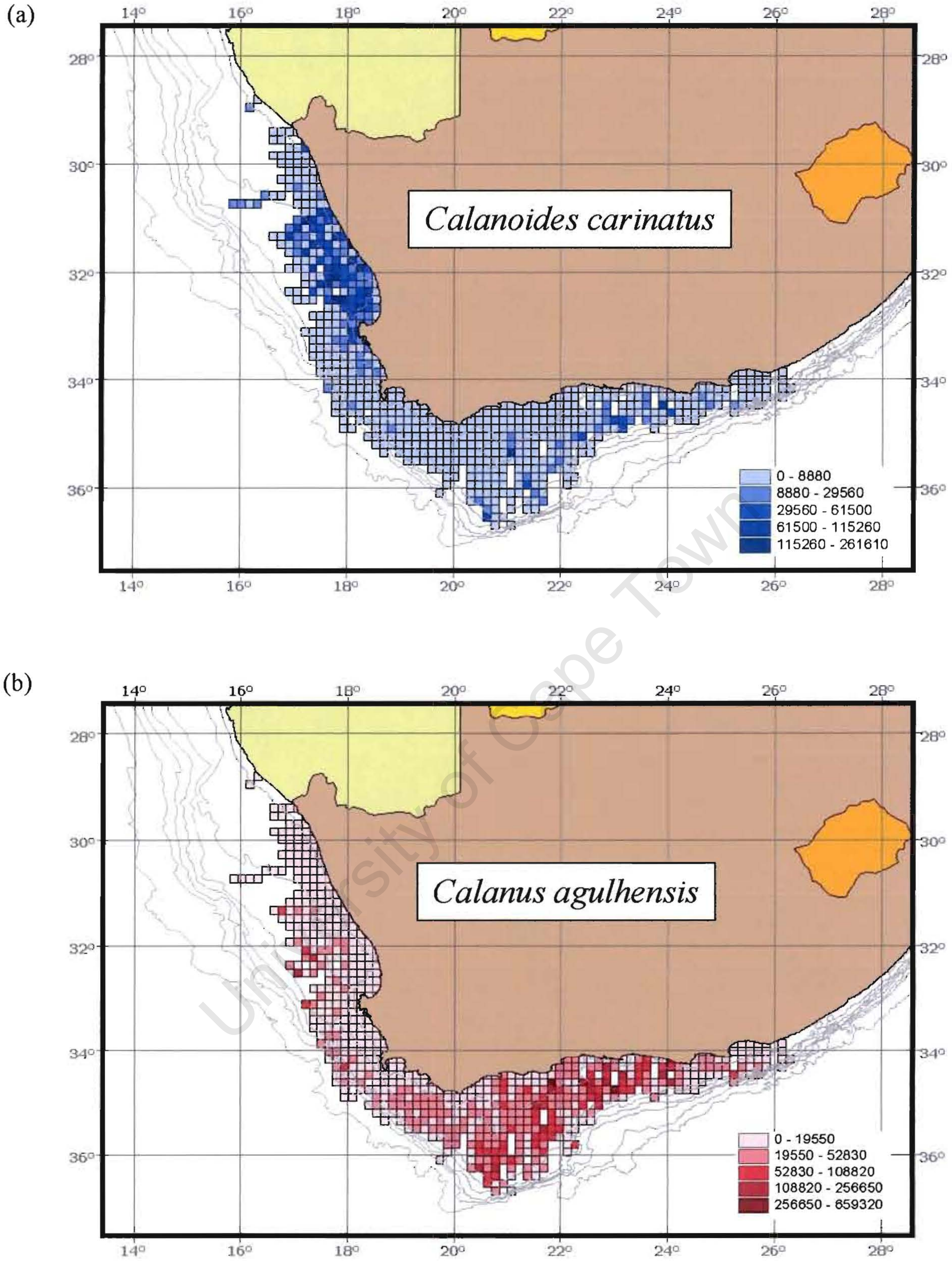


Figure 2.2. GIS maps of mean abundance (No.m^{-2}) of all copepodite stages (C1-C6) of (a) *C. carinatus* and (b) *C. agulhensis* from all summer and winter pelagic surveys from 1988 to 2000 (excluding May 2000). The 100-, 200-, 500-, 1 000-, 2 000- and 4 000-m depth contours are also shown (courtesy of L. Drapeau, IDYLE and MCM).

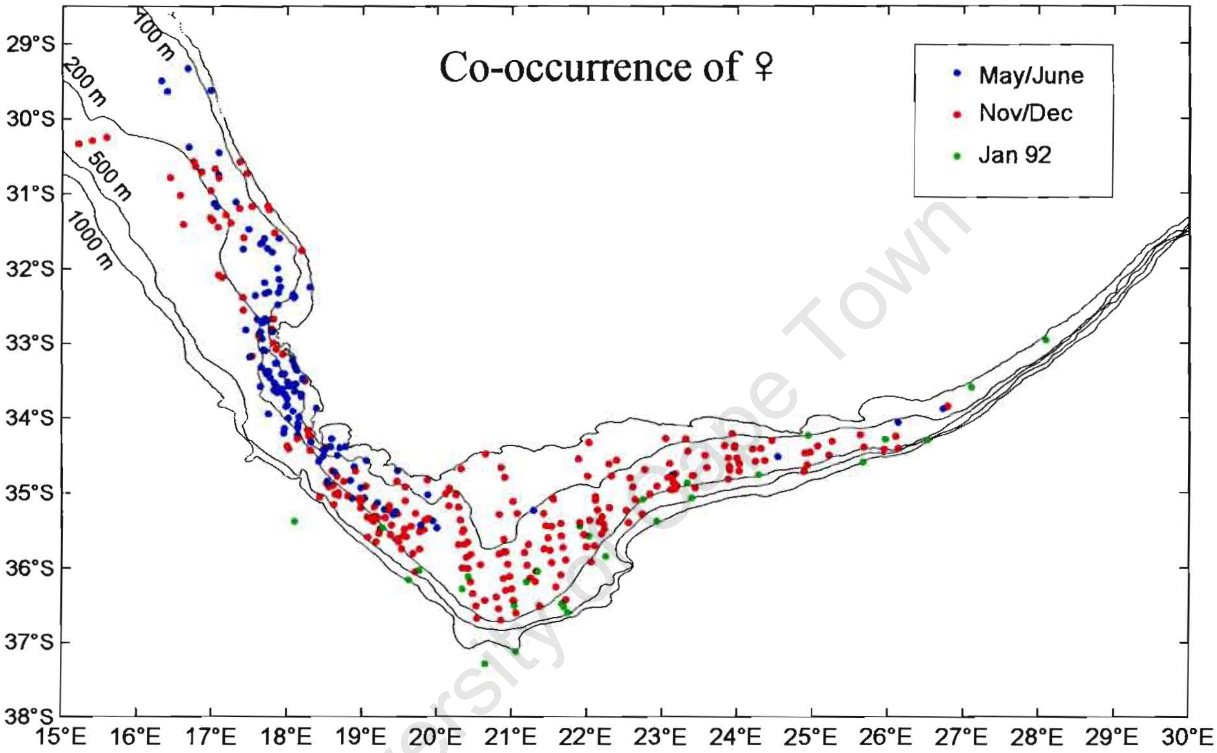


Figure 2.3. Map showing stations from all surveys where females of both *C. carinatus* and *C. agulhensis* were found to co-occur.

Table 2.3. The number of stations where samples were collected in each area, as well as the number and percentage (%) of stations where females of both species were found to co-occur; a blank indicates no samples were collected in that area.

Cruise	NWC	CWC	SWC	WAB	CAB	EAB	Total	Females of both spp. present	% co-occurrence
Nov 1988		61	42	18	16	9	146	16	11.0
Nov 1989		19	16	22	23	18	98	20	20.4
Nov 1990	11	16	12	34	21	21	115	12	10.4
Nov 1991	8	16	15	31	29	12	111	22	19.8
Nov 1992	7	20	18	23	33	21	122	28	23.0
Nov 1993		6	25	30	30	13	104	20	19.2
Nov 1994		10	10	30	34	15	99	13	13.1
Nov 1995		21	12	24	38	10	105	26	24.8
Nov 1996				34	39	26	99	19	19.2
Nov 1997	5	21	15	25			66	4	6.1
Nov 1998	6	20	17	30	52		125	45	36.0
Nov 1999	8	12	16	35	44	25	140	14	10.0
Nov 2000	6	32	10	38	49		135	6	4.4
Jan 1992				37	48	121	206	28	13.6
June 1988	11	18	21	16			66	8	12.1
June 1989	12	31	24	21			88	17	19.3
May 1990	6	16	11	9			42	8	19.0
June 1990	3	13	6	8			30	12	40.0
May 1991	9	15	6	12	12		54	4	7.4
May 1992	30	31	20	19	12		112	11	9.8
May 1993	30	44	25	41	22		162	21	13.0
May 1994	39	38	23	17	16	50	183	10	5.5
June 1995	33	49	26	20			128	14	10.9
June 1996	18	18	3				39	6	15.4
May 1997	15	15	4				34	4	11.8
June 1998	11	22	6	4			43	4	9.3
May 1999	8	17	6	16			47	2	4.3
May 2000	9	17	10	10			46	2	4.3
Total	285	598	399	604	518	341	2745	396	avg = 14.4

common along the shelf edge of the CAB and EAB due to the influence of the Agulhas Current. Coolest conditions were observed in 1988, when 16-18°C surface water extended over much of the inner Agulhas Bank from Mossel Bay eastwards (Fig. 2.4a), and in 1990, when most of the WAB and much of the EAB were covered by water cooler than 18°C (Fig. 2.4b). Warmest conditions during the time-series were observed in 1999, when most of the Agulhas Bank surface water was warmer than 20°C (Fig. 2.4c). November 2000 was unusual in that extremely warm water (>25°C) intruded onto the southernmost tip of the WAB, south of Cape Agulhas (Fig. 2.4d). SST in January 1992 was considerably warmer than usually observed during November, ranging mostly from 20 to 25°C (Fig. 2.5a). SST on the West Coast during the November surveys generally ranged from 12°C inshore to 17-18°C offshore, with colder temperatures of 10-12°C associated with the core upwelling zones.

The Agulhas Ridge, which is characterized by water colder than 17°C at 30 m (Boyd and Shillington 1994), was present in November 1988 (Fig. 2.4a), 1989, 1993, 1995 (although spatially limited; Fig. 2.5b) and 2000 (Fig. 2.4d) as well as in January 1992 (Fig. 2.5a; Table 2.4). The area of cool water varied considerably in shape, extent and location, sometimes being restricted to the inshore area adjacent to the coast, and sometimes extending away from the coast and along the 100-m isobath. The ridge was absent in November 1990 (Fig. 2.4b), 1992, 1994 (Fig. 2.5c) and 1998, weakly defined or unclear in 1991 and 1996 (Fig. 2.5c), and spatially limited or undeveloped in 1999 (Fig. 2.4c). Its prominence in November 1997 was unknown due to curtailed sampling east of Cape Agulhas.

Mean Chl *a* concentration in the upper 30 m was generally low (<2 mg m^{-3}) over the Agulhas Bank in summer, but higher in areas of coastal upwelling such as the inshore WAB (Figs 2.4a,b; 2.5a) and the EAB near Port Elizabeth (Fig. 2.5a), as well as around the cool-water ridge south of Mossel Bay (Fig. 2.4a). Moderate concentrations (1-2 mg m^{-3}) were associated with shelf-edge upwelling (Fig. 2.4b). Chl *a* concentration was much greater on the West Coast, often exceeding 5 mg m^{-3}.

Winter:

During the winter surveys, SST along the West Coast commonly ranged from 11-13°C inshore (due to upwelling) to 17-18°C farther offshore. Temperatures warmer than 18°C were sometimes observed beyond the shelf edge, probably indicative of Agulhas Bank water moving northwestwards across the outer WAB. SST on the inner WAB was occasionally as cold as 12-13°C as a result of recent upwelling, but usually ranged from 16 to 20°C. Although data east of Cape Agulhas were rarely collected during winter, the Agulhas Bank appeared to be colder on average during winter than during summer. The temperature at 30 m provided a better indication of the extent of upwelling on the West Coast during winter, with subsurface temperatures of 12-13°C common north of Cape Columbine,

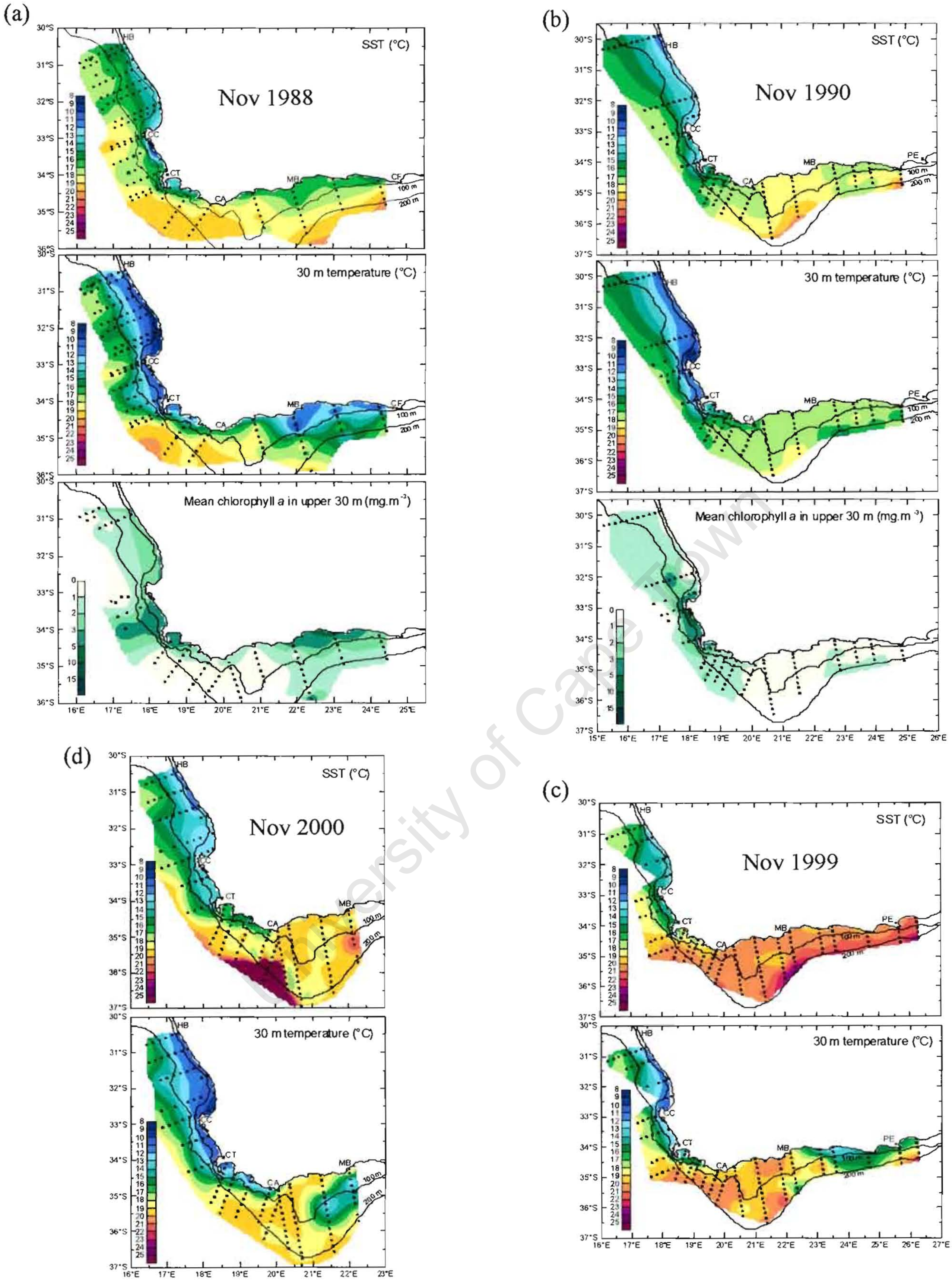


Figure 2.4. Contour plots of SST (°C), the temperature at 30 m (°C) and mean Chl a (mg m^{-3}) in the upper 30 m during (a) November 1988 and (b) November 1990. Temperature plots only are shown for (c) November 1999 and (d) November 2000.

Table 2.4. Status of the Agulhas ridge during surveys covering the Agulhas Bank

Survey	Status of ridge
November 1988	Present
November 1989	Present
November 1990	Absent
November 1991	Weakly defined – unclear
November 1992	Absent
November 1993	Present
November 1994	Absent
November 1995	Present but spatially limited
November 1996	Weakly defined – unclear
November 1997	Unknown – sampling curtailed at Cape Agulhas
November 1998	Absent
November 1999	Spatially limited
November 2000	Present
January 1992	Present
May 1994	Present

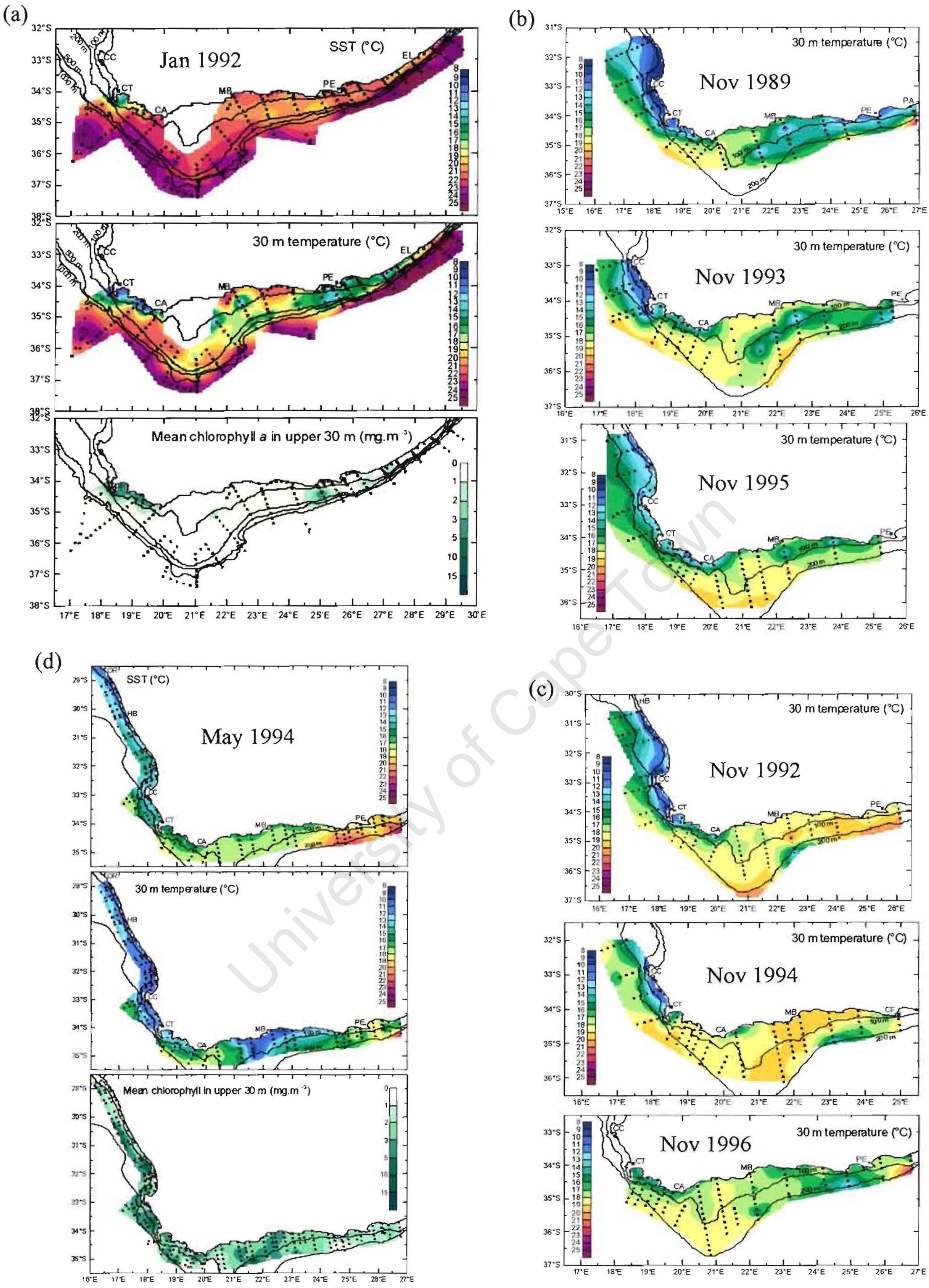


Figure 2.5. Environmental conditions during (a) January 1992, (b) November 1989, 1993 and 1995, (c) November 1992, 1994 and 1996, and (d) May 1994. Contour plots include SST (°C), the temperature (°C) at 30 m and mean Chl *a* (mg m^{-3}) in the upper 30 m.

particularly from May/June 1990 to 1992 and again in May 1994. The Agulhas Ridge was very prominent in May 1994 (Fig. 2.5d), the only winter survey to include the entire South Coast.

Maximum Chl *a* concentration on the West Coast during winter was usually >2 mg m^{-3}, but often >5 mg m^{-3}, particularly downstream from the upwelling cells. During May 1994, Chl *a* concentration along the inner Agulhas Bank was generally >2 mg m^{-3} (Fig. 2.5d), which was high relative to the concentrations normally observed during summer. Higher Chl *a* concentrations (>3 mg m^{-3}) were associated with the Agulhas Ridge.

Distribution of *C. carinatus* during summer

1. *C. carinatus* was consistently most abundant on the West Coast, in particular north of Cape Columbine, with greatest concentrations directly downstream from the Cape Columbine upwelling cell (Fig. 2.2a; Appendix 1). It did occur on the Agulhas Bank, but at relatively low abundance, and was most numerous on the outer shelf edge of the CAB and EAB, being less common on the WAB.

2. During several surveys, high concentrations of older stages, mainly C5 and adult, but sometimes C4 as well, were observed along the West Coast at inshore stations in the vicinity of newly upwelled water, as indicated by 10-12°C water at 30 m. Younger stages (C1-C3) were absent or extremely rare under these circumstances. This pattern was evident on the CWC during November 1992 and 1998 (Figs 2.6a,b), and was also apparent in 1988.

3. In some years the area of greatest abundance was spatially constant for all copepodite stages, such as during November 1990 and 1998 (Figs 2.7a and 2.6b). These "hotspots" varied in location, some being close to Cape Columbine, some farther downstream, some in St Helena Bay, and some farther offshore in the vicinity of the shelf edge at ~200 m.

4. Large concentrations of copepodite stages C4 and older were observed at a single station off Port Elizabeth near the shelf edge during November 1989, associated with cool (<18°C SST), Chl *a*-rich (>5 mg m^{-3}) water (Fig. 2.7b). Large numbers of mainly younger stages (151 000 C1s, 136 000 C2s, 109 000 C3s and 31 000 C4s.m^{-2}) were found at a mid-shelf station on the CAB during November 1988 (Appendix 1). Large numbers of the older stages (up to 84 000 C4s and 105 000 C5s.m^{-2}) were also found farther east during November 1988 in the vicinity of the cool ridge, which was particularly extensive during this survey (Fig. 2.4a).

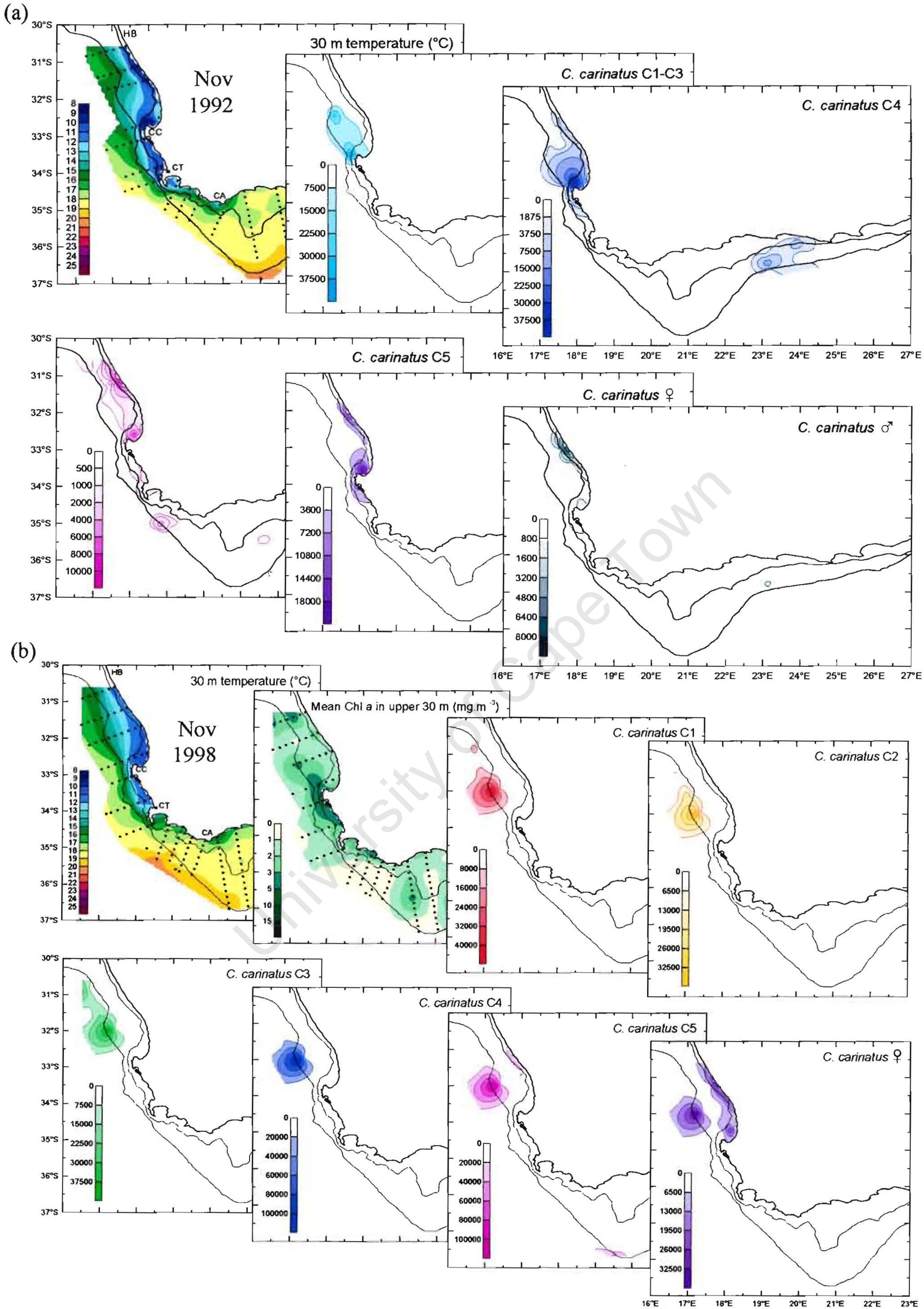


Figure 2.6. Contour plots of the temperature (°C) at 30 m, Chl *a* (mg m^{-3}) and abundance (No.m^{-2}) of *C. carinatus* copepodites during (a) November 1992 and (b) November 1998.

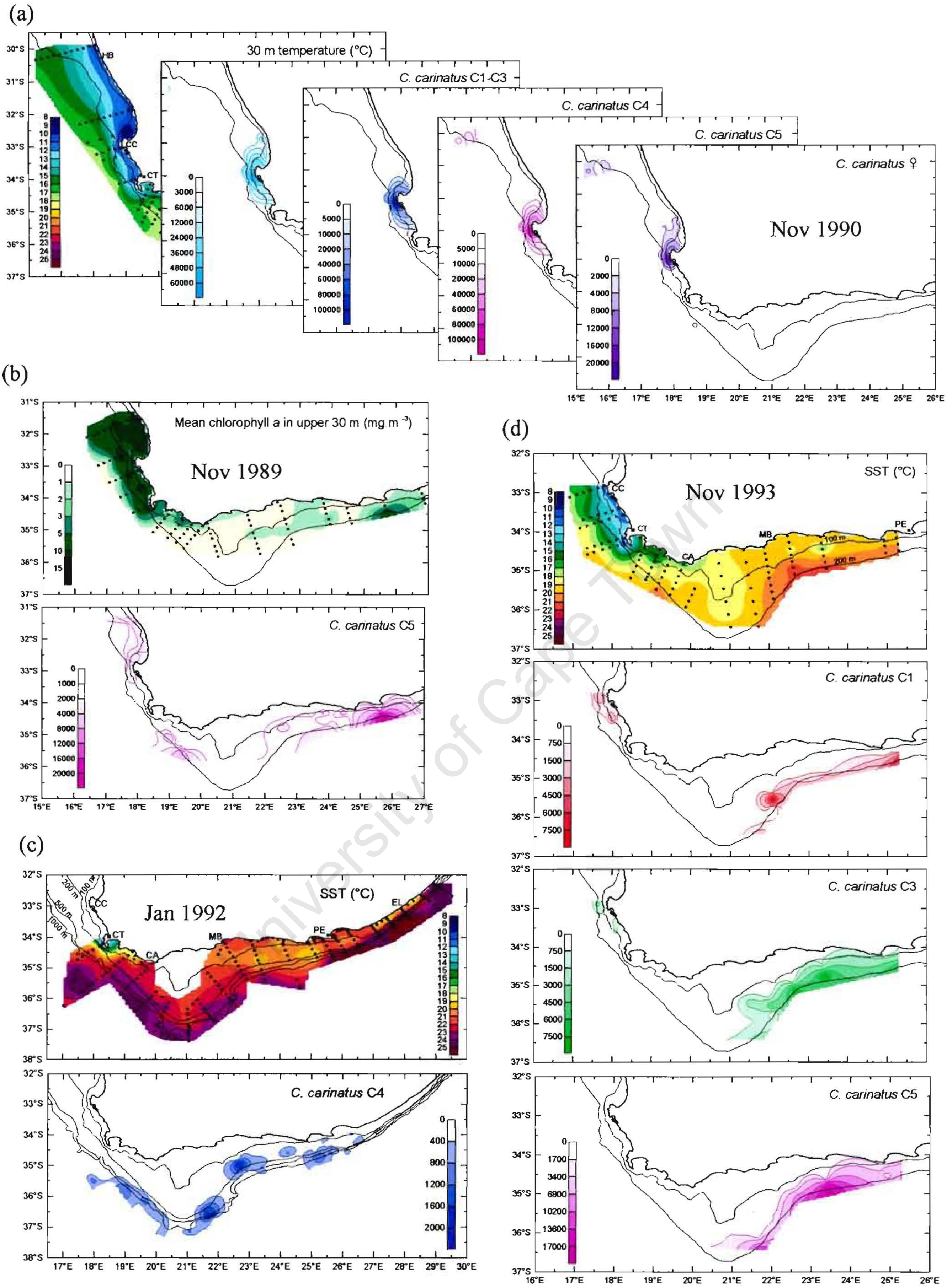


Figure 2.7. Contour plots of abundance (No.m^{-2}) of *C. carinatus* copepodites during (a) November 1990, (b) November 1989, (c) January 1992 and (d) November 1993. SST (°C), temperature (°C) at 30 m and mean Chl *a* (mg m^{-3}) in the upper 30 m are shown for some of the plots.

5. The most common distribution pattern of *C. carinatus* on the South Coast during summer was low to moderate abundances of all copepodite stages along the outer shelf and shelf edge, mainly in the Agulhas Bight region (e.g. November 1993; Fig. 2.7d) but also sometimes extending over the southern tip of the CAB and along the WAB shelf edge (as in January 1992; Fig. 2.7c). This distribution along the shelf edge often coincided with the presence of warm (>20°C) surface water of Agulhas Current origin (Fig. 2.7c,d).

Distribution of *C. carinatus* during winter

1. Abundance of *C. carinatus* was more widespread along the West Coast during winter than summer, but still appeared to be greatest in the central region (CWC), particularly downstream from Cape Columbine. Areas of high abundance were often broadly associated with elevated Chl *a* (>3 mg m^{-3}). As in summer, abundance on the WAB was usually low.

2. In June 1995, extremely high concentrations of C5 (>30 000 ind. m^{-2}) and adult stages (>200 000 females m^{-2}) were located at a single station inshore on the NWC, just south of the Orange River in cold water (11-12°C at 30 m; Fig. 2.8a). Abundances of >15 000 females m^{-2} and 11 000 C5s m^{-2} were found at adjacent stations. Very high abundances of all stages were also observed downstream of Cape Columbine in May 1991, when cold water (9-12°C) extended across nearly the entire shelf of the CWC and NWC at 30 m (Fig. 2.8b).

3. As in summer, discrete areas of high abundance of the different copepodite stages often coincided, such as the frequently observed "hotspot" off Cape Columbine (Fig. 2.9a,b).

4. During several surveys, a large proportion of the younger stages (C1-C4) were concentrated slightly farther offshore compared to the older stages, such as in June 1989 (Fig. 2.9a), May 1992 (Fig. 2.9b) and June 1996. In general, however, there were no clear stage-specific trends in cross-shelf abundance.

Distribution of *C. agulhensis* during summer

1. The distribution pattern of *C. agulhensis* on the Agulhas Bank during summer varied from year to year. It was present over the entire Bank, but was usually most abundant on the central and outer Agulhas Bank (Fig. 2.2b; Appendix 1). During a more extensive cruise in January 1992, it was found to extend as far as ~28°E, just south of East London. *C. agulhensis* was also present on the West Coast in most years, either at the shelf edge or beyond.

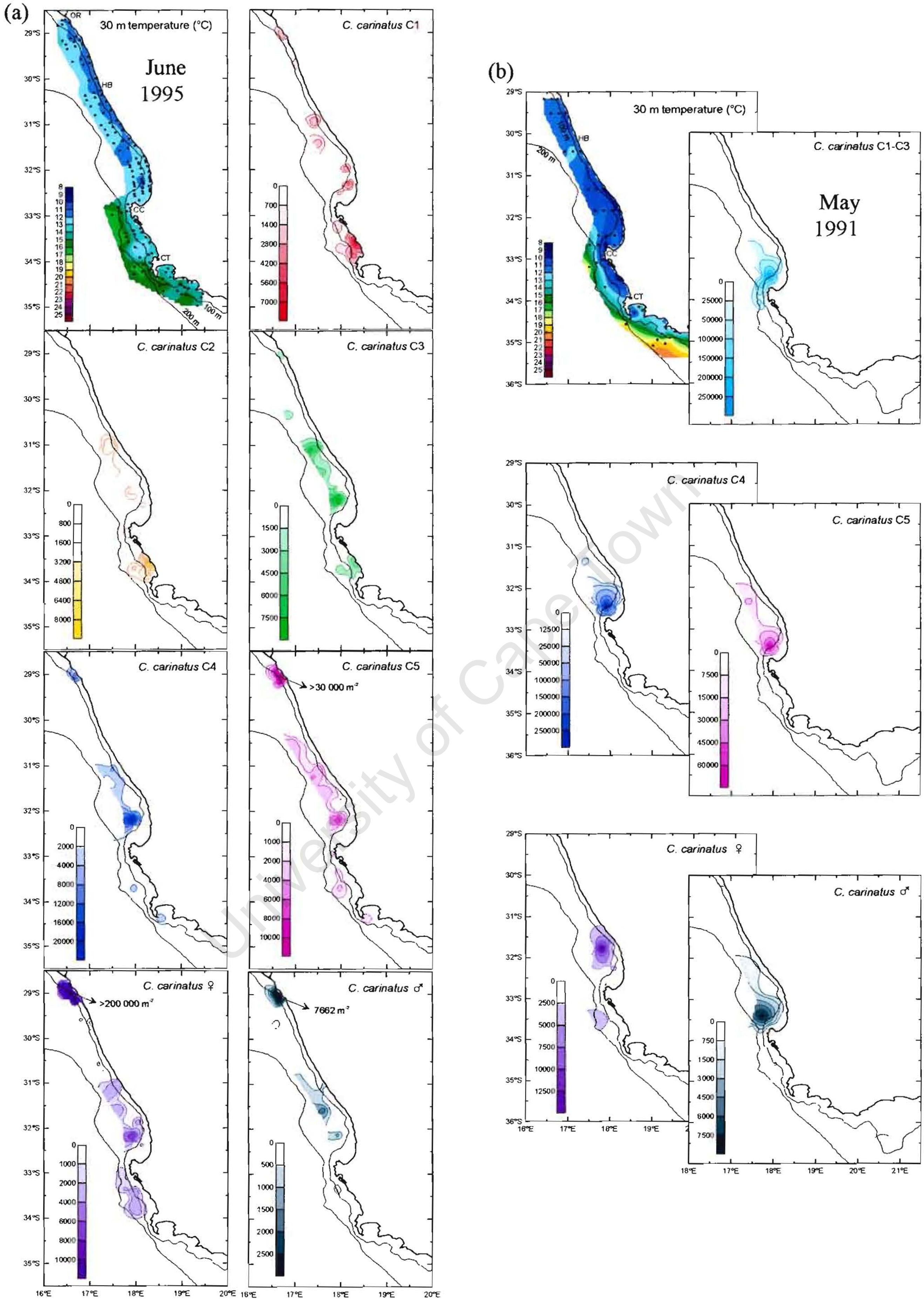


Figure 2.8. Contour plots of the temperature at 30 m (°C) and abundance (No.m^{-2}) of *C. carinatus* copepodites during (a) June 1995 and (b) May 1991.

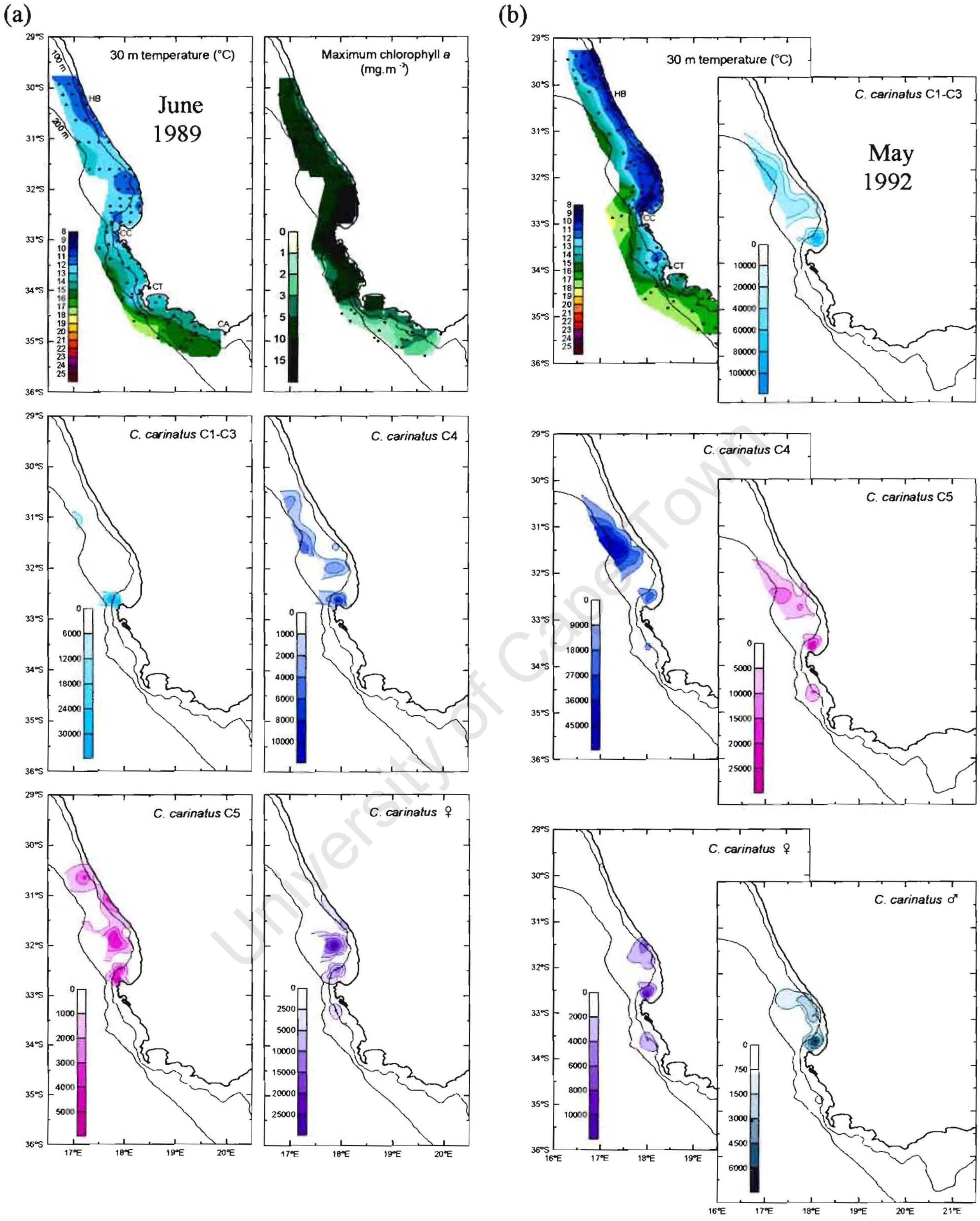


Figure 2.9. Contour plots of the temperature at 30 m (°C) and abundance (No.m^{-2}) of *C. carinatus* copepodites during (a) June 1989 and (b) May 1992. Maximum Chl *a* (mg m^{-3}) in the euphotic zone is also shown for (a).

2. In some years there was a general expansion and westward shift of the region of greatest abundance with increasing stage, as in 1988 (Fig. 2.10a), 1992, 1996 (Fig. 2.10b) and to some extent in 1998. In 1990 the distribution of the older copepodites (C4-adult) was centered on the WAB (see Appendix 1).

3. Abundance was usually low on the inner Agulhas Bank, i.e. the region shallower than 100 m (Fig. 2.2b), but greater-than-average abundance in this region was observed during 1993, 1995 and 2000 (see Appendix 1).

4. Large concentrations of the youngest copepodites (C1-C3) on the CAB and EAB were sometimes associated with, or slightly offset from, the coolest part of the Agulhas Ridge, as observed in November 1988 (Fig. 2.11a), 1989 (Fig. 2.11b), 1995 and 2000 (Fig. 2.11c), as well as in January 1992 (Fig. 2.11d). The cool water was usually associated with elevated concentrations of Chl *a*. The young copepodites observed at the extreme eastern edge of the EAB in the general vicinity of Port Elizabeth in January 1992 were also associated with cool water (Fig. 2.11d) and elevated Chl *a* (Fig. 2.5a).

5. Relatively high concentrations of mainly older copepodites (C5 and adult) were often observed along the shelf edge in the vicinity of the Agulhas Bight, usually in association with shelf-edge upwelling, which manifested as a narrow region of cool, moderately Chl *a*-rich water (Figure 2.12a,b). This combination was observed in 1990, 1992, 1994 and 1999, indicating it was fairly common, but it could not be ascertained in several years (1997, 1998 and 2000) due to the curtailment of sample collection on the CAB and EAB.

6. In some years, the distribution patterns suggested a northwestward advection of *C. agulhensis* (particularly, but not restricted to, the younger copepodites) from the WAB towards the West Coast, as in 1994, 1995, 1998 and 1999 (Fig. 2.13a-d). This was usually associated with broad-scale, northwest flow over the WAB and/or strong, northwest flow off the Cape Peninsula along or beyond the shelf edge.

Distribution of *C. agulhensis* during winter

1. *C. agulhensis* appeared to be quite abundant on the WAB during winter, with dense concentrations observed in this region from 1988 to 1995, and again in 1999. The only cruise to survey the entire coastline during winter took place in May 1994, although sampling did not extend as far offshore as during summer. During this cruise, all copepodite stages were

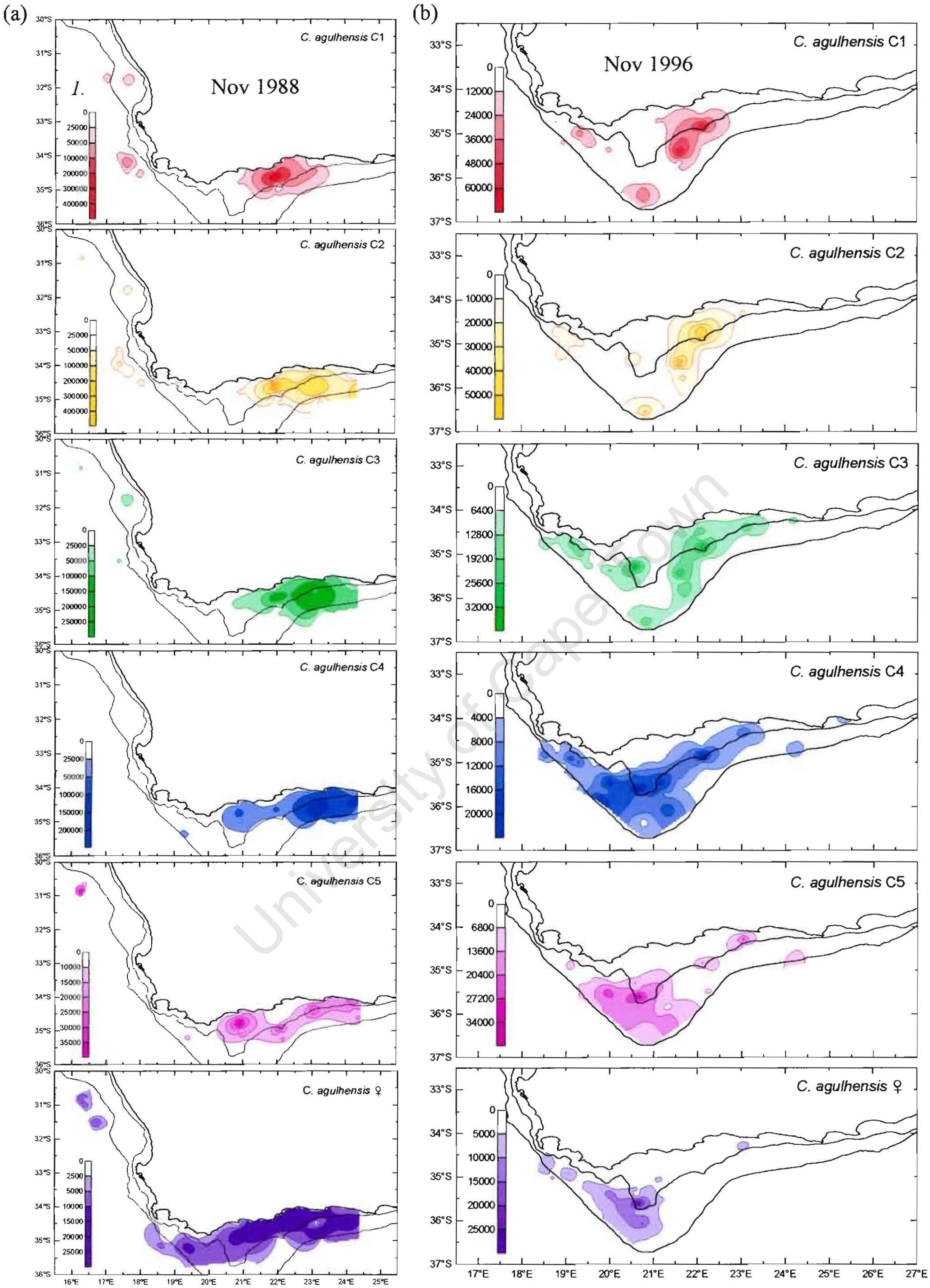


Figure 2.10. Contour plots of abundance (No.m^{-2}) of *C. agulhensis* copepodites during (a) November 1988 and (b) November 1996.

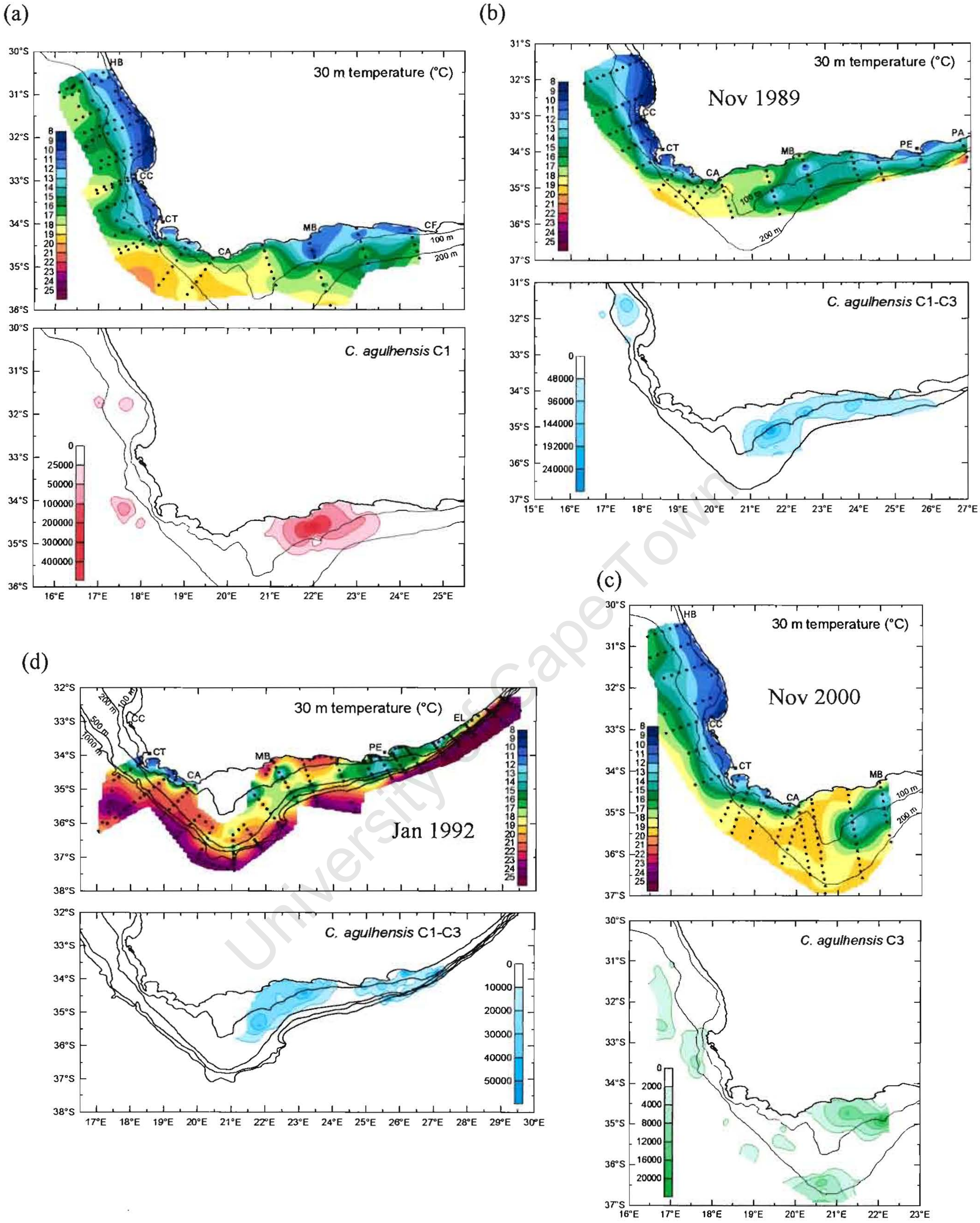


Figure 2.11. Contour plots of the temperature at 30 m (°C) and associated abundance (No.m^{-2}) of young (C1-C3) *C. agulhensis* copepodites during (a) November 1989, (b) November 1993, (c) November 2000 and (d) January 1992.

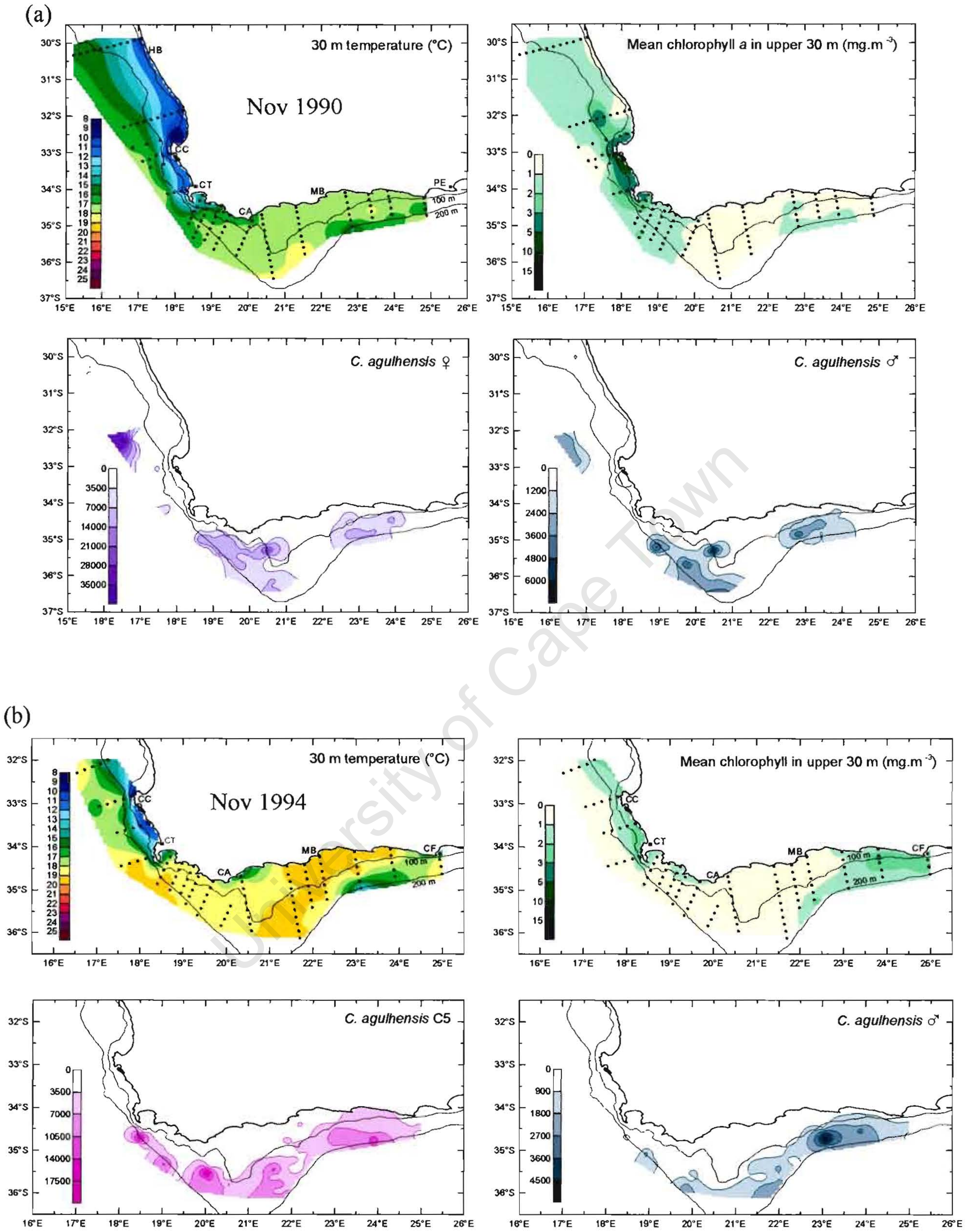


Figure 2.12. Contour plots of temperature at 30 m (°C), mean Chl *a* (mg m^{-3}) and abundance (No.m^{-2}) of some older *C. agulhensis* copepodites during (a) November 1990 and (b) November 1994. Note the higher densities along the shelf edge at 23-24°E.

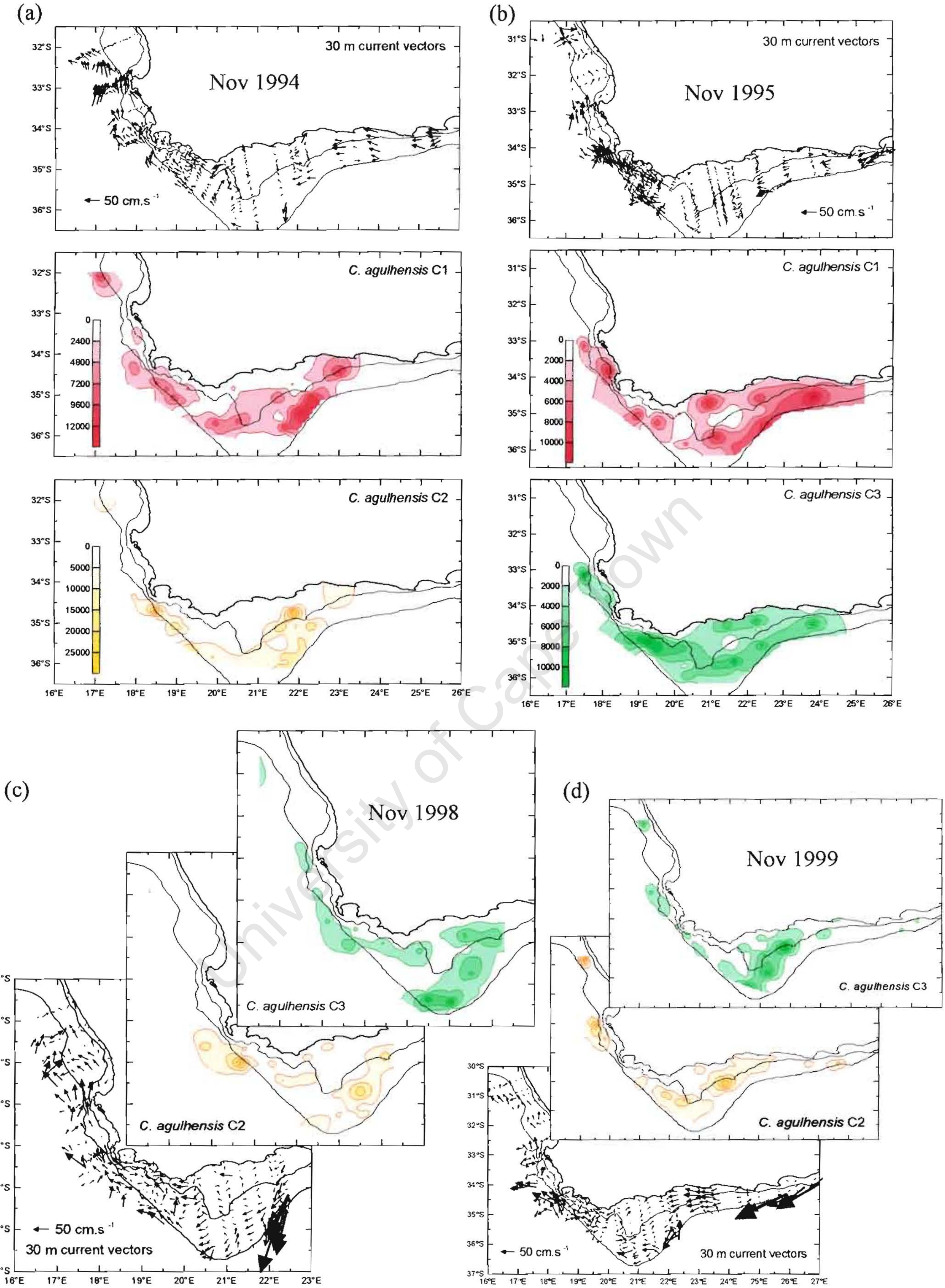


Figure 2.13. Current vector (cm s^{-1}) maps and contour plots of abundance (No.m^{-2}) of *C. agulhensis* copepodites during (a) November 1994, (b) November 1995, (c) November 1998 and (d) November 1999.

abundant from Cape Point to Plettenberg Bay (~23.5°E), whereas the older copepodites were also abundant in the vicinity of Cape St Francis and Port Elizabeth (Fig. 2.14a). Younger copepodites were most abundant surrounding the broad, subsurface ridge of cold water south of Mossel Bay.

2. *C. agulhensis* also extended up the West Coast during winter, with moderate densities extending from Cape Point to Cape Columbine during many of the cruises (Fig. 2.14b,c). Abundance was generally greater beyond the 100-m isobath, but the younger stages were also common inshore, sometimes extending into St Helena Bay. Discrete patches of *C. agulhensis* were also located farther north, on both the CWC and NWC, with the northernmost concentrations usually associated with the Hondeklipbaai upwelling region.

2.3.2 Generalized additive models (GAMs)

Of the 14 predictors included in the initial GAMs, six were found to best explain the variance associated with copepod abundance. These were: *year*, *season*, *area*, *sounding*, *sst* or *t30*, and *Chla*. The most appropriate variable describing temperature varied according to species, with *t30* being more important for *C. carinatus* and *sst* more important for *C. agulhensis*. The actual models used, plus their constraints, are provided in Table 2.5 for *C. carinatus* and in Table 2.6 for *C. agulhensis*.

A comparison of the ranges of the smoothed response functions (excluding standard errors) from the models for total abundance (top row of Fig. 2.15) indicates that the significant predictors explaining 36% of the variability in abundance of *C. carinatus* (Table 2.5) are ranked in importance as follows: 1) *t30*, 2) *area*, 3) *year*, 4) *sounding*, 5) *Chla* and 6) *season*. This ranking was similar for each copepodite stage when assessed separately, although sometimes *year* was more important than *area*. *Chla* was not important for predicting the abundance of C4s, C5s or females in this model, and season was important for all stages except the females. The significant predictors explaining 59% of the variability in total abundance of *C. agulhensis* (Table 2.6; Fig. 2.16) were ranked as follows: 1) *area*, 2) *sst*, 3) *year*, 4) *sounding*, 5) *Chla* and 6) *season*.

Year effect:

Total abundance of *C. carinatus* appeared to be relatively constant over the time-series (Fig. 2.15), with particularly low abundance during 1989 and particularly high abundance during 1998. The former was most evident for the immature copepodite stages, particularly the C1s-C3s, whereas the latter was mainly due to very large numbers of C5s and females. In contrast, total abundance of *C. agulhensis* declined over the time-series, with greatest abundance from 1988 to 1991, a sharp decrease

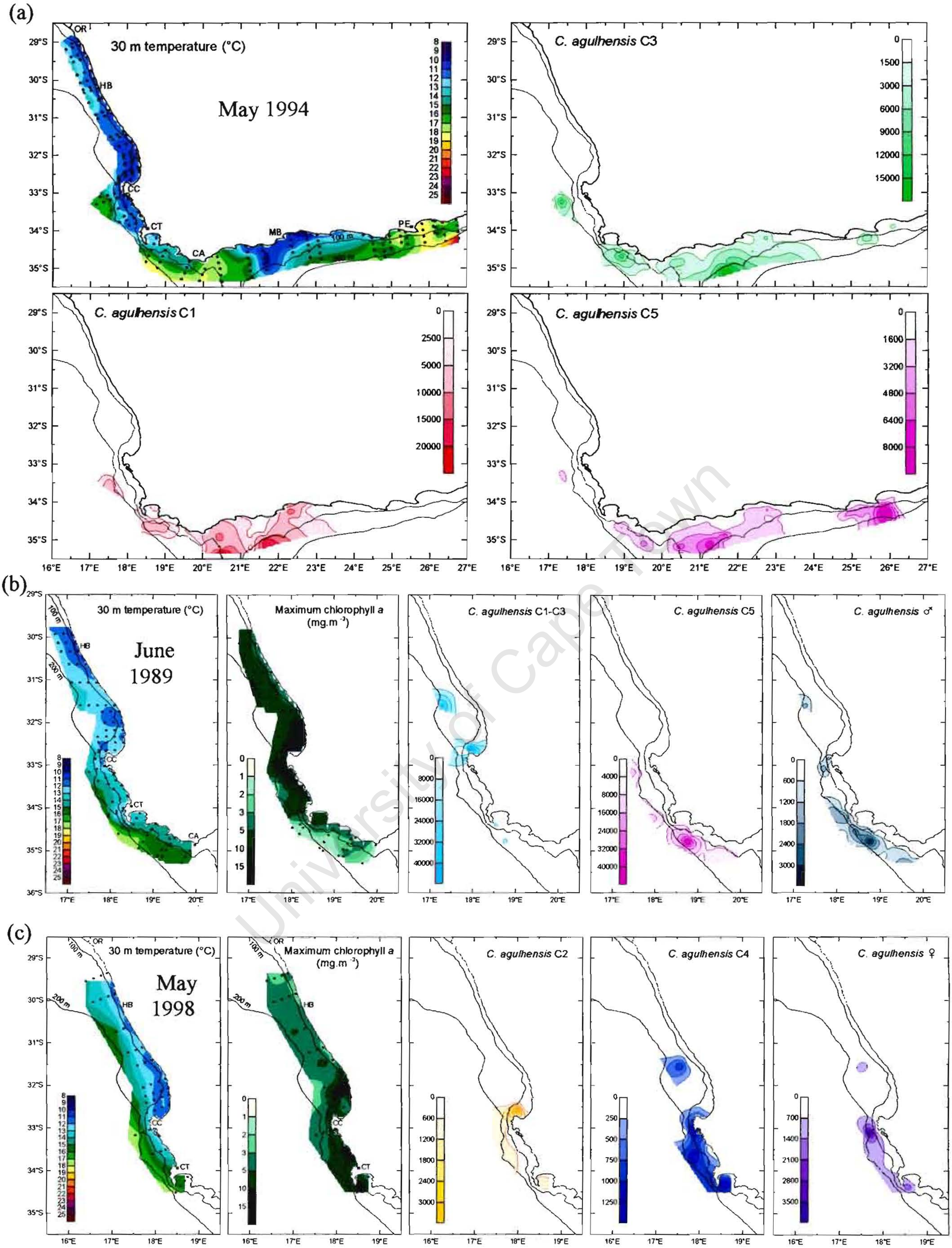


Figure 2.14. Contour plots of temperature at 30 m (°C) and abundance (No.m^{-2}) of *C. agulhensis* copepodites during (a) May 1994, (b) June 1989 and (c) May 1998. Maximum Chl *a* (mg m^{-3}) in the euphotic zone is also shown for (b) and (c).

Table 2.5. Generalized additive models used to predict abundance of *C. carinatus*.

Stage	Model	Constraints	*n*	r^2
Total	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(t30) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.36
Female	log (no+1)m^{-3} ~ year + area + lo(sounding) + lo(t30)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.27
Male	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(t30) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.18
C5	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(t30)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.29
C4	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(t30)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.29
C1-3	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(t30) + Chla	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.29

Table 2.6. Generalized additive models used to predict abundance of *C. agulhensis*.

Stage	Model	Constraints	*n*	r^2
Total	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(sst) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.59
Female	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(sst) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.40
Male	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(sst) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.26
C5	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(sst) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.51
C4	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(sst) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.53
C1-3	log (no+1)m^{-3} ~ year + season + area + lo(sounding) + lo(sst) + lo(Chla)	sounding $\leq$ 1000; Chla $\leq$ 30	2177	0.50

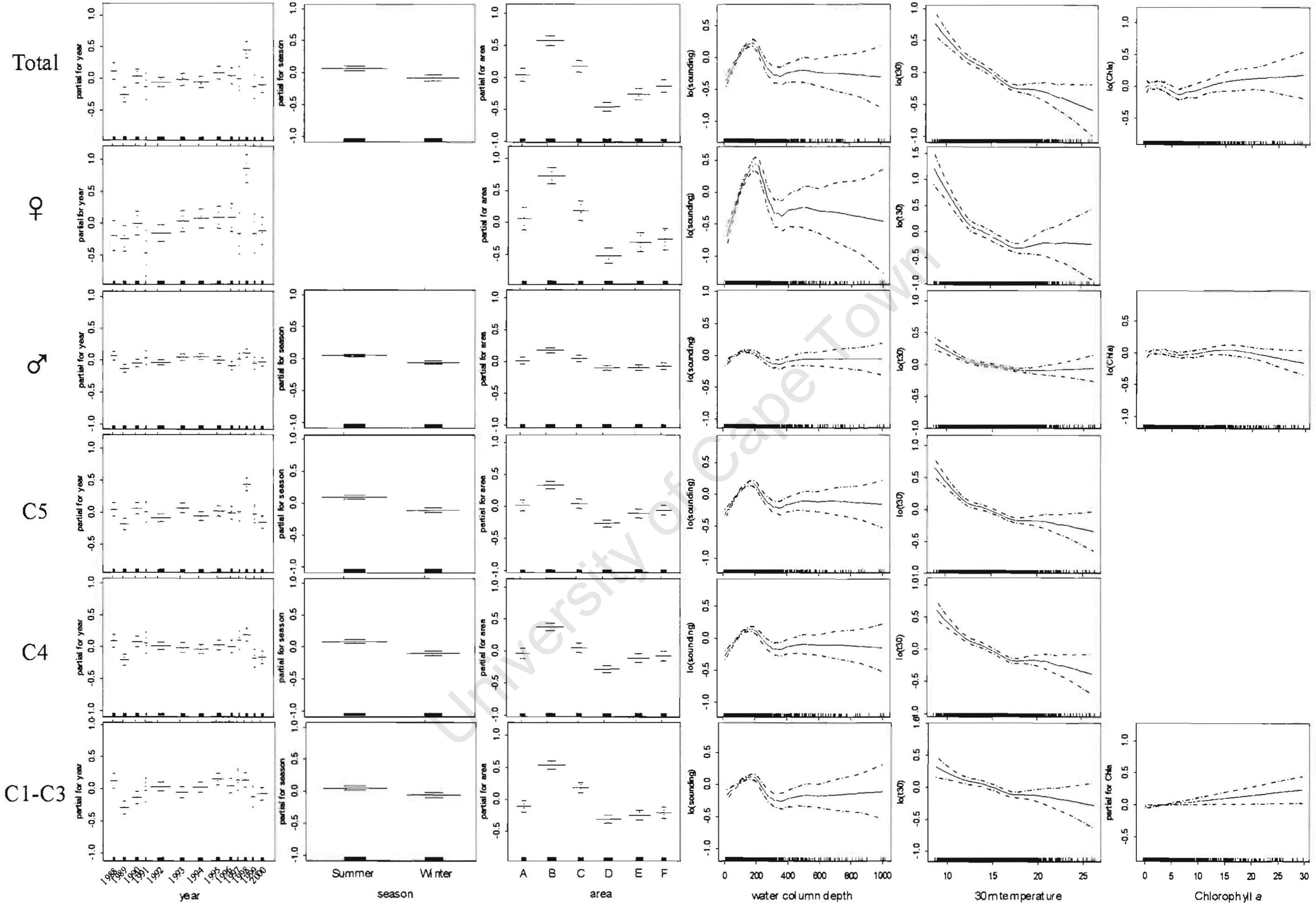


Figure 2.15. Generalized additive models of total and stage-specific abundance (log No. m^{-3} + 1) of *C. carinatus* as a function of year, season, area, water column depth (m), the temperature at 30m (°C) and Chl *a* (mg m^{-3}). A rugplot along the base of each plot shows the occurrence of each *x*-value, and 2x upper and lower standard errors are indicated by bars (categorical variables) or dotted lines (continuous variables).

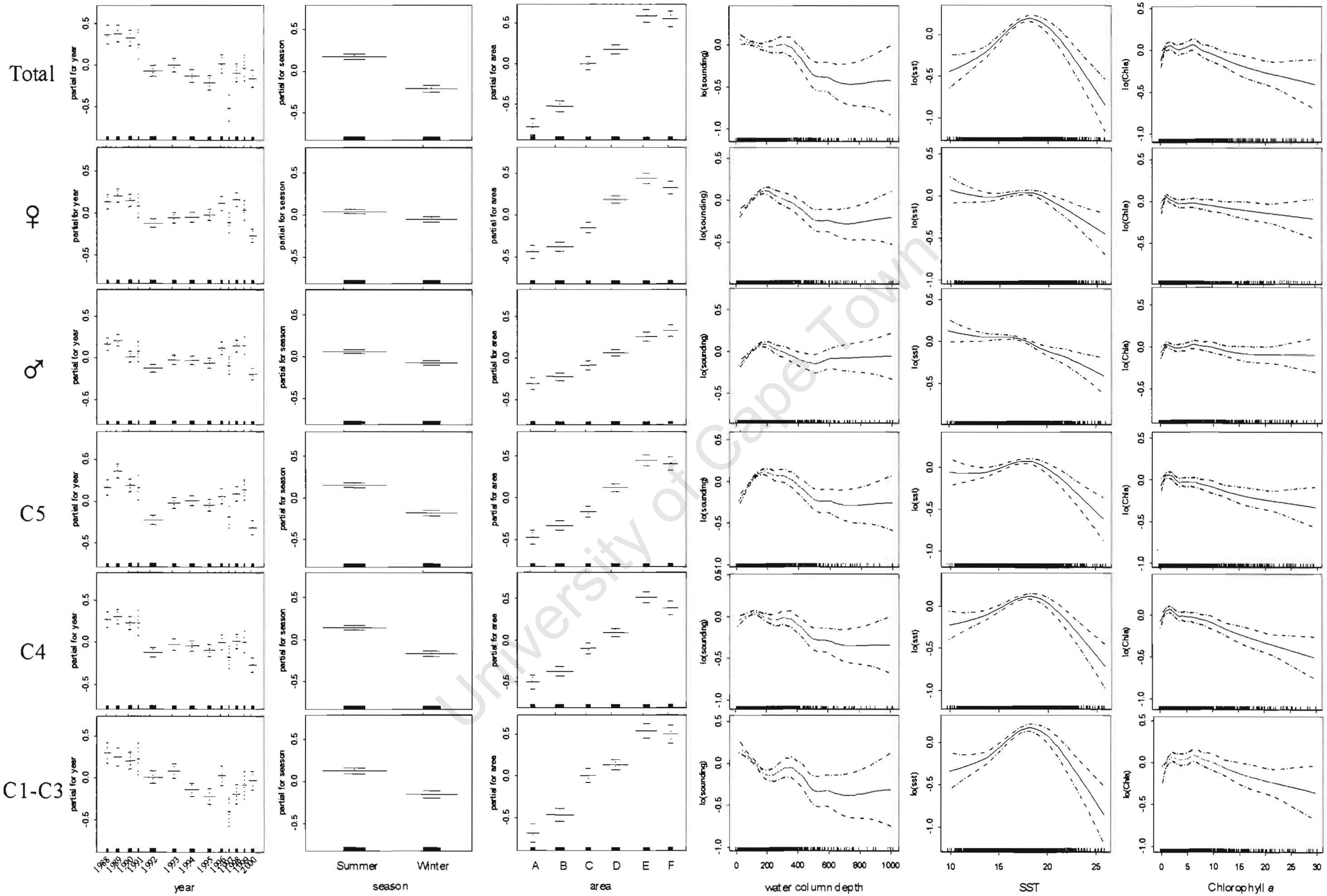


Figure 2.16. Generalized additive models of total and stage-specific abundance (log No. m^{-3} + 1) of *C. agulhensis* as a function of year, season, area, water column depth (m), SST (°C) and Chl *a* (mg m^{-3}). A rugplot along the base of each plot shows the occurrence of each *x*-value, and 2x upper and lower standard errors are indicated by bars (categorical variables) or dotted lines (continuous variables).

thereafter, and considerable interannual variability from 1996 to 2000 (Fig. 2.16). The decline in abundance was most evident for the youngest copepodite stages (C1-C3), particularly from 1988 to 1997. Total abundance was exceptionally low during 1997, mainly due to low abundance of the youngest copepodite stages (C1-C3). The older stages (C5s and adults) gradually increased in abundance after 1992, but declined sharply in 2000.

Season effect:

Season was the least important variable explaining the abundance of both species. All stages of both species (except female *C. carinatus*) were more abundant in summer than in winter (Figs 2.15 and 2.16), but the seasonal disparity was more pronounced for *C. agulhensis*. The seasonal disparity in abundance was greater for the immature *C. agulhensis* copepodites compared to the adults, but similar for the male and immature *C. carinatus* copepodites.

Area effect:

Area was the second most important variable after *t30* in explaining the abundance of *C. carinatus*, and the most important variable for *C. agulhensis*. All stages of *C. carinatus* were more abundant on the West Coast than the South Coast (Fig. 2.15), whereas the reverse was true for *C. agulhensis* (Fig. 2.16). *C. carinatus* was most abundant on the CWC, followed by the SWC and then the NWC. On the South Coast, abundance of *C. carinatus* increased from west to east. Abundance of *C. agulhensis* was greatest on the CAB, followed closely by the EAB, except for males, which were slightly more numerous on the EAB than the CAB. Abundance of this species on the West Coast declined from south to north.

Sounding effect (water-column depth):

The GAM for total abundance of *C. carinatus* indicated a well-defined peak within the shelf edge at a water-column depth of ~175 m (Fig. 2.15). Separate models for each stage revealed similar patterns, although greatest female abundance was associated with the shelf edge at the 200-m isobath. In contrast, total abundance of *C. agulhensis* was greatest near the coast, but relatively constant up to depths of 300 m, beyond which abundance declined sharply (Fig. 2.16). Separate analyses for each stage, however, indicated that greatest abundance occurred progressively farther offshore (or in progressively deeper water) with increasing age. Stages C1-C3 were most abundant close to the coast, in relatively shallow water, with a secondary node of abundance at ~350 m. Abundance of C4s peaked farther offshore at ~125 m, that of C5s and males at ~175 m and that of females just within the shelf edge at ~195 m. C4s and C5s also exhibited secondary nodes of abundance farther offshore, although for the C5s this tended to merge with the primary node of abundance.

Temperature effect:

The temperature at 30 m was the most important predictor explaining variability in abundance of *C. carinatus* (Fig. 2.15). Abundance was greatest when the temperature at 30 m was below 10°C, and decreased as temperatures increased. The effect was strongest for the females, and weakest for the males and youngest stages. The relationship between abundance and *t30* approximated an exponential decline for the females and gradually flattened to approach a gentle negative linear relationship for the youngest stages (C1-C3).

There was a clear dome-shaped relationship between total abundance of *C. agulhensis* and SST, with greatest abundance at temperatures between 15 and 20°C, peaking at ~18°C (Fig. 2.16). This was most marked for the youngest stages (C1-C3), with the dome becoming progressively flatter with increasing stage, particularly at cooler temperatures, such that older stages were more likely to be found at temperatures cooler than 15°C than younger stages. Abundance of all stages declined sharply in water warmer than 20°C.

Chl *a*:

Total abundance of *C. carinatus* was slightly higher at greater concentrations of Chl *a* at the fluorescence maximum (Fig. 2.15). Abundance of the youngest stages (C1-C3) was also positively related to Chl *a*, but that of the older stages, except for the males, were not. In contrast to *C. carinatus*, Chl *a* concentration was a significant factor explaining the abundance of all stages of *C. agulhensis*, although it was also one of the least important. GAMs for total abundance indicated nodes of relatively high abundance at concentrations of ~2 and 6 mg Chl *a* m^{-3}, and a negative relationship between abundance and Chl *a* at higher concentrations (Fig. 2.16). This pattern was also applicable for the youngest stages (C1-C3), whereas the older stages were only associated with the lower Chl *a* node.

The Agulhas Ridge effect

Models using only *longitude* as the predictor of abundance of *C. agulhensis* during summer indicated a dome-shaped distribution for the youngest stages (C1-C3) across the Agulhas Bank, with greatest abundance between ~22 and 24°E (Fig 2.17a). Greatest abundance of the older stages was distributed more broadly across the Bank, and was bimodal for the C5s and females, with peaks at 21 and 23.5°E. The westernmost peak was most prominent for the females. Separate models for four years when the

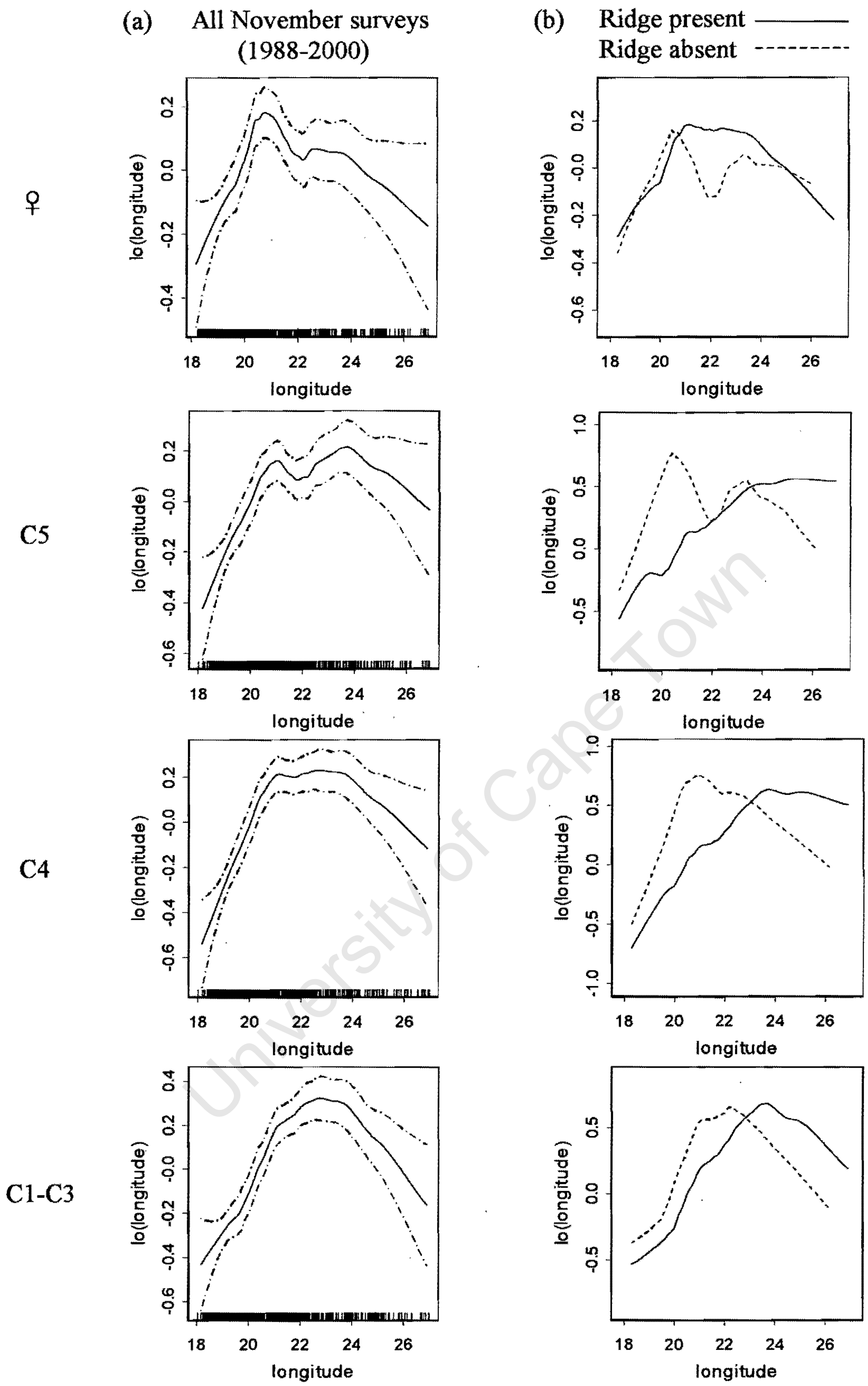


Figure 2.17. Stage-specific abundance (log No.m^{-3} + 1) of *C. agulhensis* as a function of longitude for (a) all November surveys from 1988 to 2000, and (b) for four years when the Agulhas ridge was present (1988, 1989, 1993 and 2000) and four years when it was absent (1990, 1992, 1994 and 1998). *y*-scales in (b) are accurate for years when the ridge was present, but are doubled for stages C1-C5 during years when the ridge was absent.

ridge was present compared to four years when the ridge was absent indicated a marked difference in longitudinal distribution between the two. Stages C1-C5 were most abundant towards the eastern part of the Agulhas Bank when the ridge was present, but were concentrated progressively westwards with increasing age when the ridge was absent (Fig. 2.17b). Distribution of females was unimodal when the ridge was present, but bimodal when it was absent, with greatest abundance associated with the westernmost peak. The distribution of the C5s was also bimodal but greater in the west when the ridge was absent.

2.3.3 Seasonal patterns of abundance and biomass

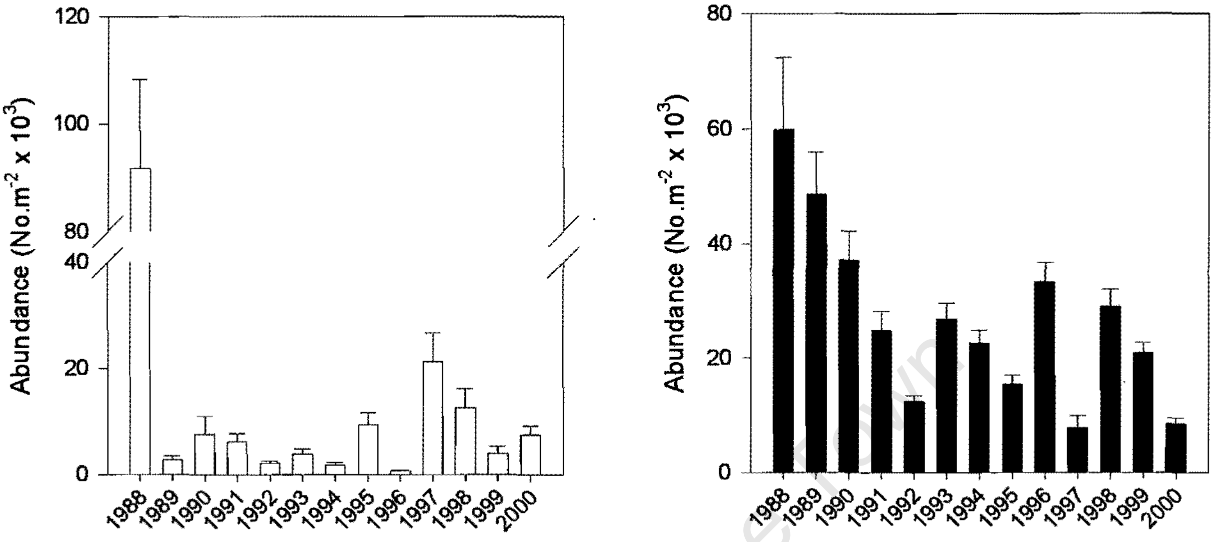
Mean annual abundance (No.m^{-2}) and biomass (g dry wt m^{-2}) of *C. carinatus* and *C. agulhensis* during both the summer and winter cruises, as well as mean biomass in each area during summer and winter, are provided here in order to complement the more descriptive results of relative abundance (No.m^{-3}) by year and area provided by the GAMs.

Interannual variability in abundance and biomass

Mean annual abundance and biomass of *C. carinatus* during summer were closely coupled (Fig. 2.18a,c), but did not display any clear trends over the time-series. Abundance of this species was exceptionally high during November 1988 (~92 000 ind.m^{-2} and 3.3 g dry wt m^{-2}), particularly on the CWC but also on the CAB and EAB (data not shown), indicating that this phenomenon was not restricted to the West Coast. Abundance was next highest in 1997 and 1998 (21 000 and 12 500 ind.m^{-2} respectively), and lowest in 1996 (700 ind.m^{-2}, equivalent to only 0.03 g dry wt m^{-2}). In contrast, mean annual abundance of *C. agulhensis* during the summer cruises appeared to decline over the time-series, with greatest abundance (60 000 ind.m^{-2}) in 1988 and smallest abundance (~8 000 ind.m^{-2}) in 1997 and 2000 (Fig. 2.18b). This trend was not evident from the mean annual biomass, however, which was high (>2.0 g dry wt m^{-2}) from 1988 to 1990, moderate (0.5-1.0 g dry wt m^{-2}) from 1991 to 1995, and highly variable (0.3-2.2 g dry wt m^{-2}) from 1996 to 2000 (Fig. 2.18d).

Mean annual abundance of *C. carinatus* copepodites during winter was greatest (although highly variable) in 1991 (~23 000 ind.m^{-2}; Fig. 2.19a), whereas biomass was greatest in 1998 (>1.0 g dry wt m^{-2}; Fig. 2.19c). Both abundance (1 000-2 000 ind.m^{-2}) and biomass (<0.1 g dry wt m^{-2}) were extremely low in 1988 and 1997, the latter year coinciding with low abundance of *C. agulhensis*. Mean annual abundance of *C. agulhensis* during winter increased from 5 000 ind.m^{-2} in 1988 to a maximum of 11 000 ind.m^{-2} in 1991, then declined to a minimum of <500 ind.m^{-2} in 1997 (Fig. 2.19b). Abundance increased again rapidly thereafter to reach nearly 10 000 ind.m^{-2} in 2000.

(a) *C. carinatus* abundance in Summer (b) *C. agulhensis* abundance in Summer



(c) *C. carinatus* biomass in Summer (d) *C. agulhensis* biomass in Summer

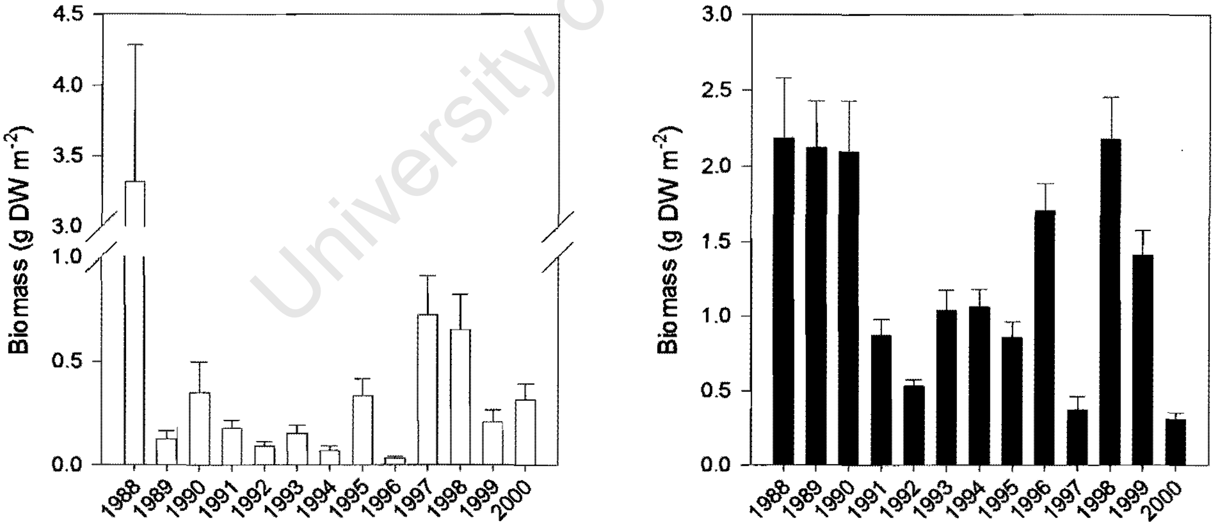
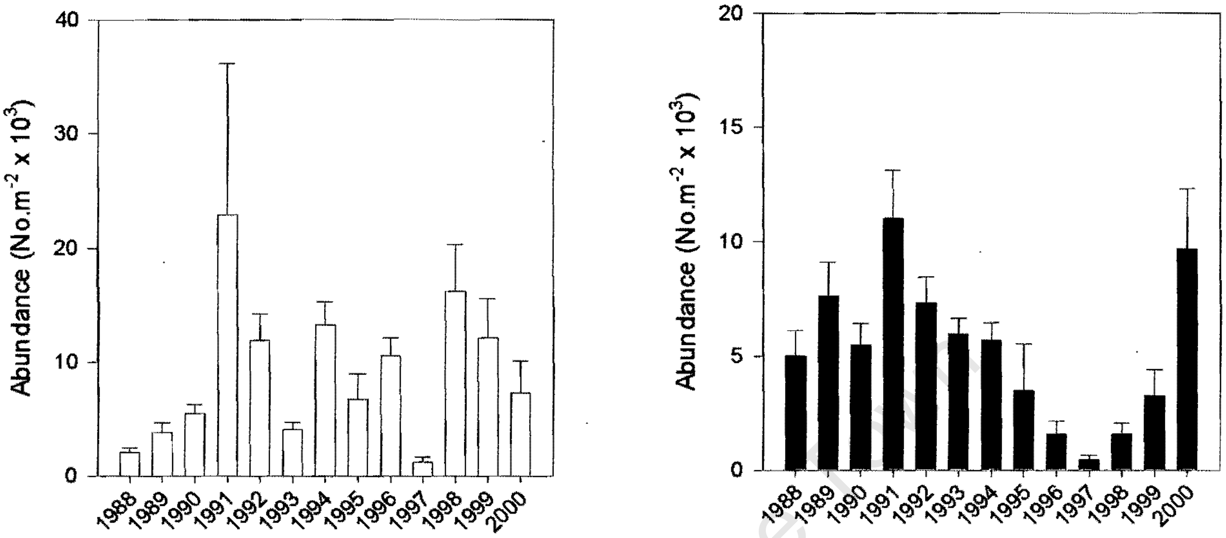


Figure 2.18. Mean annual abundance (+ 1 SE, No.m^{-2}) of all copepodite stages combined for all summer cruises for (a) *C. carinatus* and (b) *C. agulhensis*, and mean annual biomass (+ 1 SE, g dry wt m^{-2}) of all copepodite stages combined for all summer cruises for (c) *C. carinatus* and (d) *C. agulhensis* (note different scales on *y*-axes).

(a) *C. carinatus* abundance in Winter (b) *C. agulhensis* abundance in Winter



(c) *C. carinatus* biomass in Winter (d) *C. agulhensis* biomass in Winter

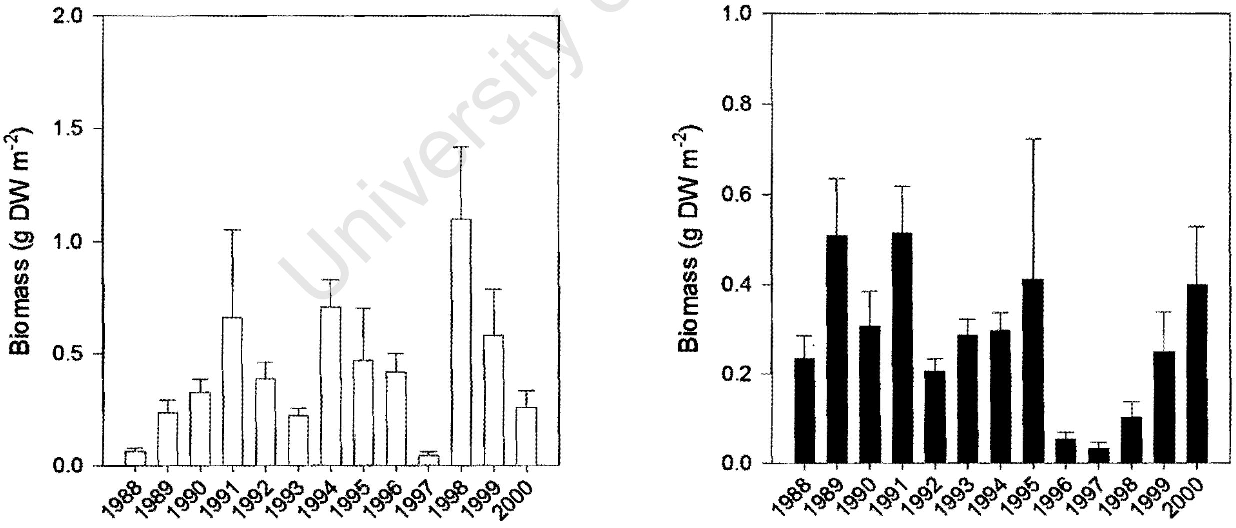


Figure 2.19. Mean annual abundance (+ 1 SE, No.m^{-2}) of all copepodite stages combined for all winter cruises for (a) *C. carinatus* and (b) *C. agulhensis*, and mean annual biomass (+ 1 SE, g dry wt m^{-2}) of all copepodite stages combined for all winter cruises for (c) *C. carinatus* and (d) *C. agulhensis* (note different scales on *y*-axes).

Fluctuations in biomass largely mirrored fluctuations in abundance, with 1992 and 1995 being exceptions (Fig. 2.19d), although biomass in 1995 was also highly variable.

Spatial patterns of biomass

As a result of the exceptionally high biomass of *C. carinatus* during November 1988 (Fig. 2.18a), data from this survey were excluded from the calculations of mean biomass over the time-series presented in Table 2.7. Regarding the core areas of abundance of both species, mean biomass of *C. agulhensis* on the South Coast during summer (1.38 g dry wt m^{-2}) was double that of *C. carinatus* on the West Coast (0.66 g dry wt m^{-2}), and was also greater during winter (0.79 versus 0.58 g dry wt m^{-2}). Mean biomass of *C. carinatus* on the CWC was 1.02 g dry wt m^{-2} during summer and 0.73 g dry wt m^{-2} during winter, compared to 1.82 and 0.87 g dry wt m^{-2} respectively for *C. agulhensis* on the CAB. These results are consistent with the greater seasonal disparity in abundance of *C. agulhensis* compared to *C. carinatus* indicated by the GAMs (Figs 2.15 and 2.16).

Considering the non-core areas of abundance, mean biomass of *C. carinatus* on the South Coast was very low during both summer and winter, not exceeding 0.1 g dry wt m^{-2} in any of the areas (Table 2.7). In contrast, biomass of *C. agulhensis* on the West Coast was quite substantial during summer, measuring >0.4 g dry wt m^{-2} in all three areas. Biomass on the West Coast during winter was greatest on the SWC (0.31 g dry wt m^{-2}), declining substantially to the north.

2.3.4 Relationships between copepod and fish biomass

There were no clear relationships between the biomass of *C. carinatus* and that of pelagic fish on the West Coast during the winter recruitment season (Fig. 2.20a-c) except for a weak relationship between *C. carinatus* on the CWC and sardine biomass north of Cape Columbine (CWC and NWC combined; Fig. 2.20d), which explained 23% of the variance. In contrast, mean annual biomass of *C. agulhensis* during summer, when spawning pelagic fish are concentrated on the Agulhas Bank, was negatively related to the mean biomass of adult anchovy on both the WAB ($r^2 = 0.61$) and CAB ($r^2 = 0.46$), but not the EAB ($r^2 = 0.02$; Fig. 2.21a). *C. agulhensis* biomass was also negatively related to total pelagic fish biomass on both the WAB and CAB ($r^2 = 0.62$ and 0.34 respectively, not shown) during summer, but not to sardine (Fig. 2.21b) or round herring (not shown).

Table 2.7: Mean total biomass (g dry wt m^{-2}) of *C. agulhensis* and *C. carinatus* off the west and south coasts of South Africa from all summer and winter cruises between 1988 and 2000, excluding November 1988. Sample size (n) is also shown.

	C. carinatus		*C. agulhensis*		*n*	
	Summer	Winter	Summer	Winter	Summer	Winter
West Coast	**0.66**	**0.58**	**0.48**	**0.11**	**409**	**761**
NWC	0.68	0.41	0.41	0.02	51	223
CWC	1.02	0.73	0.56	0.06	192	351
SWC	0.24	0.50	0.41	0.31	166	187
South Coast	**0.08**	**0.05**	**1.38**	**0.79**	**1110**	**303**
WAB	0.05	0.08	1.01	0.84	392	187
CAB	0.10	0.01	1.82	0.87	438	66
EAB	0.10	0.02	1.21	0.49	280	50

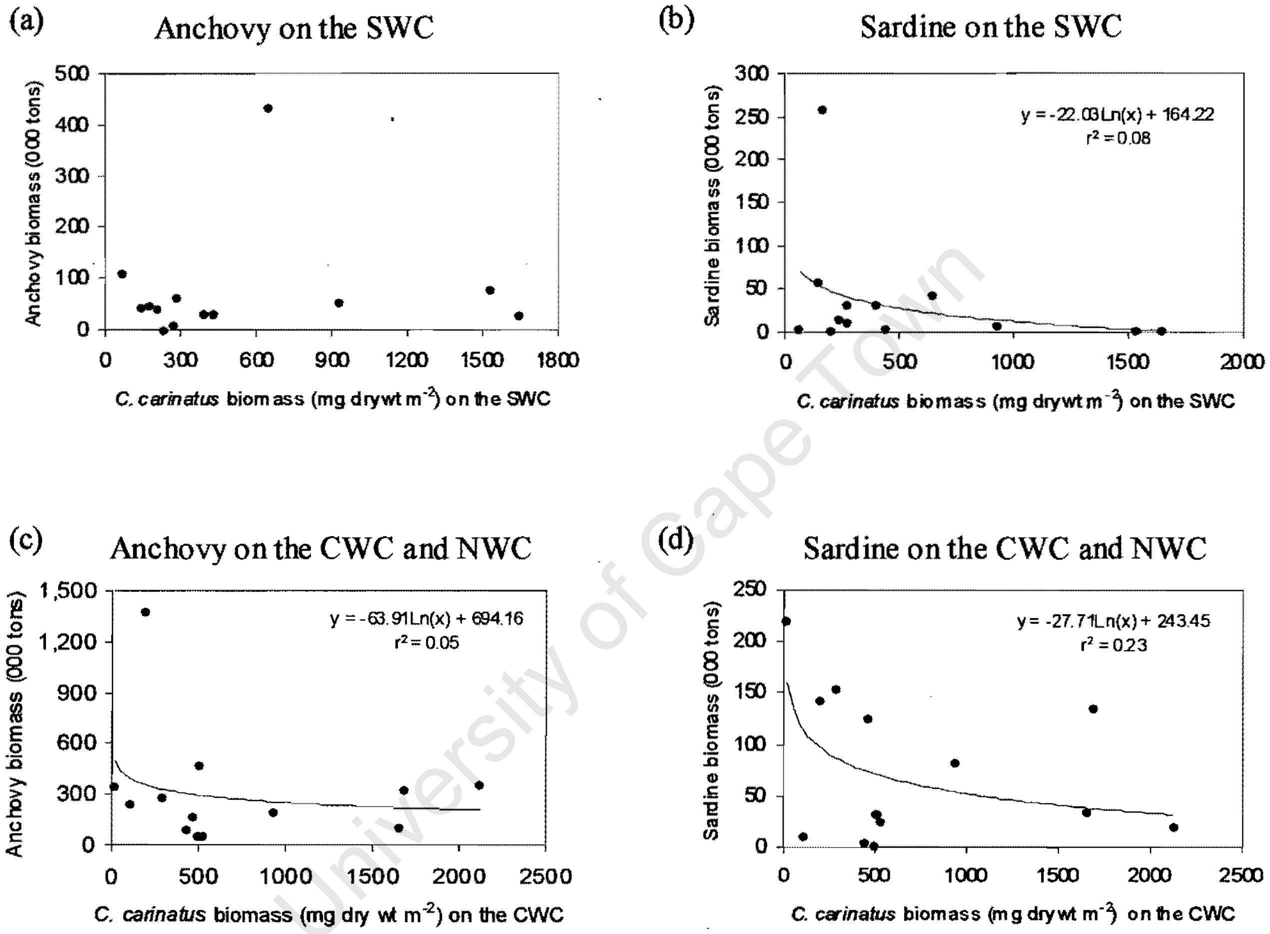


Figure 2.20.. Relationships between mean (a) anchovy and (b) sardine biomass (000 tons) on the SWC and the mean annual biomass (mg dry wt m^{-2}) of all copepodite stages of *C. carinatus* on the SWC, and between (c) anchovy and (d) sardine biomass on the CWC and NWC combined and the mean biomass of *C. carinatus* on the CWC, during all winter cruises (1988-2000). Logarithmic fits are shown.

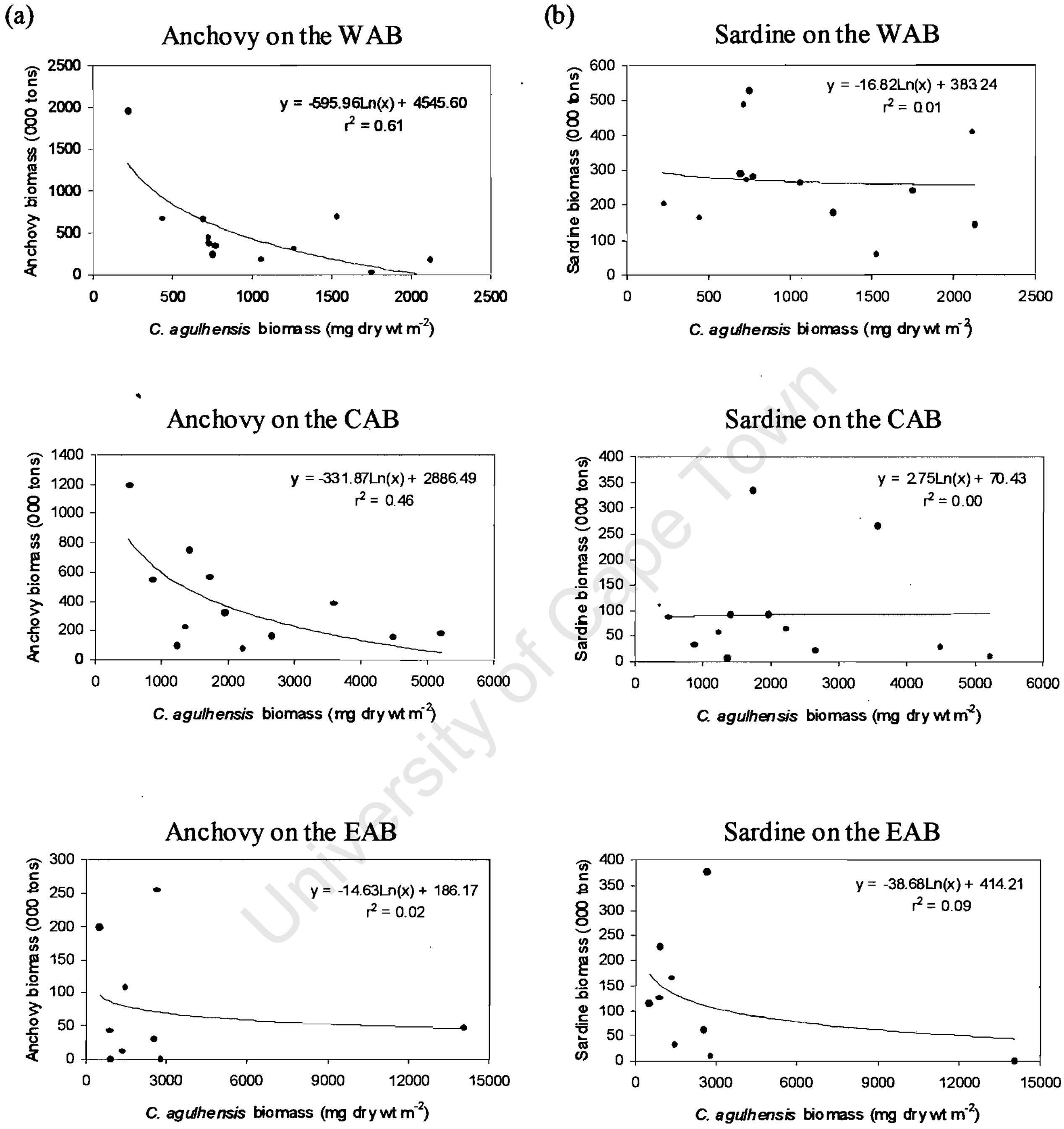


Figure 2.21. Relationships between mean (a) anchovy and (b) sardine biomass (000 tons) and the mean annual biomass (mg dry wt m^{-2}) of all copepodite stages of *C. carinatus* on the WAB, the CAB and the EAB during all summer cruises (1988-2000). Logarithmic fits are shown.

2.4 DISCUSSION

2.4.1 General patterns of distribution

This is the most comprehensive study conducted to date on the horizontal distribution and abundance of arguably the two most important large calanoid copepods found over the South African continental shelf, providing data from both summer and winter over a 13-year period. This period has been characterised by considerable interannual variability in terms of both the environment and fisheries. Previous large-scale studies (e.g. De Decker 1964, 1984) have mainly been qualitative analyses of near-surface samples, whereas this study is based on quantitative analysis of samples from the upper 200 m of the ocean.

This study confirms earlier findings that *C. agulhensis* is largely concentrated on the Agulhas Bank (De Decker 1964; De Decker *et al.* 1991; Verheye *et al.* 1994), whereas *C. carinatus* is largely concentrated on the West Coast (De Decker 1964; Verheye *et al.* 1991). It is also clear that the respective areas of dominance of the two species persist throughout both summer and winter. Of particular interest is the considerable overlap in distribution of the two species, as indicated by the co-occurrence of the females (Fig. 2.3), which includes almost the entire range of both species off South Africa. The combination of extensive spatial overlap but distinct core-areas of abundance suggests that each species is better adapted to the particular conditions characteristic of its core-area, and is able to maintain life-cycle closure in this region.

The sharp decline in abundance of *C. agulhensis* on the West Coast (its non-core area) from south to north (Fig. 2.16) suggests a major input of this species from the southernmost limit of this region, i.e. the Agulhas Bank core area, or else a decreasing gradient of losses from north to south. However, the gradual decline in abundance of *C. carinatus* from east to west on the Agulhas Bank (its non-core area; Fig. 2.15) suggests an input of this species from the easternmost region of the Bank, possibly the east African coast or southwest Indian ocean, both of which are far removed from the West Coast core area. A more detailed study of the distribution of each species in relation to circulation patterns at the extremities of the core and non-core regions, as well as to predation and other sources of loss, is required to determine whether there is evidence to support these theories.

2.4.2 Distribution of *C. carinatus*

The widespread distribution of *C. carinatus* around the South African coastline was also observed by De Decker (1984), who had previously found this species to be abundant on the Agulhas Bank, although not noticeably more so than in adjacent regions (De Decker 1973). Given the occurrence of

C. carinatus off the entire west African coast (Thiriot 1978; Peterson 1998), the south African coast and Somalia on the north-east African coast (Smith 1984), it is tempting to speculate that this species may in fact possess a continuous circum-African distribution incorporating both the Atlantic and Indian oceans, as suggested by Verheye *et al.* (1992) and Peterson (1998). Verheye *et al.* (1992) observed that the seasonal appearance of diapausal C5s would provide an ideal mechanism for long-term dispersal and large-scale colonisation of *C. carinatus* within its global area of distribution. The lack of information on copepod species composition off much of the east African coast, including Moçambique, Tanzania and Kenya, thus provides an intriguing avenue for future investigations. Genetic studies are also needed to confirm such widespread occurrence of a single species.

The location of greatest abundance (Fig. 2.15) and biomass (Table 2.7) of *C. carinatus* off the CWC is consistent with previous observations of higher densities of copepods north of Cape Columbine (Pillar 1986; Verheye *et al.* 1992), particularly in the vicinity of St Helena Bay. Enhanced plankton biomass in this region is a consequence of its location downstream from two major upwelling centres (Cape Columbine and Cape Peninsula), as well as retention mechanisms in St Helena Bay (Verheye *et al.* 1992; Verheye *et al.* 1998). The common occurrence of high abundance of all stages at various distances downstream from Cape Columbine indicates the importance of this upwelling cell as a centre of production and dispersal of *C. carinatus*, leading to the high biomass of this species observed off the CWC during summer, when upwelling-favourable winds are strongest (Shannon and Nelson 1996).

It is puzzling to note that biomass of *C. carinatus* on the CWC was not substantially lower during the winter surveys (Table 2.7), despite a reduction in upwelling winds during autumn and winter. This may be an artefact of sampling design. As sampling during the summer surveys extended much farther offshore compared to the winter surveys (Fig. 2.1), and greatest abundance of *C. carinatus* was largely restricted to the shelf (Fig. 2.2a), the area for which mean biomass of *C. carinatus* on the CWC was calculated would have included a greater proportion of stations with low or zero biomass of this species during summer compared to winter, resulting in a net "dilution" of mean biomass on the CWC during summer. If biomass calculations are restricted to measurements made on the shelf ($\leq$200 m), mean biomass of *C. carinatus* on the CWC during summer (1.5 mg DW m^{-2}) was approximately twice that during winter (0.7 mg DW m^{-2}), which is more consistent with expected seasonal differences in production.

High abundance of late-stage copepodites close to the coast north of Cape Columbine, as was observed during several of the surveys (Figs 2.6 and 2.8a), may reflect the ontogenetic layering and migratory behaviour ascribed to *C. carinatus* in the southern Benguela, whereby young copepodites occupy shallow depths, and the older stages inhabit progressively deeper depth ranges (Verheye 1991;

Verheye and Field 1992). This results in differential cross-shelf distribution of developmental stages of *C. carinatus* during contrasting phases of the upwelling cycle (Verheye *et al.* 1992). During active upwelling, wind-driven Ekman transport advects the surface-dwelling young stages northwards and offshore, while the deeper-migrating older individuals seem to be less affected by surface transport and remain closer inshore during upwelling (Verheye *et al.* 1991; see Fig. 1.11 in Chapter 1). This pattern of distribution is supported by the strong association between female and C5 *C. carinatus* copepodites and very cold subsurface (30 m) water (Fig. 2.15). This association was less important for the younger stages, which develop in the gradually warming, food-rich upwelling plume as it moves offshore, although they may return to the coast via onshore flow associated with quiescent conditions (Verheye *et al.* 1991). This scenario is also consistent with the positive relationship between Chl *a* concentration and abundance of the younger stages (C1-C3; Fig. 2.15), but not the older stages (except for a weak relationship with the males).

Discrete areas of high abundance of all stages ("hotspots") located farther offshore, such as during November 1998 (Fig. 2.6b), may be the consequence of patches of productive water containing young copepod stages becoming gradually separated from the inshore community as a result of prolonged upwelling and associated offshore advection. In November 1998 the hotspot was clearly downstream from the Cape Columbine upwelling cell, and was associated with moderate to high concentrations of Chl *a* (>2 mg m^{-3}), which are favourable for growth and reproduction. Hutchings (1981) calculated that zooplankton may be displaced 40 to 90 km offshore during active upwelling, and Pillar (1986) noted significant increases in copepod biomass 59 to 77 km offshore on the CWC during the upwelling season. These observations are consistent with the GAM results for *C. carinatus*, which indicated that greatest abundance of all stages was concentrated just within the shelf edge (Fig. 2.15).

The distribution pattern of *C. carinatus* along the outer shelf on the South Coast during summer, where SSTs are often warm due to the influence of the Agulhas Current, suggests that the presence of this species may result from some interaction with the Agulhas Current. One possible scenario is that *C. carinatus* is transported from the East Coast to the Agulhas Bank via the Agulhas Current. High numbers of juveniles are associated with upwelling centres and cyclonic eddies in the inshore/Agulhas Current boundary region off Durban and farther south, particularly during spring, from where the older stages are thought to disperse as they mature (De Decker 1964, 1973; Carter 1977). Although low densities were found in the core region of the Agulhas Current (Carter 1977), southward transport along the narrow shelf inshore of the core current towards the Agulhas Bank is likely, as has been observed for eggs and larvae of a number of linefish species that spawn on the shelf in KwaZulu-Natal (Hutchings *et al.* 2002).

Near Port Elizabeth the shelf begins to widen, and the Agulhas Current diverges from the coast, following the shelf break (Boyd and Shillington 1994). Cold-water eddies, intrusions or plumes of Agulhas Current water onto the shelf and large meanders of the Agulhas Current are common features in this region, and may either entrain biota onto the Agulhas Bank or displace them far offshore (Hutchings *et al.* 2002), whilst sporadic shelf-edge upwelling enhances the productivity along the outer margins of the Bank (Swart and Largier 1987; Hutchings *et al.* 2002). Cyclonic shear-edge eddies are prevalent along the inner edge of the current, particularly in the Agulhas Bight region. Modelling studies suggest that these eddies become trapped in the shelf bight, sandwiched between fast-moving Agulhas Current water and more sluggish water over the shelf (Lutjeharms *et al.* 2003). Although these eddies move slowly (~8 km d^{-1}) south-westward along the shelf edge, eastward flow just inshore of the current margin has been shown to be quite prevalent (Lutjeharms *et al.* 1989), providing a return flow with velocities up to 1 m s^{-2} (Boyd *et al.* 1992). Net movement of near-surface water to the north-east (Boyd and Shillington 1994) may thus facilitate the retention of biota inshore of the Agulhas Current on the relatively shallow Agulhas Bank (Boyd *et al.* 1992; Hutchings *et al.* 2002), as has been observed for kingklip eggs and larvae (Roberts *et al.* 2002). At the apex of the Agulhas Bank, an offshoot of the Agulhas Current travels northwestwards, along the outer edge of the WAB, and Hutchings *et al.* (2002) suggest that the apex of the Bank may also be an important retention area. It is therefore likely that these retention mechanisms contribute to the prevalence of *C. carinatus* along the shelf edge of the Agulhas Bank during summer. Although the productivity of this region is enhanced by shelf-edge upwelling, it is probably insufficient for the abundance of *C. carinatus* to attain as high levels as those common to the highly productive Benguela upwelling system.

The possibility of *C. carinatus* being upwelled directly onto the Agulhas Bank should also be considered. The bottom water on the EAB and CAB is thought to originate from Indian Ocean Central Water (Chapman and Largier 1989), which is upwelled at the shelf edge by Agulhas Current forcing to form the basal layer (<10°C) on the shelf (Swart and Largier 1987). This current-driven upwelling has several mechanisms, including frontal eddies, boundary layer veering and critical shelf waves, and is considered to be both seasonally consistent and uniform (Chapman and Largier 1989). *C. carinatus* was frequently found at depths below 700 m in Antarctic Intermediate Water, south of Madagascar, during a cruise in June/July 1961 (De Decker and Mombeck 1964). This water mass underlies Indian Ocean Central Water, which extends from 200 to 600 m (De Decker and Mombeck 1964), and which Chapman and Largier (1989) consider to be the source of water upwelled onto the EAB. Whether it is possible for animals occurring deeper than the Central Water to become incorporated in deep Agulhas Current water, and eventually be upwelled onto the Bank, is therefore uncertain. De Decker and Mombeck (1964) suggested that these deep-occurring *C. carinatus* south of Madagascar may in fact have originated from the Benguela system, via Atlantic water flowing eastward at some depth around Cape Point into the deep layers of the Indian Ocean.

Lutjeharms (1996) noted that water from the region east of Madagascar joins the Agulhas Current at depth, although water from the inshore side of the Agulhas current comes mainly from the Moçambique Channel. Both of these water masses could in theory facilitate the transport of *C. carinatus* from the Somali upwelling system, via the South Equatorial Current (see Fig. 1.2a in Chapter 1), but such transport would need to occur within a time frame of approximately four months, which is the maximum period that the lipid reserves are thought able to sustain *C. carinatus* individuals in a state of diapause or arrested development (Arashkevich *et al.* 1996). It seems more likely that the animals associated with upwelling off the East Coast of South Africa (Carter 1977) may originate from these northern sources, rather than there being any direct link with shelf-edge upwelling onto the Agulhas Bank. However, it may instead be possible for *C. carinatus* to be introduced onto the Agulhas Bank at depth via the WAB. Although surface flow off the West Coast is predominantly equatorward, deep poleward flow appears to be a regular feature, and may extend eastward around the Cape Peninsula during summer (Shannon and Nelson 1996). Furthermore, bottom water on the WAB is thought to be mainly of Atlantic origin, resulting from seasonal wind-driven upwelling of South Atlantic Central Water onto the western edge of the continental shelf (Chapman and Largier 1989), and southeastward flow onto the Agulhas Bank has been documented by Nelson and Polito (1987). This flow is thought to continue eastwards roughly following the bathymetry, but to lose its character in the southernmost region of the Agulhas Bank, where it probably mixes with other bottom water originating from the eastern Agulhas Bank. These deep flow patterns could facilitate the introduction of diapausal or resting stages of *C. carinatus* onto the WAB via shelf-edge upwelling, as suggested by moderate densities along the shelf edge during some of the cruises. However, more studies of water mass characteristics and flow patterns in this region are needed to confirm this hypothesis, and genetic analyses of animals collected from different areas and depth strata should also be pursued.

2.4.3 Distribution of *C. agulhensis*

There is now considerable evidence from the 13 summer surveys reported here to support the hypothesis that the centre of distribution of *C. agulhensis* is closely associated with the quasi-permanent ridge of cool water on the central and eastern Agulhas Bank. This feature was first described in detail by Swart and Largier (1987) as a midshelf ridge of cold water lying roughly along the 100-m isobath west of the area between Cape Seal (Plettenberg Bay) and Cape St Francis, and is thought to be fed by water that upwells in that region (Boyd and Shillington 1994). Although the presence of the ridge is usually determined from vertical thermal profiles, Swart and Largier (1987) found it to be a common feature in infra-red satellite images, occurring from summer through to autumn. When present it tends to separate the outer Agulhas Bank region influenced by intrusions of Agulhas Bank water and shelf-edge upwelling, from a region of deep mixing inshore and to the west (Boyd and Shillington 1994). These authors found the ridge to be present in November 1988 and 1989, absent in 1990, and present to a lesser extent in 1991. Besides confirming these findings, the present study also indicates that the ridge was present in November 1993, 1995 and 2000 as well as in January 1992 and May 1994, although its persistence is still unknown.

When the cool ridge is prominent, large concentrations of young copepodite stages (C1-C3) are usually associated with, or found downstream of, the ridge (Fig. 2.11). This supports the findings of Peterson and Hutchings (1995), who measured fast rates of egg production downstream of the ridge, and suggested that enhanced productivity and food concentration within and around the ridge would promote fast growth of the nauplii and juveniles. Predominantly cyclonic flow around the ridge (Boyd *et al.* 1992; Boyd and Shillington 1994) is thought to favour the retention of copepods, in particular the young stages (Peterson *et al.* 1992; Peterson and Hutchings 1995). Faster growth rates of these young stages compared to those on the WAB (Peterson *et al.* 1992; Hutchings *et al.* 1995) are stimulated by relatively high Chl *a* concentrations (2-5 mg m^{-3}) associated with the ridge, as indicated by satellite imagery (Shannon *et al.* 1984) and direct measurements (Peterson and Hutchings 1995). These features contribute to the greater biomass of *C. agulhensis* on the CAB and EAB compared to the WAB during summer (Table 2.7), in addition to the likelihood of greater predation on copepods by spawning pelagic fish on the WAB than on the CAB and EAB during summer.

The offshore and westward shift in distribution with increasing stage observed for *C. agulhensis* (Fig. 2.16) suggests a gradual ontogenetic shift away from the relatively shallow and productive cool ridge south of Mossel Bay, where the younger copepodites are most abundant, towards the gradually deepening southern region of the Agulhas Bank. Current vectors indicate a net westerly drift on the outer CAB in spring/summer, particularly near the bottom (Boyd and Shillington 1994). As *C. agulhensis* displays ontogenetically-based vertical migration (see Chapter 6), the older stages, by swimming deeper than the younger stages, would be more susceptible to this stronger westward drift and be displaced progressively farther west than the more shallow occurring younger stages.

The north-westward advection of *C. agulhensis* often extended beyond the Cape Peninsula along the shelf edge towards the West Coast. Patches of young copepodites, in particular, were associated in some years with relatively strong, convergent flow in the vicinity of the shelf-edge jet current (Fig. 2.13), which has been shown to be instrumental in the transport of fish eggs and larvae from the Agulhas Bank spawning grounds towards the west coast nursery region (Shelton and Hutchings 1982; Huggett *et al.* 1998). The secondary node of abundance at ~300-350 m observed for all stages (Fig.

2.15) may thus reflect the transport of copepods along or beyond the WAB shelf edge en route to the West Coast, a pattern often observed in distribution maps of anchovy and sardine eggs during the summer surveys (van der Lingen *et al.* 2001). Moderate concentrations of both young and old copepodites farther north, either associated with or beyond the west coast shelf edge, may be the consequence of such advection, injecting varying quantities of *C. agulhensis* into the offshore region of the west coast ecosystem.

The GAMs of longitudinally-related abundance on the Agulhas Bank during summer support the hypothesis that the centre of abundance of *C. agulhensis* is displaced westward when the Agulhas Ridge is absent (Fig. 17b). Contour maps of abundance also indicated greater densities of *C. agulhensis* on the WAB when the cool ridge was weakly defined (e.g. November 1991) or spatially restricted (e.g. November 1995). Hutchings *et al.* (1995) first noted a westward shift in biomass of *C. agulhensis* on the Agulhas Bank in November 1990, when the ridge was absent, primarily due to an increase in abundance of older stages, but also possibly due to decreased predation by the low biomass of pelagic fish on the WAB that year. In the absence of a mechanism to retain copepods in the central region of the Agulhas Bank, net westerly drift on the outer central Bank in spring/summer and convergent northwest currents on the WAB (Boyd and Shillington 1994) would tend to favour the concentration of copepod biomass on the WAB at this time of year. This is supported by the progressively deeper peak abundance of *C. agulhensis* with increasing stage when the ridge was absent (Fig. 2.17b). Furthermore, input of *C. agulhensis* from the Agulhas Bank to the West Coast is likely to be greater when the ridge is weak or absent, and the population is shifted towards the WAB. It will also be enhanced when lowered predation pressure on the WAB enables the copepods to survive longer, thus being more likely to reach adulthood and reproduce.

The concentrations of older stages occasionally observed along the shelf edge of the EAB (Fig. 2.7) may be related to the shear-edge cyclonic eddies prevalent in the Agulhas Bank shelf bight discussed previously. The main shear-edge eddy, represented by a dome of cold water, is a recurrent feature of the Agulhas Bank bight, although it may lie farther upstream or downstream, and is also present in winter according to both hydrographic and modelled data (Lutjeharms *et al.* 2003). The presence of the older stages at greater water column depths than the younger stages would make them more susceptible to becoming entrained and retained in such eddies and the associated counterflow along the shelf edge.

Whereas the summer surveys usually extend only as far eastward as Port Elizabeth or Port Alfred on the South Coast, sampling in January 1992 revealed *C. agulhensis* to be present farther east, up to and beyond East London. Concentrations of the younger copepodites were associated with cool (11-14°C) subsurface (30 m), presumably upwelled and Chl-rich water in the vicinity of Port Elizabeth as well as farther north. The presence of *C. agulhensis* within this region is not unusual, as Carter (1977) found this species to occur in the neritic community inshore of the western boundary of the Agulhas Current. It was rare off Durban, but occurred fairly frequently off Port Edward further south (just east of 30°E). Carter (1977) suggested that it was transported eastward from the Agulhas Bank area into the KwaZulu-Natal coastal region, counter to the Agulhas Current. De Decker (1964, p. 9) reported "a narrow but sometimes very rapid and appreciably colder counter current" between the warm Agulhas Current and the South-east coast, and suggested (De Decker 1973) that certain copepod species found along the coastline as far as Durban may be transported there by the cold counter current. In a later paper, De Decker *et al.* (1991) noted that populations of *C. agulhensis* had been found as far north as St Lucia (28°S) on the East Coast.

The dome-shaped relationship between *C. agulhensis* and SST, with greatest abundance between 15 and 20°C and a peak at ~18°C, particularly for the younger copepodites, reflects the predominant temperatures on the central region of the Agulhas Bank. Cooler temperatures are associated with coastal or shelf-edge upwelling, whereas warmer temperatures characterize the outer edge of the Bank influenced by the Agulhas Current. Although De Decker *et al.* (1991) suggested that C5s were tolerant of a wider temperature range than the adults, there was no evidence of this from the GAMs; they indicated instead that the adults were more likely to be found at both cooler and warmer temperatures than the younger stages. This probably reflects the greater abundance of the adults offshore and along the shelf edge, where either the temperature may be more extreme due to either shelf-edge upwelling or Agulhas Current influences.

The lower Chl *a* levels characteristic of much of the Agulhas Bank are reflected by the association of all copepodite stages with low concentrations of 1-2 mg Chl *a* m^{-3}. The youngest stages were also associated with higher concentrations of 5-6 mg Chl *a*, reflecting the elevated productivity and Chl *a* concentrations associated with the cool ridge. Although the older stages were sometimes associated with moderate concentrations of Chl *a* resulting from shelf-edge upwelling, these concentrations rarely exceeded 2 mg m^{-3}.

2.4.4 Seasonal patterns of biomass and abundance

It is interesting to note that the biomass of *C. agulhensis* on the South Coast, a region of relatively low productivity, is considerably higher than that of *C. carinatus* on the highly productive West Coast, particularly during summer (Table 2.7). This apparent paradox is probably because *C. agulhensis* is the only dominant calanoid copepod on the Agulhas Bank, accounting for roughly 50-80% of the standing stock of all calanoid copepods across the Bank (Verheye *et al.* 1994). *C. carinatus*, however, is one of approximately eight small to large calanoid species that dominate the more diverse West

Coast community (Verheye *et al.* 1992), resulting in greater competition for and partitioning of the rich food resources. During an anchor station study in St Helena Bay in autumn 1987, *C. carinatus* comprised only 13-27% of copepod numbers, and was outnumbered by four smaller calanoid species, although it was the dominant zooplankter in terms of biomass because of its greater size (Verheye 1991). The maximum proportion of the copepod biomass previously recorded for *C. carinatus* off the West Coast is 67% (Painting 1989), but in other studies this figure was usually lower, with *C. carinatus* accounting for ~15% of total mesozooplankton carbon on average (Verheye 1991).

The seasonal bias in sampling coverage is likely to have resulted in an underestimation of the biomass and abundance of both species on the South Coast during winter, due to the poor coverage of the CAB and EAB during the winter surveys, as well as of *C. agulhensis* on the West Coast during winter, due to the reduced coverage farther offshore, where *C. agulhensis* tends to be more abundant (Fig. 2.2). This may have contributed to the particularly large seasonal disparities in biomass of *C. agulhensis* for the NWC and CWC (20 × and 10 × respectively), as well as that of *C. carinatus* for the CAB and EAB (10 × and 5 ×; Table 2.7). However, these large differences could also be related to the greater variability in abundance and composition of animals outside of their core areas; seasonal differences for animals in their core areas were much smaller.

Although mean annual abundance of *C. carinatus* appeared to be consistent over the time-series (Fig. 2.15), variability in interannual abundance was much greater when viewed seasonally (Figs. 2.18 and 2.19), with exceptionally high abundance (>90 000 ind.m^{-2}) in November 1988 contrasting with <700 ind.m^{-2} in 1996 (Fig. 2.18a). The cause of such high abundance is uncertain, but may have resulted from an extended period of favourable environmental conditions conducive to fast growth and reproduction prior to the survey. Such extremes in abundance emphasize the high variability associated with the Benguela upwelling system during spring and summer. This is in sharp contrast to the Agulhas Bank, where the much smaller range in annual abundance (~8000 to 60 000 ind.m^{-2}) of *C. agulhensis* during summer (Fig. 2.18b) suggests more consistent productivity. Variability in abundance of both species during winter was similar (Fig. 2.19), and suggests greater variability on the Agulhas Bank compared to summer, but less variability on the West Coast compared to summer.

2.4.5 Density-dependent interactions with pelagic fish

The absence of any clear relationships between the biomass of *C. carinatus* and that of pelagic fish on the West coast during the recruitment surveys (Fig. 2.20) suggests that predation by planktivorous fish does not appear to be an important factor influencing the abundance of this copepod during winter. The larger copepodite stages would be vulnerable to consumption by anchovy, which feed selectively on large zooplankton (James 1988; James and Findlay 1989), whereas the smaller stages would be of suitable size to sardine, which feed primarily on microzooplankton, small copepods and phytoplankton (van der Lingen 1994; Louw *et al.* 1998). As *C. carinatus* is only one component of the zooplankton food assemblage available to pelagic fish on the West Coast, and the areas under consideration are broad, this is a rather simplistic analysis of possible density-dependent interactions, and falls outside the scope of the present study. It is possible that these fish may become food limited at times of high biomass in more localised areas, such as St Helena Bay, however (H. Verheye, MCM, pers. comm.).

In contrast to *C. carinatus* on the West Coast, there is evidence to suggest density-dependent interactions between *C. agulhensis* biomass and pelagic fish biomass, particularly anchovy, on the South Coast during summer. This is shown by the logarithmic decline in mean total biomass of *C. agulhensis* in relation to the biomass of both anchovy (Fig. 2.21) and total pelagic fish biomass (not shown) on the WAB and CAB from November 1988 to November 2000. As *C. agulhensis* may comprise over 80% of the copepod biomass on the Agulhas Bank (Verheye *et al.* 1994), it is clearly an important food source for spawning anchovy during summer. Particularly noteworthy is the extremely high biomass of anchovy during November 2000, exceeding two million tons on the WAB, which coincided with the lowest biomass of *C. agulhensis* recorded on the WAB over the 1988-2000 time-series, measuring just 224 mg dry wt m^{-2} (Fig. 2.21a).

Although predation by pelagic fish seems to provide a reasonable explanation for fluctuations in abundance of *C. agulhensis* on much of the Agulhas Bank, there are doubtless numerous other factors which play a role, including climatic and environmental influences, and interactions with other species. Even with time-series extending for more than 30 years it is difficult to recognise cause and effect of fluctuations in abundance (Mauchline 1998), and it is particularly fortuitous that the planktivorous pelagic fish stocks off South Africa have displayed such extremes in abundance over the last decade, enabling density-dependent effects to be demonstrated.

2.5 CONCLUSIONS

C. carinatus is an opportunistic species characteristic of many upwelling systems, colonizing recently upwelled water as C5s, and reproducing rapidly after moulting to adult. It is abundant during both spring/summer and autumn/winter in the highly productive southern Benguela system, with greatest abundance on the CWC. Its presence on the outer Agulhas Bank is most likely the result of transport from upwelling centres on the East Coast southward along the narrow shelf inshore of the core Agulhas Current towards the Agulhas Bank, where shelf-edge upwelling and local retention mechanisms enhance moderate levels of abundance. The source of these seed populations could also be upwelled bottom water originating from the east or the west, but this remains highly speculative, and may only be ascertained using a particle-tracking/high-resolution physical model of the region (such as that used by Huggett *et al.* 2003 to track fish eggs and larvae) in conjunction with genetic studies.

C. agulhensis has a centre of abundance closely associated with the cool ridge on the CAB, which is characterized by enhanced primary production and a quasi-permanent retention mechanism. Dispersion of copepodite stages from this centre allows it to dominate over the whole Agulhas Bank, although the centre of abundance is displaced westwards when the Agulhas Ridge is absent. Dispersion to the west and north, combined with convergent northwest flow on the WAB, results in considerable advection by the shelf-edge jet current to the West Coast during spring and summer, where high abundances of young stages suggest active reproduction in offshore waters on the WAB and SWC.

Despite the fact that the biannual surveys can best be regarded as "snapshots" in time, with little or no indication of prior environmental history, data collected from these surveys have indicated a considerable level of population stability in the core areas, but greater variability in non-core areas. High interannual variability in abundance of *C. carinatus* during summer probably reflects the inherent variability of the productive Benguela upwelling system, in contrast to more consistent productivity and greater population stability of *C. agulhensis* on the Agulhas Bank.

C. carinatus and *C. agulhensis* constitute an important food source for the large populations of pelagic fish in the southern Benguela, which utilize the Agulhas Bank as a spawning ground and the inshore West Coast as a nursery ground. Although there is as yet little evidence of density-dependent interactions between *C. carinatus* and anchovy and sardine recruits on the West Coast during winter, there appears to be a predatory, top-down interaction between spawning anchovy and *C. agulhensis* on the WAB and CAB during summer.

Although there is considerable spatial overlap in the distribution of the two copepod species, the separation of the core areas of abundance indicates there must be fundamental differences between the two species that make them better suited to their respective area of dominance, and able to maintain life-cycle closure there. Possible factors are explored in the following chapters, by comparing the functional response of both species to a range of environmental conditions, both in the field and in controlled laboratory experiments.

CHAPTER 3

The effect of temperature, food abundance and food size on egg production by *Calanoides carinatus* and *Calanus agulhensis*

3.1 INTRODUCTION

The rate at which female calanoid copepods lay eggs varies in response to extrinsic factors such as temperature (Plourde and Runge 1993; Hirche 1996; Uye and Murase 1997; Hirche *et al.* 1997), food abundance and nutritional quality (Marshall and Orr 1952; Checkley 1980a; Runge 1984, 1985; Paffenhöfer and van Sant 1985; Peterson and Bellantoni 1987; Peterson 1988), as well as intrinsic factors such as age or reproductive status of females (Ianora 1990; Plourde and Runge 1993) and their feeding history (Runge 1984; Borchers and Hutchings 1986; Peterson 1988; Attwood and Peterson 1989; Armstrong *et al.* 1991; Calbet and Alcaraz 1996). *Calanus* egg production tends to increase linearly or exponentially with temperature (Runge 1985; Hirche 1996; Uye and Murase 1997), and some studies have suggested that temperature is the primary factor limiting copepod growth and production (McLaren 1978; Huntley and Lopez 1992). Huntley and Lopez (1992) proposed that, in nature, copepods may always be able to find sufficient food to grow at maximal rates, even if "oceanographers cannot" (p. 237), and that appearances to the contrary may be a result of sampling at inappropriate scales. However, many studies have shown copepod egg production in the ocean to be food-limited (Checkley 1980b; Peterson 1988; Peterson *et al.* 1990b, 1991; Uye and Murase 1997; Richardson and Verheye 1998; Richardson *et al.* 2003). In a comprehensive study of copepod growth rates, Hirst and Lampitt (1998) concluded that weight-specific egg production by female broadcast spawners in the natural environment is independent of temperature, and is typically sub-optimal compared to those in food-saturated conditions. Food availability is now generally regarded as the most important factor influencing egg production (Mauchline 1998).

In addition to food abundance, egg production may also be affected by the quality of available food, which includes factors such as cell size (Paffenhöfer 1984; Runge 1984; Peterson and Bellantoni 1987; Berggreen *et al.* 1988; Armstrong *et al.* 1991; Walker and Peterson 1991; Uye and Murase 1997; Richardson and Verheye 1999), cell structure (Ianora and Poulet 1993) and biochemical composition or nutritional value (Paffenhöfer and van Sant 1985; Cowles *et al.* 1988; Hassett and Landry 1988; Kleppel and Burkart 1995). In addition to lowering egg production, poor food quality may also reduce egg viability or hatching success, and a recent debate has focussed on whether diatoms, traditionally considered to be the primary energy source for marine copepods through to fish in temperate and upwelling ecosystems (Ryther 1969; Cushing 1989; Pauly and Christensen 1995), may in fact have a deleterious effect on copepod egg hatching success (Ianora *et al.* 1995; Jónasdóttir *et al.* 1998; Ianora *et al.* 1999; Miralto *et al.* 1999; Irigoien *et al.* 2002). However, a collaborative study of *in situ* copepod egg hatching success in diatom-dominated phytoplankton assemblages from a wide range of ecosystems failed to demonstrate a negative relationship between hatching success and diatom biomass (Irigoien *et al.* 2002).

In Chapters 1 and 2 it was shown that *Calanoides carinatus* is most abundant off the West Coast, in the southern Benguela upwelling region, whereas *Calanus agulhensis* is most abundant on the Agulhas Bank. One possible reason for these two species having different areas of dominance is that each copepod is adapted to the particular thermal and/or food regime characteristic of its core area, and is thus likely to have greater reproductive success under these conditions compared to those that characterize its non-core area. SST on the west coast shelf commonly ranges from 12-13°C inshore to 17-18°C offshore, with colder temperatures of 10-12°C associated with core upwelling zones. Mean concentrations of Chl *a* in the upper 30 m are >2 mg m^{-3} over practically the entire west coast shelf (Fig. 3.1), with areas of high concentration (>6 mg m^{-3}) north of St Helena Bay and Hondeklip Bay (Brown 1992). This general pattern is maintained throughout the year, although the very high concentrations near the coast are not apparent in winter. SST over the Agulhas Bank is typically 17-20°C, but cooler (12-16°C) in areas characterized by coastal upwelling, particularly the inshore western Agulhas Bank. Warm water (>20°C) is more common along the shelf edge of the central and eastern Agulhas Bank due to the influence of the Agulhas Current. Mean concentrations of Chl *a* over most of the mid-shelf are moderately low (1-2 mg m^{-3}; Fig. 3.1), particularly during summer and winter, although higher Chl *a* concentrations are associated with the inshore coastal upwelling region on the western Agulhas Bank (>3 mg m^{-3}) and dynamic upwelling along the eastern shelf-edge (>2 mg m^{-3}). Highest mean concentrations of Chl *a* in the upper 30 m are found in autumn and spring, when patches of 2-4 mg m^{-3} are fairly widespread. The mean concentration of 3.5 mg Chl *a* m^{-3} on the west coast shelf (Brown 1992) is approximately twice that on the South Coast (1.7 mg Chl *a* m^{-3}). The mean seasonal range is also much greater on the West Coast, with maximum values of 16.5 mg Chl *a* m^{-3} compared to 5.6 mg Chl *a* m^{-3} on the South Coast (recalculated from Brown 1992), although individual measurements of >50 mg Chl *a* m^{-3} have been measured during dinoflagellate blooms on the West Coast (Mitchell-Innes *et al.* 2000).

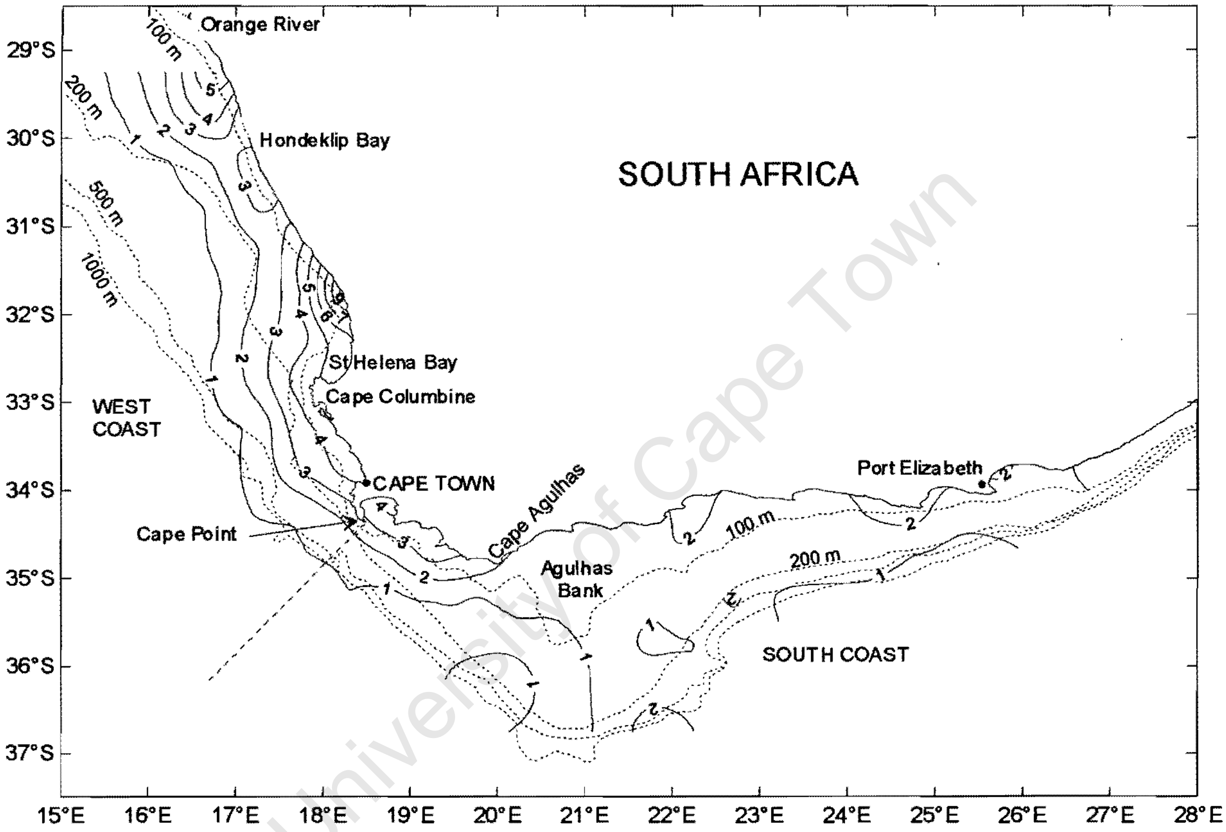


Figure 3.1. Map showing the southern Benguela upwelling region, the Agulhas Bank and locations mentioned in the text. The dashed line indicates the division between the west and south coasts. Also shown are mean concentrations of Chl *a* (mg m^{-3}) in the upper 30 m for the period 1971-1989 (after Brown and Cochrane 1991; Brown 1992).

Upwelling areas are characterised by the dominance of chain-forming and colonial diatoms, with typical cell diameters of 5-30 μm (Estrada and Blasco 1985). These diatoms grow rapidly during the period of reduced mixing and weak stratification following an upwelling event (Hutchings *et al.* 1995a). This is followed by a succession from small diatoms to large diatoms and dinoflagellates as the water column stabilizes. As stratification persists, nutrients become limited, and post-bloom oligotrophic conditions develop in which small-sized phytoplankton become dominant (Pitcher *et al.* 1991; Probyn 1992; Hutchings *et al.* 1995a). As a consequence, phytoplankton cell size increases in tandem with Chl *a* concentration in the southern Benguela (Mitchell-Innes and Pitcher 1992; Richardson and Verheye 1998). The higher concentrations of Chl *a* on the West Coast compared to the South Coast therefore suggests that large cells are likely to be more prevalent in the former region, whereas small cells may be more prevalent on the relatively Chl *a*-poor Agulhas Bank.

Field studies during spring through to autumn have shown egg production by *C. carinatus* and *C. agulhensis* to be positively related to both Chl *a* concentration and cell size (Armstrong *et al.* 1991; Walker and Peterson 1991; Richardson and Verheye 1998). Egg production by *C. agulhensis* displays a dome-shaped relationship with temperature in the field, with slower rates of egg production (≤60 eggs $♀^{-1}$ d^{-1}) for temperatures <13°C and >18°C, and faster rates (up to 120 eggs $♀^{-1}$ d^{-1}) between 13 and 18°C (Richardson and Verheye 1998). A clear relationship between egg production and temperature has not been established for *C. carinatus* (Armstrong *et al.* 1991; Richardson and Verheye 1998), although rates of egg production appear to be slower above 18°C (<85 eggs $♀^{-1}$ d^{-1}) than between 11 and 18°C (generally <120 eggs $♀^{-1}$ d^{-1}; Richardson and Verheye 1998). There are no published studies investigating egg production by either species off the South African coast during winter.

The aim of this chapter is to investigate hypotheses concerning the influence of extrinsic factors on egg production by *C. carinatus* and *C. agulhensis* that are pertinent to the contrasting food and temperature regimes of the southern Benguela and Agulhas Bank ecosystems, namely temperature, food abundance and food size. The hypotheses are (1) *C. carinatus* egg production is inhibited by warm temperatures typical of the Agulhas Bank; conversely, *C. agulhensis* egg production is reduced at cooler temperatures characteristic of the Benguela upwelling region; (2) egg production by *C. agulhensis* is satiated at lower food concentrations compared to *C. carinatus*; and (3) food size is more important for *C. carinatus* than *C. agulhensis* to achieve maximum rates of egg production. Laboratory experiments were conducted to investigate the effect of temperature on egg production under conditions of abundant food. Generalized Additive Models (GAMs), which can capture non-linear relationships, were used to explore the effect of temperature, food abundance and food size on egg production in the field during summer and winter. Previously, the effects of multiple factors on egg production were investigated using multiple linear regression (e.g. Richardson and Verheye 1998). The use of GAMs to explore these potentially non-linear relationships is thus a novel approach.

3.2 MATERIAL AND METHODS

3.2.1 Laboratory experiments: the effect of temperature on egg production

An inflatable boat was used to collect copepods from the Cape Peninsula region and St Helena Bay, on the West Coast. A plankton net (300-μm mesh; 0.25-m^2 mouth area) fitted with a 2-litre plastic, screw-on cod-end was allowed to drift at a depth of 5-10 m for about five minutes. Upon retrieval, copepods were released gently into a 20-litre bucket of ambient seawater, and returned to the temperature-controlled laboratory as soon as possible, usually within 1-2 hrs. Females that appeared healthy were selected carefully using a hand-held pipette and placed in 5-litre beakers containing excess concentrations of the diatom *Thalassiosira weissflogii* (ESD = 12.13 μm; >4 000 cells ml^{-1}, after Attwood and Peterson 1989) mixed daily using 0.2-μm filtered seawater (FSW) pre-cooled to the temperature selected for that particular experiment. Cell concentrations were measured using a Coulter Multisizer, and usually ranged between 5 000 and 6 000 cells ml^{-1}. Separate experiments were conducted at 9, 12, 15, 18 and 21°C, and fresh animals were collected for each experiment. Experiments were conducted between October 1994 and March 1995, and were done concomitantly for both species at each temperature.

After an acclimation period of five days, ten females of each species were placed singly into 1100-ml polycarbonate bottles filled with excess *T. weissflogii* and incubated on a rotating plankton wheel (end-over-end; 1 rpm) for 3 days to measure their egg production rate under food-saturation conditions. Although the bottles were not fitted with a screened partition to separate eggs and fecal pellets from females, error due to cannibalism was minimized by the high volume/female ratio (>1 000 ml $♀^{-1}$; Båmstedt *et al.* 2000). Furthermore, Peterson (1988) showed that well-fed *Calanus marshallae* (a similar-sized congener to *C. agulhensis*) females do not consume their eggs. Each day the contents of each bottle were gently poured through a 63-μm mesh to collect the female and any eggs and fecal pellets. The female was examined for condition, and if healthy, was replaced in the bottle with a freshly mixed food-suspension. Dead and moribund females were replaced with spare females from the 5-litre beakers when available. Eggs and fecal pellets were preserved in 5% buffered formalin for later enumeration. Daily egg production (*E*, eggs $♀^{-1}$ d^{-1}) was calculated (after Peterson *et al.* 1991) as:

$$E = N_e \times 24/t$$

where N_e = number of eggs, and t = the duration of the experiment (h). Experiments with dead or moribund females were excluded from calculations of egg production, but were used for calculation of mortality rates. The relative abundance of fecal pellets was used as a rough index of female condition, following the assumption that non-feeding females were in poor condition or senescent. Experiments with non-feeding females were also excluded from calculations of egg production. Mean daily egg production was calculated as the average egg production over a three-day period.

3.2.2 Field experiments: the effect of food size and abundance on egg production

Experiments to measure egg production under natural conditions were conducted during winter recruitment and summer spawner biomass surveys from 1988 to 1993, as well as during the Agulhas Bank Boundary Processes (ABBP) cruise in January 1992 (data from this cruise were included with data from the summer spawner biomass surveys). Temperature, depth and fluorescence profiles were obtained using a temperature-depth recorder in conjunction with a Chelsea Instruments Aquatracka submersible fluorometer mounted on a magnum rosette, and water samples were collected at the surface and depth of maximum fluorescence for determination of Chl *a* and particle spectra. Both total and size-fractionated (<10 µm and/or <15 µm) chlorophyll samples were analyzed on board ship according to the method of Parsons *et al.* (1984), whilst the particle-size spectra were measured using a Coulter Multisizer fitted with a 140-µm aperture tube (measures particles from 2.8-80.0 µm ESD). During all the cruises from 1988 to 1992, water samples were size-fractionated using a 15-µm mesh that was incorrectly labelled as a 10-µm mesh. Once the error was realised, both 10- and 15-µm mesh screens were used simultaneously (during the May 1993 and November 1993 cruises) in order to determine a conversion factor between the two meshes. There was a significant, positive linear relationship between the fraction of Chl *a* larger than 15 µm and that larger than 10 µm (Chl a >10 µm = 1.0104 × Chl a >15 µm + 0.1884, $n = 540$, $r^2 = 0.97$, $p < 0.001$) during the May and November 1993 cruises. This enabled the fraction of Chl *a* >10 µm from earlier cruises to be calculated.

Copepods were collected using a plankton net (300-µm mesh; 0.25-m^2 mouth area) fitted with a 2-litre plastic, screw-on cod-end, which was allowed to drift at a depth of 5-10 m for about ten minutes. Upon retrieval, the contents of the net were released gently into a 20-litre bucket of seawater at ambient surface temperature. Copepods were concentrated from this bucket using a sieve and were washed into a petri dish. Females that appeared healthy were selected using a hand-held pipette under a dissecting microscope with subdued light. Females (usually two per bottle) were placed in 1100-ml polycarbonate bottles filled with 63-µm filtered seawater from the depth of maximum fluorescence (f-max). From one to five bottles per species were incubated at each station, depending on availability of the females. Bottles were incubated on deck in darkened bins cooled with seawater pumped continuously from a depth of 6 m, as described by Hutchings *et al.* (1995b). After 24 h the contents of the experimental bottles were gently poured through a 63-µm mesh to collect the females and their eggs. The condition of the females was checked, and the eggs were preserved in 5% buffered formalin for later enumeration. Experiments with dead or moribund females were excluded from calculations of daily egg production (eggs $♀^{-1}$ d^{-1}), as described above.

Stepwise generalized additive models (GAMs) were used to investigate relationships between egg production and a number of predictors using S-Plus software (Insightful Corp. 2001). Predictors used included *Season* (winter or summer), *SST* (sea surface temperature, °C), *TotalChla* (extracted Chl *a* concentration from the f-max, mg m^{-3}), *%Chla>10* (the proportion of cells larger than 10 µm, %), *Pvol* (volume of particles at the f-max, ppm), and *%Pvol>10* (the proportion of particles larger than 10 µm, %). The concentration of Chl *a* and the total particle volume at the f-max were used as measures of ambient food availability for the copepods.

3.3 RESULTS

3.3.1 Laboratory experiments: the effect of temperature on egg production

Egg production by *C. carinatus* increased linearly with increasing temperature (Fig. 3.2a), from a mean of 28.8 (±2.8 SE, n = 18) eggs $♀^{-1}$ d^{-1} at 9°C to 87.3 (±5.8 SE, n = 15) eggs $♀^{-1}$ d^{-1} at 21°C. Egg production by *C. agulhensis* increased from 31.7 (±5.3 SE, n = 14) eggs $♀^{-1}$ d^{-1} at 9°C to 79.4 (±5.9 SE, n = 20) eggs $♀^{-1}$ d^{-1} at 18°C, but decreased again to 62.2 (±6.0 SE, n = 21) eggs $♀^{-1}$ d^{-1} at the warmest temperature (21°C). A quadratic polynomial curve gave the best fit for this species. Egg production by both species was similar at the coldest temperature used in the experiments (9°C), whereas egg production by *C. carinatus* was greater than that by *C. agulhensis* at the warmest temperature (21°C). There was a significant interaction between temperature and species (p = 0.01; Table 3.1) due to the significantly lower egg production by *C. agulhensis* at 21°C (p = 0.01, Newman-Keuls post hoc test). Egg production was significantly related to temperature (p < 0.0001), but not to species.

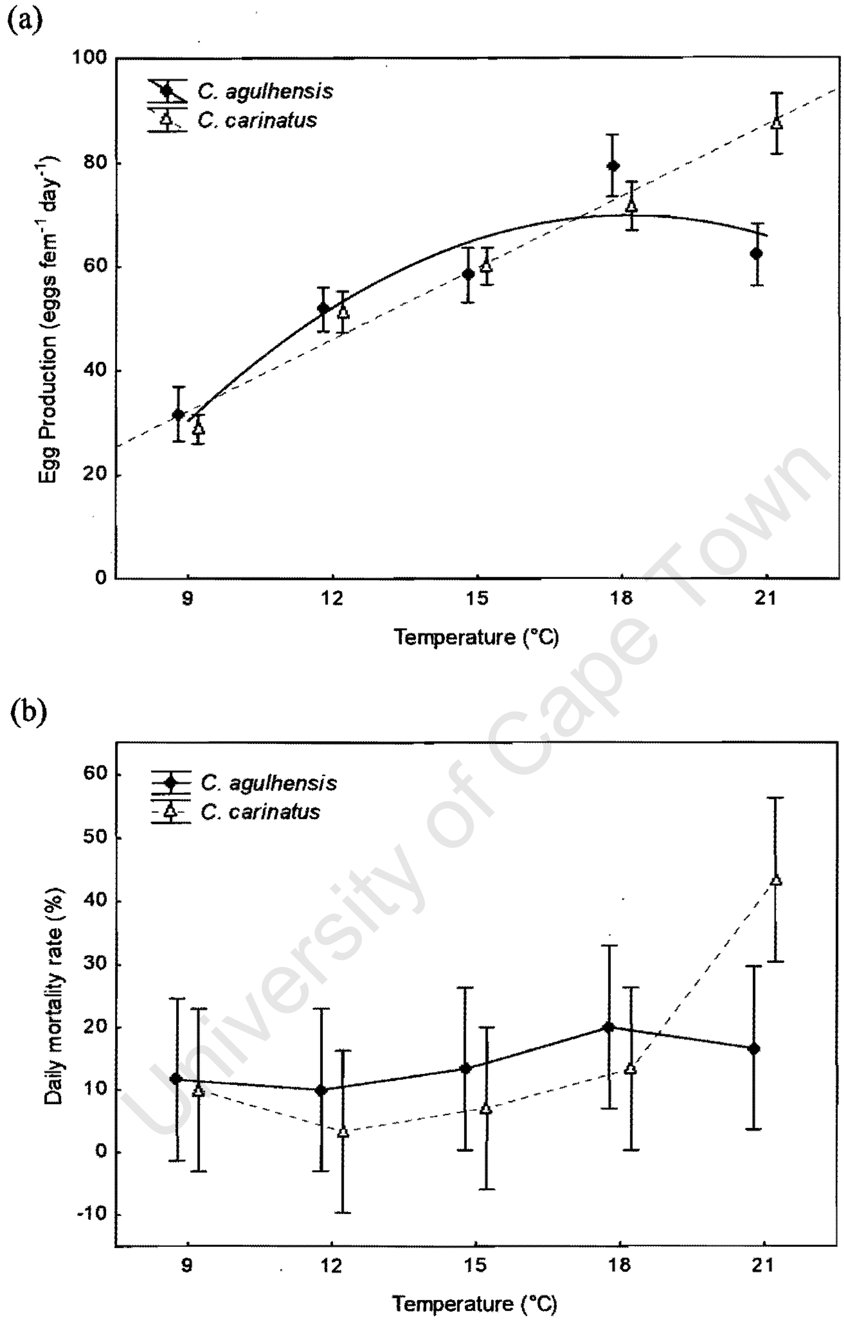


Figure 3.2. (a) Egg production rate of *C. carinatus* and *C. agulhensis* (eggs ♀$^{-1}$ d^{-1}, ± SE) in relation to temperature (°C) in the laboratory, under satiated food conditions. Equation for *C. carinatus* is $y = 4.55x - 8.24$ ($r^2 = 0.56$; $p < 0.001$), and for *C. agulhensis* is $y = -0.54x^2 + 19.25x - 100.01$ ($r^2 = 0.26$; $p < 0.001$); (b) mean daily mortality rate (%, ± 95% confidence intervals) of females of both species at each temperature over the three-day experimental period.

Table 3.1. Results of an ANOVA used to test the effect of temperature (°C) and species on the rate of egg production (eggs $♀^{-1}$ d^{-1}). Significant effects (p<0.05) are indicated in bold.

Effect	% variance explained	*SS*	*df*	*F*	*MS*	*p*
Intercept	82.03	571193.4	1	1325.23	571193.4	**0.0000**
Temperature	6.75	46984.6	4	27.25	11746.2	**0.0000**
Species	0.06	414.0	1	0.96	414.0	0.3284
Temperature × Species	0.83	5752.2	4	3.34	1438.0	**0.0117**
Error	10.34	71979.6	167		431.0	

Mean daily mortality rate over each three-day experiment ranged from 10.0 to 20.0% for *C. agulhensis*, and from 3.3 to 43.3% for *C. carinatus* (Fig. 3.2b). There was a marginally significant interaction between temperature and species ($p = 0.06$; Table 3.2). These effects were clearly a result of the significantly greater mortality rate of *C. carinatus* at 21°C compared to *C. agulhensis* ($p = 0.02$, Newman-Keuls post hoc test), as mortality rates of the two species were similar at all other temperatures, although slightly lower for *C. carinatus* (Fig. 3.2b). Mortality rate was significantly related to temperature ($p < 0.001$), but not to species.

3.3.2 Field experiments: the effect of food abundance, cell size and temperature on egg production

Mean egg production by *C. carinatus* and *C. agulhensis* during the field experiments was 18.6 (±0.4 SE, $n = 1520$) and 10.5 (±1.2 SE, $n = 333$) eggs ♀$^{-1}$ d^{-1} respectively, with respective maxima of 91.0 and 130.0 eggs ♀$^{-1}$ d^{-1} (Table 3.3). The minimum egg production rate was 0.0 eggs ♀$^{-1}$ d^{-1} for both species. Egg production by both species was significantly greater during winter than in summer (*t*-test, $t = -2.98$, $df = 331$, $p = 0.003$ for *C. carinatus*; *t*-test, $t = -1.99$, $df = 1518$, $p = 0.047$ for *C. agulhensis*; Table 3.3), and was significantly greater on the West Coast compared to the South Coast (*t*-test, $t = -4.05$, $df = 331$, $p < 0.001$ for *C. carinatus*; *t*-test, $t = -8.61$, $df = 1518$, $p < 0.001$ for *C. agulhensis*).

The mean concentration of both Chl *a* and particle volume at the f-max was significantly greater on the West Coast (5.88 mg m^{-3}; 2.15 ppm) than the South Coast (1.63 mg m^{-3}; 0.83 ppm) during the field experiments (*t*-test, $t = -18.83$, $df = 1463$, $p < 0.001$ for Chl *a*; *t*-test, $t = -19.50$, $df = 1735$, $p < 0.001$ for particle volume). The proportion of Chl *a* greater than 10 μm on the West Coast (48.5%) was not significantly different from that on the South Coast (49.5%; *t*-test, $t = 0.72$, $df = 1435$, $p = 0.47$), but the proportion of particle volume greater than 10 μm was significantly greater on the West Coast (69.6%) compared to the South Coast (61.4%; *t*-test, $t = -8.45$, $df = 1732$, $p < 0.001$).

The GAM using Chl *a* as a measure of food abundance to explain the variability of egg production by both species is shown in Fig. 3.3. *TotalChla* was the most important predictor of egg production for both species, whereas *%Chla>10* and *SST* were of lesser but similar importance. *Season* was important for *C. carinatus* but not for *C. agulhensis*. The models explained 29 and 28% of the variability of egg production for *C. carinatus* and *C. agulhensis* respectively (Table 3.4).

Egg production by *C. carinatus* increased rapidly with Chl *a* at the f-max, but the rate of increase began to slow at ~10 mg m^{-3}, and appeared to reach an asymptote at ~15 mg m^{-3} (Fig. 3.3a). Egg

Table 3.2. Results of an ANOVA used to test the effect of temperature (°C) and species on daily mortality rate (%). Significant effects ($p<0.05$) are indicated in bold.

Effect	% variance explained	*SS*	*df*	*F*	*MS*	*p*
Intercept	54.16	6633.8	1	57.07	6633.8	**0.0000**
Temperature	16.54	2026.1	4	4.36	506.5	**0.0407**
Species	0.07	8.7	1	0.07	8.7	0.7878
Temperature × Species	10.25	1255.0	4	2.70	313.7	0.0601
Error	18.98	2324.9	20		116.2	

Table 3.3. Mean and maximum rates of egg production (EP) by *C. carinatus* and *C. agulhensis* in the field off South Africa, and under food-satiated conditions in the laboratory.

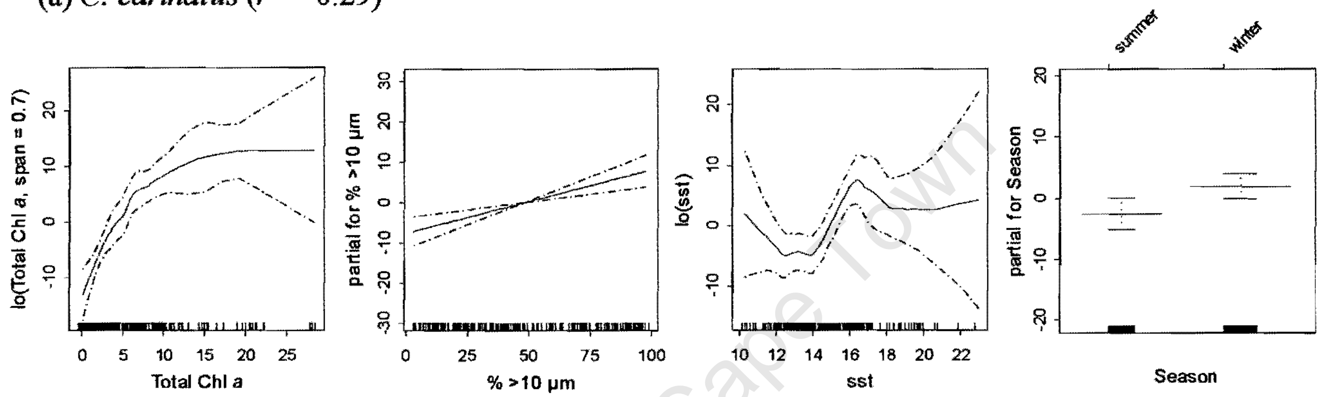
Species	Mean EP	Max EP	Food conditions	Reference
C. carinatus	18.6 (14.8/21.8; 20.4/6.6)	91.1	Field measurements (summer/winter; West Coast/South Coast)	this study
	28.0	54.6	Field measurements (Egg Ratio method)	Armstrong *et al.* 1991b
	21.1/4.4		Field measurements (diatom/microflagellate-dominated stations)	Walker and Peterson 1991
	23.7	143.5; 73.7[a]	Field measurements; >16 mg Chl a m^{-3}	Richardson 1998; Richardson and Verheye 1998
	70.0	120/154[b]	*Pseudoisochrysis paradoxa* (5-7 mg C l^{-1}; 18°C)	Borchers and Hutchings 1986
	74.5		*Thalassiosira weisflogii* (8000 cells ml^{-1}; 15°C),	Peterson *et al.* 1990a
	55.8	90/101[c]	*Thalassiosira weisflogii* (>4000 cells ml^{-1}; 15°C)	this study (Chapter 4)
C. agulhensis	50.5/9.0		Field measurements (Chl *a* = 17.2/3.8 mg m^{-3})	Peterson *et al.* 1990b
	30.9/4.6		Field measurements (diatom/microflagellate-dominated stations)	Walker and Peterson 1991
	19.0	130.8; 69.4[a]	Field measurements; >20 mg Chl *a* m^{-3}	Richardson 1998; Richardson and Verheye 1998
	10.5 (10.1/12.0; 16.7/8.7)	130.0	Field measurements (summer/winter; West Coast/South Coast)	this study
	27.6	40.0	*Thalassiosira weisflogii* (4000 cells ml^{-1}; 15°C)	Attwood and Peterson 1989
	51.1	81/99[c]	*Thalassiosira weisflogii* (>4000 cells ml^{-1}; 15°C)	this study (Chapter 4)

[a] asymptotic egg production g_a related to Chl *a* concentration from Ivlev curve $g = g_a(1 - e^{-k \times c})$

[b] continuously fed/intermittently fed

[c] not starved/previously starved

(a) *C. carinatus* ($r^2 = 0.29$)



(b) *C. agulhensis* ($r^2 = 0.28$)

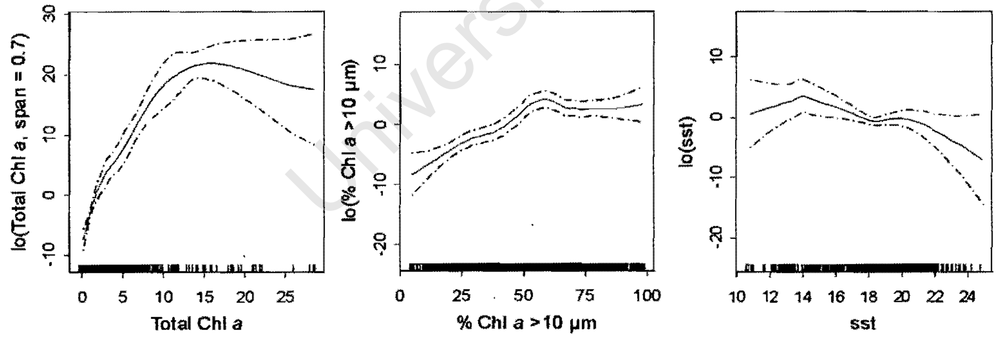


Figure 3.3. Stepwise GAMs of egg production by (a) *C. carinatus* and (b) C. *agulhensis* as a function of Total Chl *a* (mg m^{-3}), % Chl *a* > 10 µm, SST (°C) and Season during 7 winter and 7 summer cruises. A rugplot along the base of each plot shows the occurrence of each *x*-value, and 2 × upper and lower standard errors are indicated by dotted lines (continuous variables) or bars (categorical variables).

Table 3.4. Generalized additive models used to predict egg production of *C. carinatus* and *C. agulhensis*. "Chla" refers to the concentration of chorophyll *a* at the depth of maximum fluorescence, "%Chla>10" to the percentage of chlorophyll *a* >10μm, "Pvol" to particle volume (ppm) at the depth of maximum fluorescence, "%Pvol>10" to the percentage of particles >10μm, and sst to sea surface temperature (°C).

Species	Model	Constraints	n	r^2
C. carinatus	egg prod ~ lo(Chla,span=0.7) + %Chla>10 + lo(sst) + season	Chla ≤ 30	1149	0.29
	egg prod ~ lo(Pvol,span=0.7) + lo (%Pvol>10)	Pvol ≤ 7	1415	0.37
C. agulhensis	egg prod ~ lo(Chla,span=0.7) + lo (%Chla>10) + lo(sst)	Chla ≤ 30	306	0.28
	egg prod ~ lo(Pvol,span=0.7) + lo (%Pvol>10) + sst + season	Pvol ≤ 7	301	0.32

production displayed a positive linear relationship with the proportion of cells >10 µm. There was considerable variability in egg production at extreme temperatures (<12°C and >18°C) in the Chl *a* model due to fewer data at these temperatures (Fig. 3.3a), but egg production increased at intermediate temperatures, with fastest rates of egg production at 16-17°C. Egg production was greater during winter compared to summer.

Egg production by *C. agulhensis* also increased rapidly with Chl *a* at the f-max, reaching an asymptote at a concentration of ~15 mg m^{-3} (Fig. 3.3b). Egg production also increased with cell size, reaching a maximum when more than 50% of the cells were >10 µm, thereafter remaining constant. Egg production and SST were weakly related, but a slight decline in egg production with increasing temperature was apparent. Season was not important for egg production in this model.

The models using particle volume as a measure of food abundance explained 37 and 32% of variability in egg production by *C. carinatus* and *C. agulhensis* respectively (Table 3.4). Egg production by *C. carinatus* increased with increasing particle volume (Fig. 3.4a) up to a value of ~3 ppm, but was relatively constant thereafter. Particle size was the most important predictor of egg production, which increased exponentially with large-cell dominance (>50% of the particles larger than 10 µm). Neither season nor SST was important in this model.

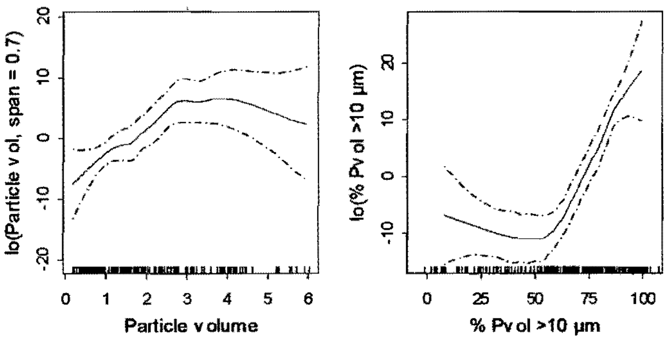
Egg production by *C. agulhensis* also increased smoothly with increasing particle volume (Fig. 3.4b), and approached an asymptote at ~3-4 ppm. Particle size appeared to be of minor importance to egg production by *C. agulhensis* compared to that by *C. carinatus*, although egg production was slightly enhanced when most of the particles were greater than 10 µm. There was a negative linear relationship between egg production and SST. Egg production by *C. agulhensis* was slightly greater during summer than in winter in this model.

3.4 DISCUSSION

3.4.1 The effect of temperature

Under conditions of abundant food in the laboratory, egg production by *C. carinatus* and *C. agulhensis* increased linearly with temperature between 9 and 18°C, although decreased egg production by *C. agulhensis* at 21°C suggests a more dome-shaped relationship with temperature overall. Positive linear relationships between egg production and temperature have also been observed for *Calanus* congeners

(a) *C. carinatus* ($r^2 = 0.37$)



(b) *C. agulhensis* ($r^2 = 0.32$)

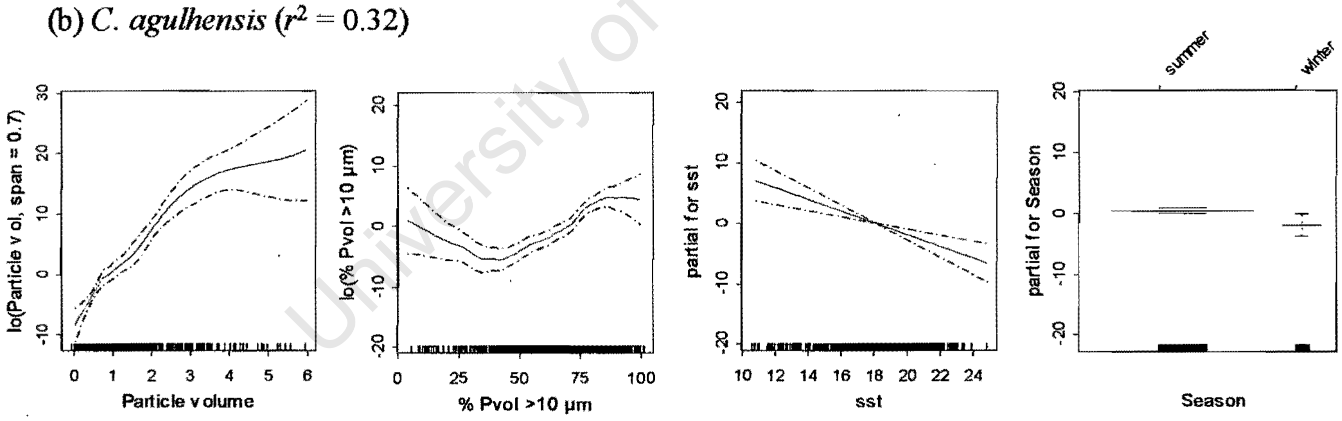


Figure 3.4. Stepwise GAMs of egg production by (a) *C. carinatus* and (b) *C. agulhensis* as a function of Particle volume (ppm), % particles > 10 µm, SST (°C) and Season during 7 winter and 7 summer cruises. A rugplot along the base of each plot shows the occurrence of each *x*-value, and 2 × upper and lower standard errors are indicated by dotted lines (continuous variables) or bars (categorical variables).

C. finmarchicus and *C. pacificus* between 5 and 15°C (Runge 1985; Hirche 1996; Hirche *et al.* 1997), and for *C. sinicus* between 5 and 20°C (Uye and Murase 1997). As food-satiated rates of egg production were similar for both *C. carinatus* and *C. agulhensis* across a broad temperature range, the hypothesis that *C. carinatus* egg production is inhibited by warm temperatures typical of the Agulhas Bank must therefore be rejected, particularly since *C. carinatus* had faster rates of egg production than *C. agulhensis* at the warmest temperature investigated (21°C; Fig. 3.2a). However, the faster egg production by *C. carinatus* at warm temperatures is likely to be mitigated by a greater natural mortality rate (Fig. 3.2b), which may result in a lower net production compared to *C. agulhensis*. The two copepods had similar egg production and mortality rates at the coldest experimental temperature (°C), indicating that the converse hypothesis that *C. agulhensis* egg production is reduced at cooler temperatures characteristic of the Benguela upwelling region should also be rejected.

Although egg production by both species was linearly related to temperature (from 9-18°C) under food-satiated conditions in the laboratory (Fig. 3.2a), the relationship between egg production and temperature in the field was more complex. Whereas egg production by *C. carinatus* appeared to increase at intermediate temperatures (Fig. 3.3a), an inverse relationship with temperature was suggested for *C. agulhensis* (Figs 3.3b and 3.4b). There are two likely reasons for these differences. Firstly, animals in the laboratory studies were acclimated to constant food and temperature conditions for five days prior to their egg production being measured, whereas both the feeding and thermal history of animals collected in the field was unknown. Previous feeding history has a major influence on both ingestion rate and egg production (Runge 1980; Hassett and Landry 1983; Donaghay 1985; Borchers and Hutchings 1986; Huntley 1988; Peterson 1988; Atwood and Peterson 1989; Calbet and Alcaraz 1996; Hirche *et al.* 1997; Båmstedt *et al.* 1999). Whereas Chl *a* concentration and particle volume at the f-max may provide a reasonable index of recent food availability, particularly in a more stable area such as the Agulhas Bank, SST may not be an adequate index of recent thermal exposure. If the animals migrate vertically, SST may be an adequate index of the temperature at which animals feed in the (usually) upper food-rich layer at night, but it will not reflect time spent at depth in colder water during the day, or whilst migrating. Secondly, animals incubated on deck in bins filled with a constant supply of subsurface seawater are subjected to temperature fluctuations as the ship steams alternately inshore and offshore along transects roughly perpendicular to the coast. Such uncertainty with regard to thermal history, compounded by its inherent variability due to diel vertical migratory behaviour, suggests that the feasibility of discerning clear relationships between egg production and temperature in the ocean may be unrealistic.

Richardson and Verheye (1998) were unable to detect a linear relationship between egg production by *C. carinatus* or *C. agulhensis* and temperature using multiple regression, but observed a roughly dome-shaped relationship between *C. agulhensis* egg production and temperature in the field, with relatively low rates of egg production associated with cool (<13°C) and warm (>18°C) temperatures. They suggested that this was a result of the dome-shaped relationship between Chl *a* and temperature, with low Chl *a* concentrations associated with cool and warm temperatures. Cool temperatures (<13°C) are indicative of newly upwelled water, characterized by low Chl *a* concentration (Brown and Hutchings 1987), whereas warm temperatures (>18°C) are typically dominated by low-biomass, microflagellate-dominated microbial communities (Mitchell-Innes and Pitcher 1992). A similar dome-shaped relationship between Chl *a* and temperature was observed during the present study (Fig. 3.5a), although greatest concentrations of Chl *a* were observed at slightly cooler temperatures (~11-17°C), possibly because of the inclusion of winter sampling. There was also a dome-shaped relationship between particle volume and temperature, with greatest measurements of particle volume associated with temperatures between 11 and 17°C (Fig. 3.5b). These relationships correspond to a large degree with elevated rates of egg production by *C. carinatus* (Fig. 3.5c) and *C. agulhensis* (Fig. 3.5d) between 11 and 17°C during the present study. However, these patterns did not emerge when food concentration was accounted for in the GAMs (Figs 3.3 and 3.4), confirming findings from earlier studies that the influence of temperature on egg production in the ocean is outweighed by the importance of food concentration (Peterson and Hutchings 1995; Kleppel *et al.* 1996; Pond *et al.* 1996; Hirst and Lampitt 1998; Richardson and Verheye 1998), notwithstanding the variability in egg production introduced through variations in temperature experienced by migrating copepods on a daily basis, as discussed above.

3.4.2 The effect of food abundance

Food abundance was the most important predictor of egg production in the ocean for both species, whether measured as Chl *a* (Fig 3.3) or particle volume (Fig. 3.4). Furthermore, both species showed a similar response to food concentration in terms of egg production, with a near-linear increase with Chl *a* up to ~10 mg m^{-3}, and an apparent satiation effect at ~15 mg m^{-3}. In terms of particle volume, asymptotic rates of egg production were attained at ~3-4 ppm (Fig. 3.4). Based on these data, the hypothesis that egg production by *C. agulhensis* is satiated at lower food concentrations compared to *C. carinatus* is rejected.

Similar relationships between egg production and food concentration have previously been observed for *C. carinatus* (Armstrong *et al.* 1991; Hutchings and Field 1997; Richardson and Verheye 1998) and *C.*

agulhensis (Richardson and Verheye 1998), as well as for other *Calanus* species, including *Paracalanus parvus* (Checkley 1980 a, b), *C. pacificus* (Runge 1984, 1985), *C. chilensis* (Peterson and Bellantoni 1987), *C. marshallae* (Peterson 1988), *C. finmarchicus* (Plourde and Runge 1993; Runge and Plourde 1996) and *C. sinicus* (Uye and Murase 1997). Both rectilinear and curvilinear (hyperbolic) models have been used to describe these relationships, with a linear increase in egg production with Chl *a* up to a critical food concentration, which varies according to species, and beyond which egg production is relatively constant. Armstrong *et al.* (1991) were unable to determine this critical concentration for *C. carinatus* because of variability in the data, but their results indicated that egg production was food-limited at concentrations below 6 mg Chl *a* m^{-3}. Comparable findings to the present study were found for *C. marshallae* (10 mg Chl m^{-3}; Peterson 1988) and *C. pacificus* (15 mg Chl *a* m^{-3}; Runge 1985). Both of these similarly-sized species belong to the *Calanus helgolandicus* species group, as does *C. agulhensis,* which is considered to be most similar morphologically to *C. pacificus* (De Decker *et al.* 1991). They occur in the northeast Pacific and California Current upwelling region, and require high concentrations of phytoplankton relative to other species to achieve maximum rates of egg production (Runge 1984; Peterson 1988). A much lower critical concentration in terms of integrated standing stock was found for *C. finmarchicus* (25 mg Chl *a* m^{-2}; Plourde and Runge 1993) compared to *C. pacificus* (~130 mg integrated Chl *a* m^{-2}; Runge 1985), suggesting different empirical responses by these two species. For some species, thresholds have only been reported in terms of a particular size-fraction of phytoplankton biomass, or for below-maximum egg production, making comparisons difficult. For example, a critical concentration of 5 mg Chl m^{-3} of the >20 μm size fraction was reported for *C. chilensis* (Peterson and Bellantoni 1987), and *C. sinicus* was reported to attain ~90% of maximum egg production rates at 5 mg Chl *a* m^{-3} for the >5 μm size fraction (Uye and Murase 1997).

The dome-shaped relationships between food abundance (in terms of Chl *a* concentration and particle volume) and temperature during this study (Figs 3.5 a and b) demonstrate the typically greater food concentrations associated with the West Coast upwelling regime compared to the South Coast (Brown 1992), which support significantly greater rates of egg production for both species (Table 3.3).

3.4.3 The effect of food size

Food size was an important factor affecting egg production by *C. carinatus and C. agulhensis,* particularly the former species (Figs 3.3 and 3.4). Whereas egg production by *C. carinatus* increased linearly with the proportion of Chl *a* >10 μm (Fig. 3.3a), egg production by *C. agulhensis* increased linearly to ~55% of Chl *a* >10 μm and then was constant when large cells dominated (Fig. 3.3b). In terms of particle volume, *C. carinatus* egg production increased exponentially with an increasing proportion of large cells (Fig. 3.4a), in contrast to a less dramatic response by *C. agulhensis* (Fig. 3.4b). In this model, particle volume and particle size explained a greater proportion of the variance in egg production by *C. carinatus* (37%; Table 3.4) compared to all four factors for *C. agulhensis* (32%). Collectively, these results suggest that although both copepod species prefer larger cells, the hypothesis that food size is more important for *C. carinatus* than *C. agulhensis* to achieve maximum rates of egg production cannot be rejected.

The optimal size of food particles is generally related to copepod size (Berggreen *et al.* 1988; Mauchline 1998), with larger copepods preferring larger phytoplankton cells, and previous field studies have shown faster rates of egg production by both *C. carinatus* and *C. agulhensis* when large phytoplankton cells were dominant. Walker and Peterson (1991) observed an almost five-fold improvement in daily egg production by *C. carinatus* in areas dominated (in terms of carbon) by large cells (diatoms and dinoflagellates) over areas dominated by small cells (microflagellates and ciliates), and an almost seven-fold improvement for *C. agulhensis* (Table 3.3). Armstrong *et al.* (1991) measured high *in situ* rates of egg production (>40 eggs $♀^{-1}$ d^{-1}) by *C. carinatus* during a monospecific bloom of the large (200-300 µm diameter, 40 µm height) diatom *Coscinodiscus gigas*, but near-zero rates of egg production during a bloom of small (mostly <6 µm) microflagellates. In some studies, the >5 µm or >10 µm chlorophyll fraction has been found to be a better predictor of copepod egg production than total chlorophyll (Runge 1985; Peterson and Bellantoni 1987; Armstrong *et al.* 1991; Uye and Murase 1997). Uye and Murase (1997) found that particles smaller than 5 µm could not be utilized by *C. sinicus*, and the minimum size of particles effectively captured by female *C. pacificus* in laboratory experiments was about 8-10 µm (Frost 1972). However, Båmstedt *et al.* (1999) found that *C. finmarchicus* was able to attain maximum rates of egg production when feeding on high concentrations (>800 mg C m^{-3}) of algae as small as 4-8 µm.

Chl *a* concentration is positively related to cell size off the west coast of South Africa, as well as on the western Agulhas Bank (Mitchell-Innes and Pitcher 1992; Richardson and Verheye 1998), so the effect of cell size on growth tends to be confounded with the effect of Chl concentration. Although chlorophyll size did not differ significantly between the West and South Coasts in this study, particle size was significantly larger on the West Coast. Richardson and Verheye (1998) suggested that, when small phytoplankton cells dominate the phytoplankton assemblage, growth of copepods in the field may not be limited by cell size *per se*, but by the typical concentrations of these cells (≤2 mg Chl *a* m^{-3}, equivalent to ≤82 mg C m^{-3}). This supports the finding that *Calanus* species may attain maximum rates of egg production on small cells if they are sufficiently abundant (Båmstedt *et al.* 1999).

3.4.4 The effect of season

Previous studies of egg production in the southern Benguela have been conducted during autumn, summer and spring, so this is the first study to include measurements made during winter. Season was the least important predictor of egg production in the models, and was only retained as a significant variable in the Chl *a* model for *C. carinatus* (Fig. 3.3a), indicating greater egg production during winter, adjusting for the other factors in the model. This is supported by the significantly greater rates of egg production by this species during winter (Table 3.3). In contrast, it was only significant in the particle volume model for *C. agulhensis* (Fig. 3.4b), indicating slightly greater egg production during summer. The reason for these seasonal differences is uncertain, and may relate to factors not tested in the GAMs, such as variability in food abundance. Variability in phytoplankton abundance is likely to be considerable in the wind-driven southern Benguela upwelling system, and this factor is explored further in Chapter 4. However, the minor importance of season compared to the other variables as a predictor of egg production suggests that it can be largely disregarded in future attempts to predict egg production from environmental variables.

3.4.5 General findings

The relatively low mean rates of egg production measured during this study are comparable to field measurements by other workers in the region (e.g. Armstrong *et al.* 1991; Walker and Peterson 1991; Richardson *et al.* 2001; Table 3.3), and confirm previous findings that egg production in the field is typically much lower than maximum rates of egg production measured under conditions of abundant food in the laboratory (e.g. Borchers and Hutchings 1986 for *C. carinatus*) or the ocean (Richardson and Verheye 1998; Richardson *et al.* 2001; Table 3.3). This appears to be largely a result of food-limitation, whether due to the relatively low food abundance characteristic of the Agulhas Bank, where *C. agulhensis* is most abundant, or to the inherent variability in food abundance that typifies upwelling ecosystems such as the southern Benguela, where temporal mismatches in peak phytoplankton and copepod abundance (Hutchings 1992) tend to limit the productive capacity of even opportunistic species such as *C. carinatus*.

Only ~30% of the variance in egg production by both species was explained by the factors considered in this study (Table 3.4), namely food abundance (in terms of phytoplankton abundance), cell size, temperature and season. This indicates the importance of other factors in determining rates of egg production, such as feeding history, and other indicators of food quality besides food size. Huntley (1988) proposed that feeding history may be more important than present environmental conditions in determining egg production, and a number of studies have shown that previous feeding conditions may influence rates of egg production (Runge 1980; Huntley 1988; Peterson 1988; Calbet and Alcaraz 1996; Hirche *et al.* 1997), including those by *C. carinatus* (Borchers and Hutchings 1986) and *C. agulhensis* (Attwood and Peterson 1989). Båmstedt *et al.* (1999) suggested that food conditions may influence ingestion rates for 1-2 weeks, and the influence of varying periods of starvation on rates of egg production is explored in Chapter 4.

Although many calanoid copepods are considered to be predominantly herbivorous, hence the emphasis on feeding in terms of available chlorophyll, studies have shown that omnivory comprises an important but largely unexplored role in their diet. Ohman and Runge (1994) found relatively high rates of egg production by *C. finmarchicus* in low-chlorophyll water to be due to predation on microzooplankton, particularly aloricate ciliates, and Gifford and Dagg (1988) also found that copepods may utilize ciliates to supplement their diet when phytoplankton concentrations are low or of unsuitable size. During a field study in the southern Benguela, Peterson *et al.* (1990b) concluded that *C. agulhensis* supplemented its diet through omnivory, since only 30% of the energy required for the observed rates of egg production could be met by ingestion of phytoplankton. The extent of omnivory thus remains an important area for further study in the southern Benguela ecosystem, where the microbial foodweb is thought to play an important role in recycling nutrients between upwelling events (Probyn 1992; Painting *et al.* 1992, 1993).

The results from this study emphasize the value of GAMs in exploring non-linear relationships between biological rates and environmental variables that would not be detected using traditional linear methods. Using multiple regression, Richardson and Verheye (1998) found egg production by *C. carinatus* and *C. agulhensis* to be significantly related to both Chl *a* and the proportion of cells >10 μm, but not to temperature. However, the GAMs indicate that temperature does indeed have a significant effect on egg production in the field, but that it is largely overridden by the greater influence of food abundance on egg production.

3.5 CONCLUSIONS

Food abundance, food size, temperature and season all have a significant influence on egg production by *C. carinatus* and *C. agulhensis*. Food abundance is the most important of these variables, and results from this study as well as many others indicate that egg production in the ocean is frequently food-limited. Although egg production by both species tends to increase linearly with temperature under conditions of abundant food in the laboratory, faster rates of egg production by *C. carinatus* were observed at warm temperatures (21°C), although this may be mitigated by greater natural mortality at these temperatures. The low abundance of phytoplankton at extreme temperatures results in a dome-shaped relationship between egg production and temperature in the field. However, this effect is largely overridden by the greater importance of food abundance in the field, and the considerable thermal variability experienced by migrating copepods in their diel cycle. Egg production by both species reaches asymptotic levels at ~10-15 mg Chl *a* m^{-3} and 3-4 ppm. Although both species have higher rates of egg production when large cells (>10 μm) are dominant, food size may be more important for *C. carinatus* to achieve maximum rates of egg production. Significantly higher rates of egg production were observed for both species on the West Coast, where phytoplankton food abundance is significantly greater, and particle size is significantly larger. The hypotheses that *C. carinatus* egg production is inhibited by warm temperatures typical of the Agulhas Bank, and that egg production by *C. agulhensis* is satiated at lower food concentrations compared to *C. carinatus*, are rejected. However, the hypothesis that food size is more important for *C. carinatus* than *C. agulhensis* to achieve maximum rates of egg production cannot be rejected.

CHAPTER 4

Effect of pulsed food availability on egg production of *Calanoides carinatus* and *Calanus agulhensis*

4.1 INTRODUCTION

The oceanography of the west coast of South Africa is dominated by coastal upwelling (Shannon 1985), with the main upwelling centres off Cape Columbine and the Cape Peninsula, and a secondary centre off Hondeklip Bay. Wind-induced upwelling is seasonal and strongly pulsed (Nelson and Hutchings 1983; Borchers and Hutchings 1986), reaching a maximum during spring and summer (Andrews and Hutchings 1980; Shannon 1985). Upwelling winds exhibit a periodicity of 5-10 days, with reversals of 1-3 days (Pitcher *et al.* 1996). Considerable variability in wind-forcing results in a pulsed supply of nutrients to the euphotic zone (Hutchings *et al.* 1995a). Drogue studies indicate subsequent phytoplankton bloom development cycles of 6-7 days, with Chl *a* increasing from <1 mg m^{-3} in upwelling water to 10-20 mg m^{-3} at the peak of the bloom, before decreasing to 1-3 mg m^{-3} thereafter (Brown and Hutchings 1987; Pitcher *et al.* 1996). Mean concentrations of Chl *a* in the upper 30 m are >2 mg m^{-3} over practically the entire west coast shelf (see Fig. 3.1 in Chapter 3), with areas of high concentration (>6 mg m^{-3}) north of St Helena Bay and Hondeklip Bay (Brown 1992). This general pattern is maintained throughout the year, although the very high concentrations near the coast are not apparent in winter. The overall mean concentration of Chl *a* on the West Coast is 3.5 mg m^{-3}, with a mean seasonal range of 0.2–16.5 mg m^{-3} (recalculated from Brown 1992). Individual measurements may yield much higher concentrations than average values, with exceptionally high Chl *a* concentrations of 139 and >175 mg m^{-3} recorded during nearshore dinoflagellate blooms in late summer and autumn (Walker and Pitcher 1991; Mitchell-Innes *et al.* 2000). The abundance of food for herbivorous zooplankton can therefore vary considerably, with periods of high food abundance alternating with periods of near starvation.

By contrast, the Agulhas Bank provides a more stable environment, with a seasonal water column structure typical of temperate, western-boundary continental shelf systems. Hydrological conditions are primarily a function of forcing by the Agulhas Current and wind-driven coastal upwelling (Probyn *et al.* 1994). The western inner shelf (<100 m) between Cape Point and Cape Agulhas forms a natural continuation of the west-coast upwelling system (Shannon 1985), with upwelling-favourable winds in summer generally persisting for 2-4 days, although occasionally up to several weeks (Largier *et al.* 1992). The outer shelf (100-200 m) of both the western and central/eastern regions, however, where the bulk of the *C. agulhensis* population is found (see Chapter 2), is strongly influenced by oceanic flow. During summer this whole area is characterised by strong thermal stratification, with thermoclines generally located at 40-60 m over the western part of the Bank, and 20-40 m farther east (Boyd and Shillington 1994; Largier *et al.* 1992; Probyn *et al.* 1994). During winter, storms create a uniformly well-mixed, deeper (>70 m) upper layer. Although higher Chl *a* concentrations are associated with the inshore coastal upwelling region on the western Agulhas Bank (>3 mg m^{-3}) and dynamic upwelling along the eastern shelf edge (>2 mg m^{-3}), mean concentrations over most of the mid-shelf (see Fig. 3.1) are moderately low (1-2 mg m^{-3}), particularly during summer and winter. Highest mean concentrations of Chl *a* in the upper 30 m are found in autumn and spring, when patches of 2-4 mg m^{-3} are fairly widespread. The overall mean concentration of Chl *a* on the South Coast is 1.7 mg m^{-3}, with a mean seasonal range of 0.3-5.6 mg m^{-3} (recalculated from Brown 1992).

C. carinatus and *C. agulhensis*, considered to be predominantly herbivorous, clearly inhabit areas with very different food regimes. Food abundance on the Agulhas Bank is generally lower than on the West Coast, but less variable, whereas on the West Coast food abundance is generally much greater than on the Agulhas Bank, but extremely variable, although less so in winter. As a typical upwelling species, *C. carinatus* is considered to be well adapted to a pulsed food regime (Borchers and Hutchings 1986; Armstrong *et al.* 1991). It therefore seems reasonable that *C. agulhensis*, originating from a more stable food environment, may be at a disadvantage if advected or entrained into the highly variable West Coast upwelling environment.

The effect of various periods of starvation (1-9 days) on *C. agulhensis* egg production was previously investigated by Attwood and Peterson (1989). Similar work on *C. carinatus* is lacking, except for one experiment in which a single female was starved for 5 days (Borchers and Hutchings 1986). It has therefore not been possible to compare the effect of both short and long periods of starvation on egg production of the two species.

In this chapter, the hypothesis is tested that *C. carinatus* is better adapted than *C. agulhensis* to the pulsed food environment characteristic of the southern Benguela upwelling region. Females of both species were subjected to varying periods of starvation, following the method of Attwood and Peterson (1989), and the time taken for egg production to resume satiated levels was measured.

4.2 MATERIAL AND METHODS

4.2.1 Collection of animals

Owing to limited laboratory resources and the time-consuming nature of the research, the entire experiment could not be performed on both species simultaneously. Thus, a number of sub-experiments were conducted in order to complete several replicates of each starvation period for both species, with new animals collected for each experiment. Moreover, by conducting several experiments, the likelihood of biases in the data due to varying copepod condition is reduced. The starvation-recovery experiments were conducted during austral summer and autumn, from March to May 1993 and January to April 1994.

An inflatable boat was used in the collection of copepods off the Cape Peninsula and in St Helena Bay, off the west coast of South Africa. A plankton net (300-µm-mesh; 0.25-m^2 mouth area) fitted with a 2-litre plastic, screw-on cod-end was allowed to drift at a depth of 5-10 m for about five minutes. On retrieval, the sample was gently released into a 20-litre bucket of ambient seawater and returned to the laboratory as soon as possible, usually within 1-2 hrs. On each sampling occasion, copepods were collected from visually dense patches of phytoplankton, dominated by genera such as *Chaetoceros*, *Coscinodiscus*, *Nitzschia* and *Ceratium*, suggesting a non-limited feeding history prior to capture.

4.2.2 Experimental procedure

The laboratory was maintained at a constant temperature of 15°C with a natural dark/light cycle. Exponentially growing cultures of the diatom *Thalassiosira weissflogii* were maintained at 20°C in 40-litre plastic bags, using Walne's medium. Freshly caught copepods were placed into 100-litre flow through tanks and fed excess (food-saturated) concentrations of *T. weissflogii* (>4000 cells ml^{-1}). Peterson (1988) determined food-saturated concentrations of *T. weissflogii* to be ≥3500 cells ml^{-1} for *Calanus marshallae*, a similar-sized congener of *C. agulhensis*. Food suspensions were made daily using 0.2-µm filtered seawater (FSW) pre-cooled to 15°C. Cell concentrations were measured using a Coulter Multisizer.

Initially, the daily egg production by both species under food-saturated conditions was measured. After an acclimation period of five days, five or six females of each species were placed singly into 1100-ml polycarbonate bottles filled with the food suspension and incubated on a rotating plankton wheel (end-over-end; 1 rpm) for 4-5 days. For the starvation-recovery experiments, batches of 20 females of each species were placed in 5-litre beakers containing 0.2-µm FSW for varying periods of time, namely 1, 3, 5, 7 and 9 days. The FSW was replaced daily to minimize coprophagy, while the food suspension was replaced every other day.

Each day the contents of each bottle were gently poured through a 63-µm mesh to collect the female and any eggs and faecal pellets. The female was examined, and was returned to the bottle if healthy. Dead and moribund females were replaced, when possible, with spare females with identical feeding history (i.e. females captured at the same time and exposed to an identical feeding and starvation regime in the laboratory). Eggs were preserved in 4% formaldehyde for later enumeration. The presence or absence of faecal pellets was also noted to determine whether the females were feeding. The incubation method did not prevent egg cannibalism, but filtrates were examined for empty egg cases. Each experiment was terminated when the rate of egg production had returned to the observed ("normal") satiated rate.

Females that did not produce fecal pellets i.e. were not feeding and therefore probably damaged or senescent, were excluded from the analysis, as were females that died during the experiments. Two or three separate sets of experiments were conducted for each starvation period, and results were combined. A total of 74 *C. carinatus* and 88 *C. agulhensis* females were used in the data analysis.

Separate experiments were conducted during December 2000 and February 2001 to investigate the termination of egg production by previously fed *C. carinatus* and *C. agulhensis* females incubated in FSW. Freshly caught females were acclimated to excess food at 15°C under a natural light/dark cycle for at least 6 days, and then incubated in 0.2-µm FSW for 4-5 days. Females were housed in 1500-ml perspex containers divided by a 300-µm mesh to enable any eggs laid to fall through the mesh into the bottom third of the containers, thus preventing egg cannibalism by starved females. Daily egg production of starved females was measured as described above until it had declined to zero.

4.3 RESULTS

The mean rate of egg production (±SE) by satiated (non-starved) females was 55.8 (±2.0, $n = 70$) eggs $♀^{-1}$ day^{-1} for *C. carinatus* and 51.1 (±1.7, $n = 69$) eggs $♀^{-1}$ day^{-1} for *C. agulhensis*. There was no evidence of egg cannibalism by females incubated on the plankton wheel with excess food, as was also noted by Peterson (1988) for well-fed female *C. marshallae*. Mortality rates during recovery varied between 6.7% and 26.7% for *C. carinatus*, and between 16.7% and 55.0% for *C. agulhensis* females

(Table 4.1). Highest mortalities were observed for *C. agulhensis* females starved for 9 days (55.0%), but mortality was found to be independent of both starvation period and species ($\chi^2 = 18.72$, $v = 16$, $p > 0.25$).

Egg production rates of females starved for 1, 3, 5, 7 and 9 days and then fed with excess food are shown in Figure 4.1. As the relationship between egg production and days following starvation was variable for different starvation periods, lines were fit using the distance-weighted, least-squares smoothing procedure (StatSoft 2002). This procedure gives the best fit to the data without any *a priori* constraints. Recovery time for each period of starvation was then calculated as the time (in days) when the least-squares curve intersected the line equivalent to the 99% confidence interval of the mean egg production rate of non-starved females (Fig. 4.1; see Table 4.2 for values). The response of egg production by both species to various periods of starvation is summarized by plotting the mean recovery time against the starvation period (Fig. 4.2). Mean recovery time following starvation increased linearly with increasing starvation period for both *C. carinatus* ($r^2 = 0.72$, $n = 5$, $p < 0.1$) and *C. agulhensis* ($r^2 = 0.99$, $n = 4$, $p < 0.01$). The slopes of straight lines fitted to these data were significantly different (ANCOVA test of parallelism, $F = 55.55$, $n = 9$, $p < 0.001$), implying different responses by the two species. The lines intersected at 4.25 days of starvation.

Egg production by *C. carinatus* following one day of starvation was depressed (Fig. 4.1a) and only returned to normal following 2.8 days of excess food (Fig. 4.2), whereas egg production by *C. agulhensis* females returned to normal after approximately one day of excess food (Figs 4.1b and 4.2). After 3 days without food, egg production of both species was depressed one day after the re-introduction of food (Figs 4.1c and d), with mean egg production being close to zero for *C. carinatus*. *C. carinatus* egg production recovered after ~3 days of excess food, whereas *C. agulhensis* egg production recovered after 2.4 days (Fig. 4.2).

Following ~4 days of starvation, there was a change in the relative recovery of the two copepod species, with *C. carinatus* now recovering faster than *C. agulhensis* (Fig. 4.2). When starved for 5 days, *C. carinatus* required only 3.4 days of excess food for egg production to resume normal levels (Figs 4.1e and 4.2), whereas *C. agulhensis* egg production returned to non-starved levels after 3.8 days of excess food (Figs 4.1f and 4.2). When starved for 7 and 9 days, *C. carinatus* recovered after only 3.7 and 4.0 days of feeding respectively (Figs 4.1g, i and 4.2). By contrast, *C. agulhensis* required 5.2 days of excess food for egg production to return to normal following 7 days of starvation (Figs 4.1h and 4.2). Furthermore, most female *C. agulhensis* did not recover after 9 days of starvation (Fig. 4.1j).

Table 4.1. Mortality rates (%) during experiments

Starvation period	0 days	1 day	3 days	5 days	7 days	9 days
Calanoides carinatus	6.7	13.3	26.7	20.0	22.2	23.1
Calanus agulhensis	16.7	20.0	16.7	16.7	27.8	55.0

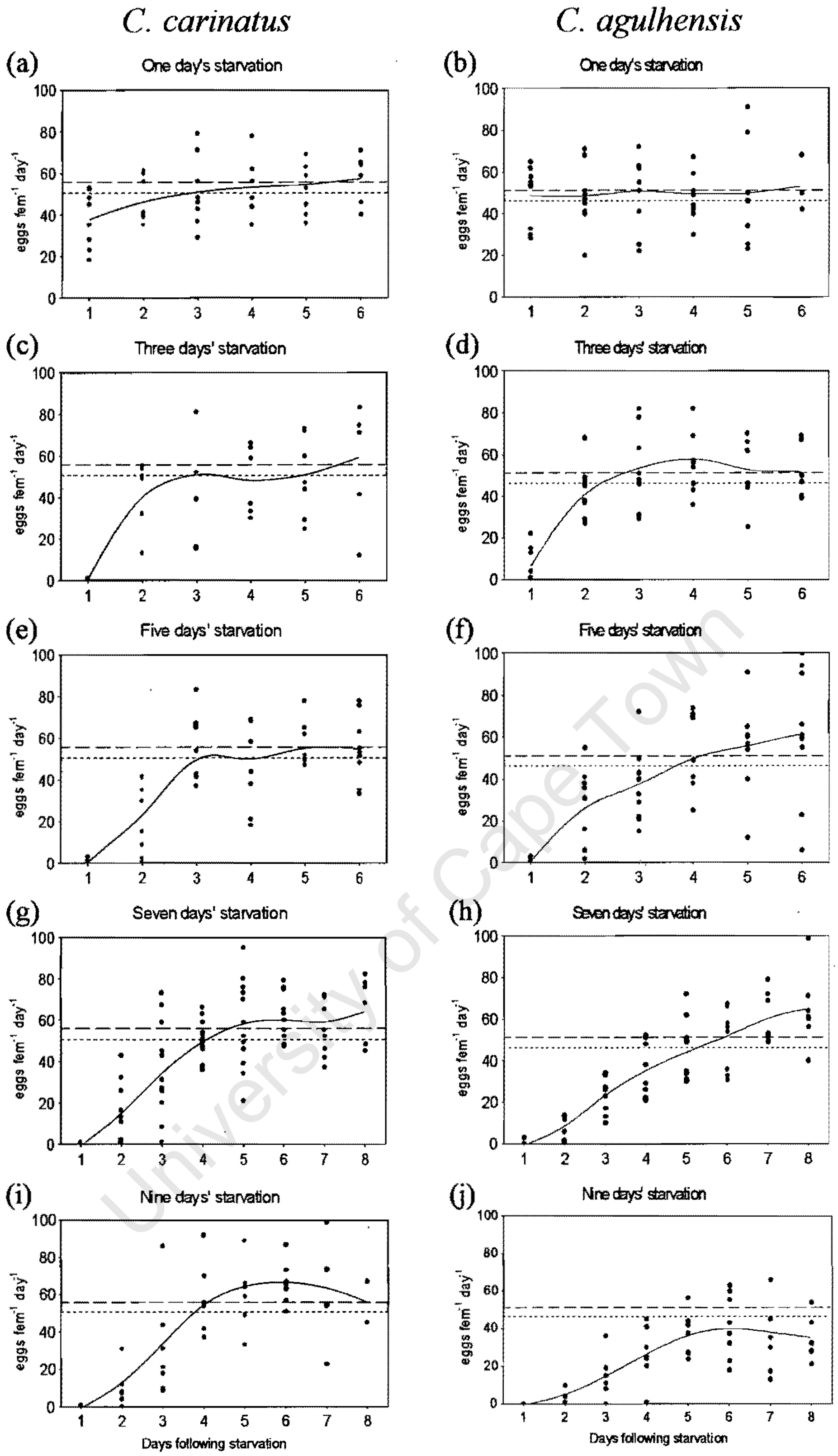


Figure 4.1. Egg production (eggs ♀$^{-1}$ day^{-1}) by *C. carinatus* and *C. agulhensis* females when fed excess *T. weissflogii* following 1, 3, 5, 7 and 9 days of starvation. The solid curve is the distance-weighted, least-squares smoothed fit to the data. The dashed line indicates mean egg production by unstarved females (55.8 and 51.1 eggs ♀$^{-1}$ day^{-1} respectively), and the dotted line corresponds to the lower 99% confidence interval of mean egg production by unstarved females (50.6 and 46.3 eggs ♀$^{-1}$ day^{-1} respectively).

Table 4.2. Effect of starvation on calanoid copepod egg production

Species	Habitat	Temp. (°C)	Starvation Period (days)	Termination of egg production (days)	Resumption of egg production (days)	Recovery of egg production (days)	Reference
Calanoides carinatus	Southern Benguela	15	1	2	1	2.8	this study
			3		1-2	3.1	
			5		1-2	3.4	
			7		1-3	3.7	
			9		1-3	4.0	
Calanoides carinatus	Southern Benguela	18	5	immediate	2	3	Borchers and Hutchings (1986)
Calanus agulhensis	Southern Benguela	15	1	5	immediate	0.9	this study
			3		1-2	2.4	
			5		1-2	3.8	
			7		1-3	5.2	
			9		2-4	most did not recover	
Calanus agulhensis	Southern Benguela	15	1-5	2 (≤4 eggs.d^{-1} within first 24h)	immediate	~5	Attwood and Peterson (1989)
			7		-	7.7	
			9		-	16	
Calanus glacialis	Arctic (78-83°N)	0	3	3-6 (eggs not viable > 3).	immediate	10	Hirche and Bohrer (1987)
			8	Constant within 24h; decreased rapidly thereafter.	-	-	
Calanus finmarchicus	North Atlantic (72-79°N)	0	2	sharp decrease after 3	2	2.9	Hirche (1990)
			4		1 (4 when senescent)	2.7 (8 when senescent)	
			7		1	7.6	
Calanus finmarchicus	Westspitsbergen Current (N. Atlantic)	0	12	sharp decrease after 3 (0°C), 2-3 (5°C) and 1 (10°C), but spawning continued up to 21	-	-	Hirche *et al.* (1997)
		5	12		3	5	
		5	23		-	-	
		10	8		-	-	
Calanus finmarchicus	SW Scotland	5	15	sharp decrease after 2; few laying after 7; only 1 egg laid after 15	immediate	sharp increase after 4	Marshall and Orr (1952)
			35		-	-	
Calanus marshallae	Oregon	10	1	immediate	immediate	-	Peterson (1988)
			4		3	-	
			5		3	5	
			6		3-4	5	
			8		4	-	
			10		6	-	
Calanus pacificus	Puget Sound, Washington	12	3.5	-	immediate	2	Runge (1984)
			14		3	6-7	
			21		4	6-7	

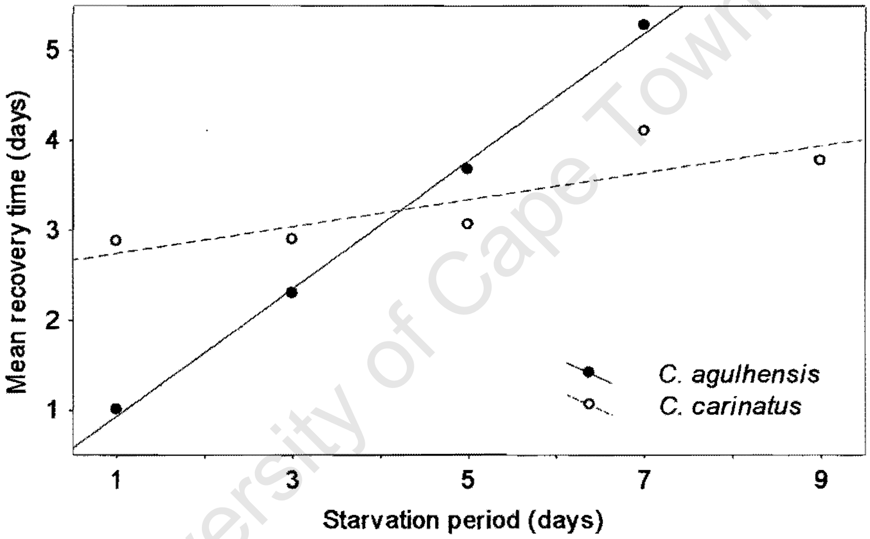


Figure 4.2. Mean time (days) for egg production by *C. carinatus* and *C. agulhensis* to return to normal following various periods of starvation (days). The parameters for the fitted lines are: $y = 0.15x + 2.60$ ($r^2 = 0.72$, $n = 5$, $p < 0.10$) for *C. carinatus*, and $y = 0.71x + 0.22$ ($r^2 = 0.99$, $n = 4$, $p < 0.01$) for *C. agulhensis*. Note that, on average, *C. agulhensis* did not regain normal rates of egg production following nine days of starvation.

In the experiments where previously fed females were incubated in filtered seawater, *C. carinatus* stopped laying eggs before *C. agulhensis*. *C. carinatus* egg production declined by 69% after one day of starvation and terminated after 2 days in filtered seawater (Fig. 4.3a). By contrast, *C. agulhensis* egg production declined by just 29% following one day of starvation (Fig. 4.3b), with females continuing to lay eggs following 2-4 days of starvation, although at a slower rate. *C. agulhensis* egg production terminated after 5 days without food.

4.4 DISCUSSION

4.4.1 Response of egg production to short periods of starvation

The faster recovery by *C. agulhensis* following short periods of starvation (1-3 days; Fig. 4.2) suggests that it is better adapted to, or more able to tolerate, short-term variability in food availability compared to *C. carinatus*. This may be linked to the fact that *C. agulhensis* did not immediately terminate egg production after being placed in filtered seawater, but continued to lay eggs following up to 4 days of starvation (Fig. 4.3b). Continued egg laying during starvation, i.e. delayed termination of egg production, has been observed for other *Calanus* species (Table 4.2). *Calanus glacialis* females from the Arctic (incubated at 0°C) took up to 3-6 days to stop spawning when starved (Hirche and Bohrer 1987), and previously fed *Calanus finmarchicus* females sporadically laid low numbers of eggs up to 21 days later (Hirche 1990; Hirche *et al.* 1997). Similar results were found for *C. finmarchicus* collected off the southwest coast of Scotland (Marshall and Orr 1952).

By comparison, *C. carinatus* displayed a more rapid response to starvation, with markedly depressed rates of egg production after one day in filtered seawater, and no eggs laid thereafter (Fig. 4.3a). Laboratory experiments by Borchers and Hutchings (1986) showed a similar rapid response for *C. carinatus*, with elevated rates of egg production when food was abundant and immediate cessation of egg production when females were placed in filtered seawater. The same response was observed for *Calanus marshallae*, an inhabitant of the Oregon upwelling system, which immediately terminated egg production when starved (Peterson 1988).

Delayed termination of egg production in response to the absence of food, as demonstrated by *C. agulhensis*, may be a more efficient strategy in a system characterized by fairly constant food availability, such as the Agulhas Bank. If periods of food deprivation are generally brief, it might be

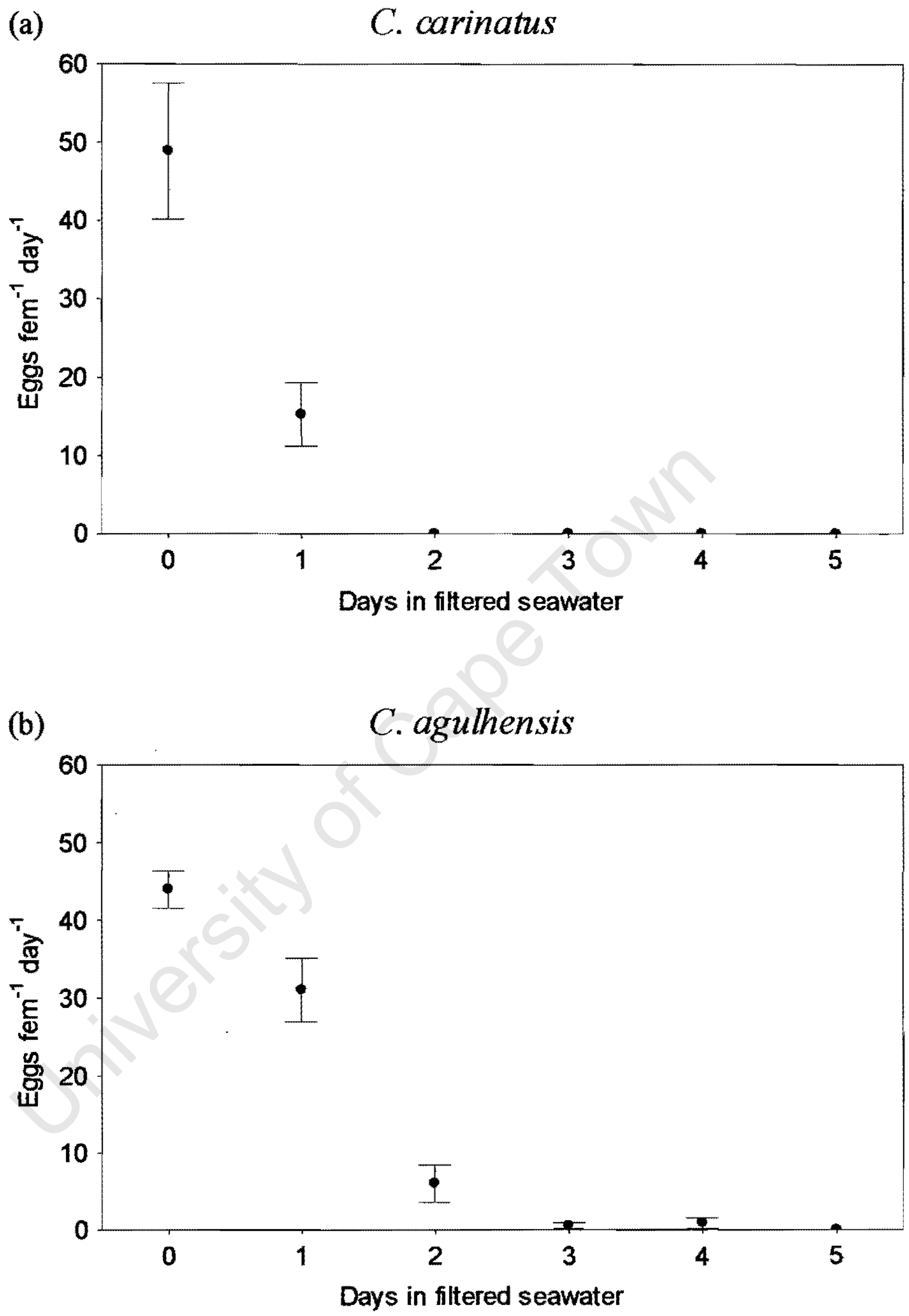


Figure 4.3. Mean egg production (eggs ♀$^{-1}$ day^{-1}) ±SE by previously fed (a) *C. carinatus* and (b) *C. agulhensis* females when placed in filtered seawater. Note that no eggs were laid by *C. carinatus* females after 2 days in filtered seawater.

energetically more efficient to maintain egg production, albeit at a lower rate, rather than to stop and then resume egg production within a short period of time. In a similar context, Hassett and Landry (1983) suggested that it might be energetically optimal for copepods experiencing short-term food patchiness to maintain higher levels of digestive enzymes at low food concentrations in order to exploit higher concentrations of food when encountered. Thus, *C. agulhensis* may recover faster than *C. carinatus* from short (<4 day) interruptions in the food supply, because egg production has not yet been terminated. If periods without food are often prolonged, however, it might be energetically more efficient to cease egg production immediately and wait for better conditions. This appears to be the strategy used by *C. carinatus* in the southern Benguela upwelling region and *C. marshallae* in the Oregon upwelling system.

4.4.2 Response of egg production to long periods of starvation

C. carinatus recovered faster than *C. agulhensis* following 5-9 days without food (Fig. 4.2). Subsequent to a 9-day period without food, most *C. carinatus* females regained their maximum reproductive output after only 4 days of abundant food, with one female laying 82 eggs on the third day (Fig. 4.1i). By contrast, most *C. agulhensis* females could no longer regain normal levels of egg production after 9 days without food, although some individuals did recover (Fig. 4.1j). Rapid recovery from long periods without food supports previous observations that *C. carinatus* is well suited to a pulsed upwelling environment (Borchers and Hutchings 1986; Armstrong *et al.* 1991), where interruptions in food availability are erratic and may be lengthy.

Results from the present study are similar to those reported by Borchers and Hutchings (1986) for *C. carinatus*. In their study, one female that was starved for 5 days regained normal levels of egg production (approximately 70 eggs $♀^{-1}$ day^{-1}) after 3 days of excess food. This recovery time matches that of females starved for 5 days in the present study (3.1 days; Figs 4.1e and 4.2), with the higher rate of satiated egg production probably a result of the higher experimental temperature (18°C as opposed to 15°C in the present study), and/or better quality food.

4.4.3 Resumption of egg production following the reintroduction of food

Many previously starved copepod species, including *C. agulhensis* and *C. carinatus,* resume egg production almost immediately when returned to abundant food conditions (Table 4.2), particularly following short periods of starvation. However, the resumption of egg production becomes increasingly variable with longer starvation periods for both *C. agulhensis* and *C. carinatus* females, with up to 3 days separating faster from slower individuals resuming egg production after 7-9 days without food. *C. marshallae* females laid eggs within 1 day of feeding following 1 day of starvation, but after 4-10 days without food, an interval of 0.4 times the starvation interval was required before egg production resumed (Peterson 1988). Both *C. agulhensis* and *C. carinatus* recovered faster than *C. marshallae* (Table 4.2), although this may have been a consequence of the higher incubation temperature (15°C in the present study compared to 10°C for *C. marshallae*). Termination of egg production by *C. finmarchicus* following starvation was temperature dependent (Hirche *et al.* 1997), with response time decreasing with increasing temperature.

4.4.4 Recovery of egg production following starvation

The time required for post-starvation egg production by *C. agulhensis* and *C. carinatus* to return to normal levels was proportional to the starvation period (Fig. 4.2). This was also true for *Acartia grani* females starved for 3-5 days (Calbet and Alcaraz 1996). However, it seems that this relationship will only hold up to a certain point, beyond which egg production can never completely recover. This threshold point, which is species-, temperature- and probably also food quality-specific, was not reached by *C. carinatus* during the present study, but was reached by *C. agulhensis* when starved for 9 days. The least squares curve in Fig. 4.1j did not intersect with the 99% confidence interval of mean, satiated egg production (46.3 eggs $♀^{-1}$ day^{-1}) for these females. A similar but more gradual decline in the maximum rate of egg production with increasing starvation period was noted by Runge (1984) for *C. pacificus* females. In his study, maximum egg production at 12°C declined from a food-satiated rate of ~55 eggs $♀^{-1}$ day^{-1} (which was regained after 3.5 days of starvation) to ~50 eggs $♀^{-1}$ day^{-1} after 14 days of starvation, and to ~35 eggs $♀^{-1}$ day^{-1} after 21 days of starvation. The time required for egg production both to resume and to reach a maximum was similar following both 14 and 21 days of starvation, indicating that the decline in maximum rate of egg production was not caused by senescence in this case. A more likely cause is degeneration of the reproductive system. Marshall and Orr (1952) noted that *C. pacificus* females starved for more than 30 days had shrunken oviducts, and Runge (1984) found that ovaries of *C. pacificus* had regressed to an undeveloped state after 14 days of starvation. Extending the structural weight concept presented by Carlotti *et al.* (1993), Hirche *et al.* (1997) suggested that, after prolonged starvation, females may use freshly ingested material to restore their internal structures rather than investing in egg production, and may switch to reproduction only when a critical weight is reached.

It is interesting to note that the recovery times of starved *C. agulhensis* females in the present study differ from those reported by Attwood and Peterson (1989), who found that considerably longer recovery periods were required (Table 4.2). Furthermore, egg production by non-starved *C. agulhensis* females in their study was approximately half of that found in the present study. This suggests that the animals they used were in poorer condition, possibly because they were collected during winter, when females may have had a poor feeding history.

4.4.5 Implications of pulsed food availability for copepods in the southern Benguela

The pulsed nature of upwelling in the southern Benguela is considered to lead to a mismatch in both space and time between the production of phytoplankton and that of zooplankton (Hutchings 1992). Wild C5 *C. carinatus* copepodites had similar lipid contents to intermittently-fed animals reared in the laboratory (Borchers and Hutchings 1986), suggesting that they are food limited to some extent during development. Animals fed intermittently, such that they experienced starvation for half of their development time, took approximately twice as long to develop. Older (larger) copepod stages in the southern Benguela are more likely to be food-limited (Richardson and Verheye 1998), but this may be balanced by increased starvation tolerance with development of both naupliar and copepodite stages (Borchers and Hutchings 1986; Tsuda 1994).

Despite the constraints imposed by high variability of food abundance in the southern Benguela upwelling system, *C. carinatus* has a number of characteristics that enable it to thrive in this environment. Firstly, *C. carinatus* C5s have a higher lipid content than most other calanoid copepod species (Borchers and Hutchings 1986), which enables the older stages to tolerate starvation. Preliminary results from lipid analyses suggest that a much greater proportion of the lipid content of *C. carinatus* is comprised of wax esters (68% for females and 87% for C5s) compared to *C. aguhensis* (24% for females and 32% for C5s; W. Hagen and H. Verheye pers. comm.), which allow efficient energy storage by marine herbivorous copepods, and are particularly vital in ecosystems with a periodically limited food supply (Hagen 2000). These reserves are probably not used to sustain egg production when food is in short supply, but instead enable the female to survive adverse feeding conditions (Armstrong *et al.* 1991). The females can then become reproductively active almost immediately when conditions are more favourable, enhancing the probability of survival of their offspring. This strategy has been proposed for other species, including *C. pacificus* (Marshall and Orr 1952), *C. glacialis* (Hirche and Bohrer 1987) and *Metridia longa* (Buskey and Stearns 1991). Exhaustion of lipid reserves, and subsequent degeneration of the reproductive system, could explain why egg production of *C. agulhensis* females starved for 9 days failed to return to satiated levels.

Secondly, *C. carinatus* development time from egg to adult is 2 days faster than that of *C. agulhensis* at 15.5°C and 4 days faster at 19.5°C under saturated food conditions (Peterson and Painting 1990). Furthermore, *C. carinatus* has the most rapid development of any calanoid studied to date, and of most other copepod species as well (Mauchline 1998, his Table 47).

Finally, as this study has shown, *C. carinatus* is able to recover more rapidly from long (7-9 day) periods of starvation compared to *C. agulhensis,* which is no doubt a result of its greater lipid reserves, and the greater wax-ester content of the lipid compared to *C. agulhensis*. The ability to tolerate and recover quickly from long periods of starvation, combined with a faster development time and a higher rate of egg production than *C. agulhensis*, thus provides *C. carinatus* with a strong competitive advantage in a highly variable food environment. These characteristics enable *C. carinatus* to outnumber *C. agulhensis* in the upwelling environment off the west coast of South Africa.

CHAPTER 5

Comparative ingestion rates, food-size selection and diel feeding patterns of *Calanoides carinatus* and *Calanus agulhensis*

5.1 INTRODUCTION

Copepod feeding behaviour is a vast subject, but much of our knowledge derives from studies of calanoid copepods, and of *Calanus* in particular, such as the classic study of *C. finmarchicus* by Marshall and Orr (1955). Factors that influence copepod feeding have been the focus of a number of reviews, including those by Paffenhöfer (1988) on zooplankton feeding behaviour, Huntley (1988) on feeding biology of *Calanus*, Kleppel (1993) on the diets of calanoid copepods, Harris (1996) on feeding ecology of *Calanus*, and most recently Mauchline (1998) in his book on the biology of calanoid copepods. Broadly speaking, copepod feeding behaviour is influenced by the physical and physiological condition of the animal (e.g. life-history stage and mouthpart development, seasonal cycle, feeding history and nutritional state), the food available to it (e.g. abundance, size, nutritional quality, growth phase and spatial distribution), and the environmental conditions under which feeding occurs (e.g. temperature, light and turbulence; Mauchline 1998).

Copepod feeding is usually expressed as ingestion rate (the amount of food ingested per unit time and copepod), clearance rate (the volume of water cleared per unit time and copepod), or daily ration (the mass of food ingested per day as a percentage of copepod body mass; Båmstedt *et al.* 2000). Ingestion rates increase with body weight and developmental stage (Paffenhöfer 1971; Runge 1980; Huntley 1981; Peterson *et al.* 1990b), temperature (Huntley and Boyd 1984; White and Roman 1992) and food concentration (Frost 1972, 1985; Gamble 1978; Huntley 1981; Dagg and Walser 1987; Turner and Tester 1989; Hansen *et al.* 1990; Dam and Peterson 1991; Irigoien *et al.* 1998; Båmstedt *et al.* 1999 amongst many others). Frost (1972) used a rectilinear model to describe the relationship between ingestion rate and food concentration, with a linear increase in ingestion rate up to an asymptote or "critical concentration", beyond which the ingestion rate is constant and maximum, also referred to as a "saturation response" (Hassett and Landry 1983; Mauchline 1998). In later studies a curvilinear (hyperbolic) relationship was considered to be more appropriate (Frost 1985), and variations of the Ivlev curve are widely used to describe the functional response to food concentration (Parsons *et al.* 1967; Hansen *et al.* 1990; Dam and Peterson 1991; Båmstedt *et al.* 1999; Båmstedt *et al.* 2000). Frost

(1972) also proposed that clearance rate was a function of particle size below the critical concentration, and was independent of food concentration. While this appears to be generally true for well-fed copepods, Runge (1980) found that starved *C. pacificus* removed diatoms of different sizes at different relative efficiencies compared to continuously feeding animals. Other studies have documented elevated clearance rates by copepods exposed to short-term (1-14 h) periods of starvation (Ishii 1990; Tiselius 1998) or long-term (12-14 d) acclimation to low food concentration (Hassett and Landry 1983). The latter is thought to explain the seasonal change in maximum feeding rates and digestive enzyme activity observed for *C. pacificus* at the onset of the spring bloom (Hassett and Landry 1990). Båmstedt *et al.* (1999) concluded that feeding history may significantly affect ingestion on a time scale of 1-2 weeks, and Huntley (1988) proposed that feeding history may be more important than present forcing conditions in determining feeding behaviour.

Calanus spp. are generally considered to prefer large phytoplankton cells (Frost 1972, 1977; Peterson and Bellantoni 1987; Walker and Peterson 1991), although *C. finmarchicus* is able to utilise small (<10 µm) cells (Huntley 1981; Nejstgaard *et al.* 1997; Båmstedt *et al.* 1999) if they are sufficiently abundant. The traditional view of copepods as passive, mechanical filter-feeders (Frost 1977), with the size of ingested particles purely a function of the morphology and geometry of the mouthparts (the "leaky-sieve hypothesis"; Boyd 1976), was altered with the advent of high-speed microcinematography (Paffenhöfer *et al.* 1982; Strickler 1982). These cinematographic studies showed that food particles above a certain size (e.g. 12 µm diameter for *Eucalanus pileatus* and *Paracalanus parvus*; Price *et al.* 1983) are detected individually, and collected using at least four out of five feeding appendages (Paffenhöfer and Lewis 1989). Smaller particles are collected by low-amplitude movement of the second maxillae, from a water current created by the other appendages (Båmstedt *et al.* 2000). These studies also highlighted the role of chemosensory perception in feeding encounters, providing evidence that copepods can detect algal cells from a distance of several hundred microns (Koehl and Strickler 1981; Paffenhöfer *et al.* 1982; Price *et al.* 1983).

The importance of food quality to copepod feeding has been increasingly recognized. In addition to preferring larger food, copepods have shown a preference for algae over polystyrene beads (Donaghay and Small 1979; Huntley *et al.* 1983), exponentially growing algae over senescent algae (Mullin 1963; Paffenhöfer and Van Sant 1985; Houde and Roman 1987), nutritionally rich cells over nutritionally poor cells (Cowles *et al.* 1988), and certain algal species over others (Håkanson 1984), notably certain dinoflagellate species over others (Huntley *et al.* 1983, 1987; Sykes and Huntley 1987). Whereas *Calanus* species were previously considered to be predominantly herbivorous, it is now recognized that phytoplankton often only represents a part of zooplankton diet, and that microzooplankton often comprises an important fraction (Barthel 1988; Gifford and Dagg 1988; Stoecker and Capuzzo 1990; Kleppel 1993; Ohman and Runge 1994; Nejstgaard *et al.* 1997). Dietary diversity and nutritional optimization are now considered the rule rather than the exception (Kleppel 1993).

In previous chapters it was shown that *Calanoides carinatus* is most abundant in the cool, variable but generally food-rich environment of the West Coast upwelling regime, whereas *Calanus agulhensis* is most abundant in the warmer, more stable but generally less food-rich environment of the Agulhas Bank. Whereas both species appear to need relatively high concentrations of Chl *a* to achieve maximum rates of egg production, food size may be more important to *C. carinatus* than to *C. agulhensis* in attaining high fecundity rates. This suggests that the two species may have different food-size or food-type preferences, or else different feeding behaviours or feeding efficiencies when in the same food environment.

Both field and laboratory studies have found ingestion rate by female *C. carinatus* to be related to food concentration (Peterson 1989; Peterson *et al.* 1990a) and cell size (Peterson *et al.* 1990a) in the southern Benguela. Daily ingestion rates of *C. carinatus* were also linked to chlorophyll concentration in the northern Benguela (Timonin *et al.* 1992). Although diel variation in gut pigment content of this species has not been observed in the laboratory (Peterson *et al.* 1990a), ingestion rates in the field were 1.5 to 3 times higher during nighttime than during the day, and were linked to body size and stage, with highest rates measured for females (Timonin *et al.* 1992). Ingestion rates off North-West Africa were higher on weak-linked diatom chains compared to strong-linked chains, as well as on the largest cells in 8 out of 10 laboratory experiments (Schnack 1982). Off Somalia, cells comprising the largest proportion eaten by female *C. carinatus* were generally between 36 and 85 μm (largest dimension; Smith 1982).

Studies on feeding by *C. agulhensis* in the ocean are relatively scarce, but suggest that ingestion rate is also related both to phytoplankton cell size and concentration (Peterson 1989; Verheye *et al.* 1992; Verheye *et al.* 1994), as well as to ontogenetic stage (Peterson *et al.* 1990b). A diel feeding rhythm was observed on the West Coast, with low gut pigment content during daylight hours, increasing rapidly approximately one hour before sunset (Peterson *et al.* 1990b). Individuals were often food limited, with slow mean ingestion rates under low Chl *a* concentrations (<3 mg m^{-3}), and faster mean ingestion rates under high Chl *a* concentrations on both the West Coast and the Agulhas Bank (Verheye *et al.* 1994). The high Chl *a* concentrations often observed on the West Coast (Brown *et al.* 1991; Brown 1992) thus appear likely to support faster ingestion rates than the generally low Chl *a* concentrations characteristic of the Agulhas Bank.

The aim of this study was to investigate whether *C. carinatus* and *C. agulhensis* have different feeding behaviours in terms of (1) ingestion rate in relation to food abundance, including the hypothesis that *C. agulhensis* attains satiation at a lower food concentration than *C. carinatus*, (2) food-size or food-type preference, including the hypothesis that *C. agulhensis* feeds less efficiently on small cells (<10 µm) compared to *C. carinatus*, and (3) diel feeding patterns. The ingestion rate and size preference of each species was determined during shipboard incubation experiments using ambient food. Diel feeding behaviour was investigated by measuring the gut pigment content of various stages of each species over a 24-hr cycle, during two cruises.

5.2 MATERIAL AND METHODS

5.2.1 The effect of food size and abundance on ingestion rates

Shipboard experiments were conducted on several cruises off both the West and South coasts to compare the ingestion rates and food-size selection of *C. carinatus* and *C. agulhensis* under natural food conditions. A magnum rosette sampler comprising six 18-l bottles, and fitted with a Chelsea Instruments Aquatracka submersible fluorometer, was used to collect incubation water from the depth of the fluorescence maximum. Copepods were collected using a plankton net (300-µm mesh; 0.25 m^2 mouth area) fitted with a 2-litre plastic, screw-on cod-end, which was allowed to drift at a depth of 5-10 m for about ten minutes. Upon retrieval, the contents of the net were released gently into a 20-litre bucket of seawater at ambient surface temperature. Copepods that appeared healthy were selected carefully using a hand-held pipette. Between 4 and 10 animals of the same stage (mostly females) and species were placed in 1100-ml polycarbonate bottles ("experimental" bottles) containing 200-µm filtered seawater from the depth of the fluorescence maximum ("initial" water). For each experiment, four experimental bottles and two "control" bottles (excluding animals) were incubated on a water-driven, slowly rotating axis in darkened bins cooled with seawater pumped from a depth of 6 m. After 24 h the contents of the experimental bottles were gently poured through a 200-µm mesh to collect the animals and check their condition. The Chl *a* concentration (total and <10 µm fraction), particle concentration and size spectrum of the incubation water was measured both before (initial water) and after (control and experimental bottles) each grazing experiment. The two species were sufficiently abundant for their ingestion rates to be measured simultaneously during 9 out of a total of 26 experiments conducted.

Total ingestion rates during each experiment were measured by the removal of Chl *a* and particle volume, according to the equations of Frost (1972). These results could not be corrected for possible microzooplankton grazing effects as suggested by Nejstgaard *et al.* (1997, 2001), as supplementary phytoplankton and microzooplankton cell counts were not routinely made. The functional response of ingestion rates to food concentration in terms of Chl *a* (mg m^{-3}) and particle volume (ppm) was described by an Ivlev curve without a threshold (as used by Richardson and Verheye 1998; Bamstedt *et al.* 1999):

$$I = I_{max}\,(1 - e^{-k \times c})$$

where

I = ingestion rate,

I_{max} = asymptotic ingestion rate,

k = the rate at which I approaches I_{max},

c = food concentration

Several experiments (when the two species co-occurred) were selected to compare particle removal when the food environment was dominated volumetrically by small cells (~8 µm equivalent spherical diameter [ESD]), large cells (~45 µm ESD), and a bimodal distribution of particles (~12 and 25 µm ESD). The size spectrum of the particles removed by the animals during each experiment was calculated as the difference between the particle volume in each size channel (128 initial channels, grouped into 32 channels) from particle spectra of water in the experimental bottles, and that in the control bottles after 24 hours. The identification of phytoplankton species during these experiments (see below) enabled species selection by both copepods to be compared.

5.2.2 Phytoplankton species selection

Sub-samples (100 ml) of water from the initial, control and experimental bottles were preserved in 0.5% acid Lugol's solution for the large-cell dominated and bimodal size distribution experiments, which were conducted during January 1991, and in 4% buffered formalin for the small-cell dominated experiment, which was conducted during November 1992 (Lugol's solution was not available during this cruise). Phytoplankton and microzooplankton species were enumerated using the Utermöhl method (Hasle 1978). Cell counts were made by B. Mitchell-Innes and M. Weilbach, MCM, using a Zeiss inverted microscope.

A measure of relative abundance of prey in the diet compared to relative abundance of phytoplankton in the environment was obtained using Vanderploeg and Scavia's (1979) selectivity coefficient W_i, as described by Lechowicz (1982):

$$W_i = \frac{\frac{r_i}{p_i}}{\sum r_i p_i}$$

where r_i is the relative abundance (as a proportion) of prey type i in the diet, and p_i is the relative abundance (as a proportion) of prey type i in the environment. The expected value for random feeding is $1/n$, where n is the number of prey types included in the analysis. The coefficient varies between 0 and 1, with values greater than $1/n$ indicating preference, and those less than $1/n$ indicating avoidance. The Vanderploeg and Scavia (1979) selectivity coefficient is vulnerable to sampling error for items rare in the environment or in the diet, as are most feeding selectivity indices, but has the advantage of being unaffected by the relative abundance of food types, which allows meaningful comparisons between samples (Lechowicz 1982). Selectivity coefficients were calculated for phytoplankton and microzooplankton species that comprised at least 5% of the total species abundance, in order to minimize possible errors associated with enumeration of rare species.

5.2.3 Diel feeding

The gut fluorescence method was used to measure the gut pigment content (GPC) of animals at different times of the day during two cruises: The Agulhas Ridge survey in March 1994, and a drogue-tracking cruise off the West Coast in February 1995. Copepods were collected using a plankton net (300-µm mesh; 0.25 m^2 mouth area) fitted with a 2-litre plastic, screw-on cod-end, which was allowed to drift at a depth of 5-10 m for about ten minutes. Upon retrieval, the contents of the net were released gently into a 20-litre bucket of seawater at ambient surface temperature. In the ship's laboratory, copepods were immediately concentrated onto a 10-cm diameter, 120-µm mesh sieve. The sieve was placed on the stage of a dissecting microscope, and individuals were picked rapidly under a cool light-source by grasping them by the antennules or furcal rami, using jeweler's forceps. Picking was terminated after 15-20 minutes, or at the first sign of defecation. At least 10 individuals per stage were picked, when possible, and placed into a plastic centrifuge tube. Once picking was completed, 90% acetone was added to each tube, the contents of which were homogenized with a clean glass rod and stored in the dark at –20°C for at least 24h. Tubes were then centrifuged for 10 minutes at 4000 rpm, and the pigment content of the acetone extract was measured with a Turner Designs fluorometer before and after acidification with 10% HCl. Pigment content per individual copepod was calculated as described in Dagg and Walser (1987). As noted in Peterson *et al.* (1990b), this yields an estimate of the total pigment (chlorophyll + phaeopigment) in units of ng pigment per copepod, and does not include any correction for background (body tissue) fluorescence, as previous work indicated this to be negligible (Peterson *et al.* 1990b).

5.3 RESULTS

5.3.1 Ingestion rate

Mean daily ingestion rates of bulk phytoplankton by females and late stage copepodites in the field were consistently faster for *C. agulhensis* than for *C. carinatus* under conditions of both low ($\leq$3 mg Chl *a* m^{-3}) and high (>3 mg Chl *a* m^{-3}) Chl *a* concentration (Table 5.1), although fewer data were available for the latter species. An ANOVA showed that this difference between the species was not significant, however (Table 5.2). There was also no significant stage effect, but ingestion rates of both species were significantly faster under high concentrations of Chl *a*. Mean daily rations were similar for the females of both species, averaging 1% and 2% of body carbon for *C. carinatus* and *C. agulhensis* respectively under low Chl *a* concentrations, and 23% and 21% of body carbon respectively under high Chl *a* concentrations (Table 5.1). Maximum daily rations of female *C. carinatus* and *C. agulhensis* were 79% and 47% of body carbon respectively (Table 5.1).

Ingestion rates of females of both species increased with food concentration in the ocean (Figs 5.1 and 5.2), but were highly variable. Although there were relatively few measurements of ingestion rate at high concentrations of Chl *a*, both species appeared to achieve maximum rates at ~15 mg Chl *a* m^{-3}. Fig 5.1 shows the asymptotic rates of ingestion, as fitted by an Ivlev function, with a wide scatter of rates particularly at high levels of food. The ingestion rate of *C. carinatus* in terms of Chl *a* reached ~360 ng Chl *a* $♀^{-1}$ d^{-1}, equivalent to 14 ng C ind^{-1} d^{-1} assuming C:Chl *a* = 40. Although the mean ingestion rate by females was 331 ng Chl *a* $♀^{-1}$ d^{-1} at relatively high concentrations of Chl a (>3 mg m^{-3}; Table 5.1), a maximum of 1124 ng Chl *a* $♀^{-1}$ d^{-1} was measured during one experiment. The asymptotic ingestion rate of *C. agulhensis* females estimated by the Ivlev function (868 ng Chl *a* $♀^{-1}$ d^{-1}, equivalent to 354 ng C $♀^{-1}$ d^{-1}) was approximately double that estimated for *C. carinatus* (Fig. 5.1), and was closer to the maximum rate measured in the field (960 ng Chl *a* $♀^{-1}$ d^{-1}; Table 5.1). The Ivlev curve also explained a greater proportion of the variance in ingestion rate for *C. agulhensis* compared to *C. carinatus* (80% vs. 52%).

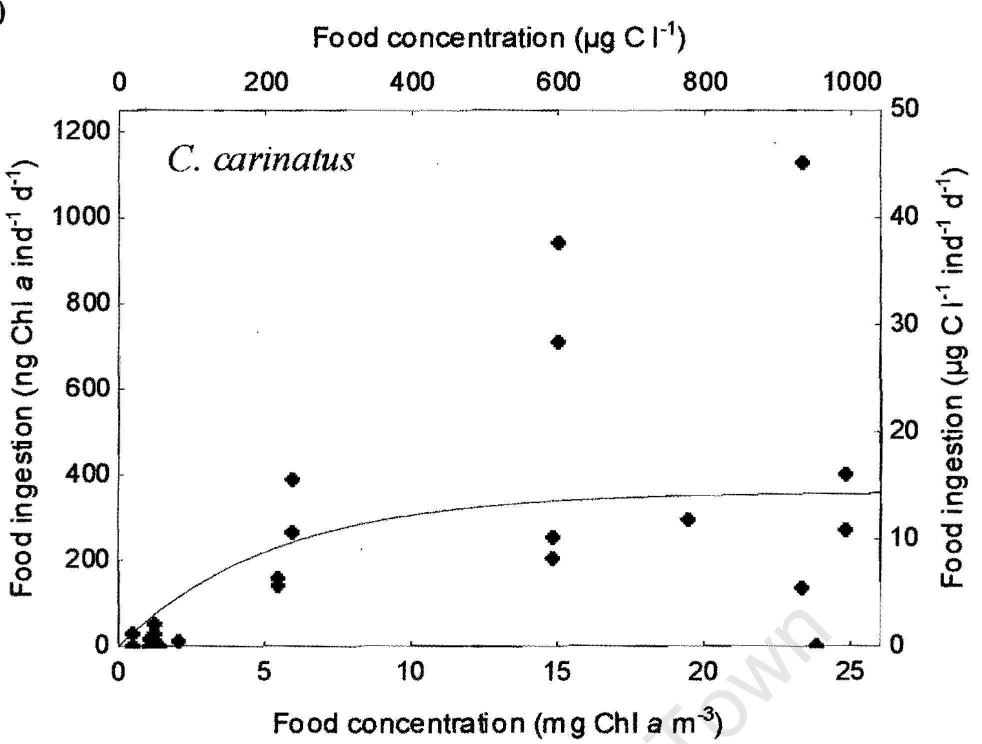
Table 5.1. Mean daily ingestion rates (ng Chl *a* ind^{-1} d^{-1} and µg C ind^{-1} d^{-1}, assuming C:Chl *a* = 40) and daily ration (% body carbon d^{-1}) of female, C5 and C4 *C. carinatus* and *C. agulhensis* under low ($\leq$3 mg Chl *a* m^{-3}) and high (>3 mg Chl *a* m^{-3}) concentrations of Chl *a*. Daily rations were calculated using dry weight and C:dry weight measurements from Verheye (1991) for *C. carinatus,* and body carbon values from Peterson *et al.* (1990b) for *C. agulhensis*. The range of measurements is indicated in brackets.

	C. carinatus				*C. agulhensis*			
Stage	ng Chl *a* ind^{-1} d^{-1}	µg C ind^{-1} d^{-1}	% body carbon d^{-1}	*n*	ng Chl *a* ind^{-1} d^{-1}	µg C ind^{-1} d^{-1}	% body carbon d^{-1}	*n*
	Low Chl *a*							
Fem	15.6 (0.0-48.4)	0.6 (0.0-1.9)	1.1 (0.0-3.3)	9	48.6 (0.0-176.9)	1.9 (0.0-7.1)	2.3 (0.0-8.8)	37
C5	10.5 (10.0-11.0)	0.4 (0.4)	1.3 (1.3)	2	62.0 (0.0-145.2)	2.5 (0.0-5.8)	6.4 (0.0-14.9)	14
C4	-	-	-	-	76.9 (4.1-145.2)	3.1 (0.2-5.8)	17.2 (1.1-32.2)	6
	High Chl *a*							
Fem	330.6 (0.0-1124.4)	13.2 (0.0-45.0)	23.2 (0.0-79.2)	16	425.4 (63.8-959.7)	17.0 (2.6-38.4)	21.0 (3.2-47.4)	13
C5	267.0 (0.0-426.8)	10.7 (0.0-17.1)	33.9 (0.0-54.1)	3	454.8 (252.2-657.4)	18.2 (10.1-26.3)	46.7 (25.9-67.4)	2

Table 5.2. Results of an ANOVA performed on ingestion rate (ng Chl *a* ind^{-1} d^{-1}) in relation to species (*C. carinatus* or *C. agulhensis*), stage (C5 or female), and either low (≤3 mg Chl *a* m^{-3}) or high (>3 mg Chl *a* m^{-3}) food concentration at the fluorescence maximum. Significant effects ($p < 0.05$) are indicated in bold.

Effect	% variance explained	*SS*	*df*	*MS*	*F*	*p*
Intercept	27.93	1549451	1	1549451	48.48	**0.0000**
Species	1.44	80071	1	80071	2.51	0.1170
Stage	0.01	401	1	401	0.01	0.9111
Chl	19.28	1069174	1	1069174	33.45	**0.0000**
Species × Stage	0.13	7379	1	7379	0.23	0.6321
Species × Chl	0.42	23343	1	23343	0.73	0.3951
Stage × Chl	0.02	1068	1	1068	0.03	0.8554
Species × Stage × Chl	0.06	3297	1	3297	0.10	0.7488
Error	50.71	2812469	88	31960		

(a)



(b)

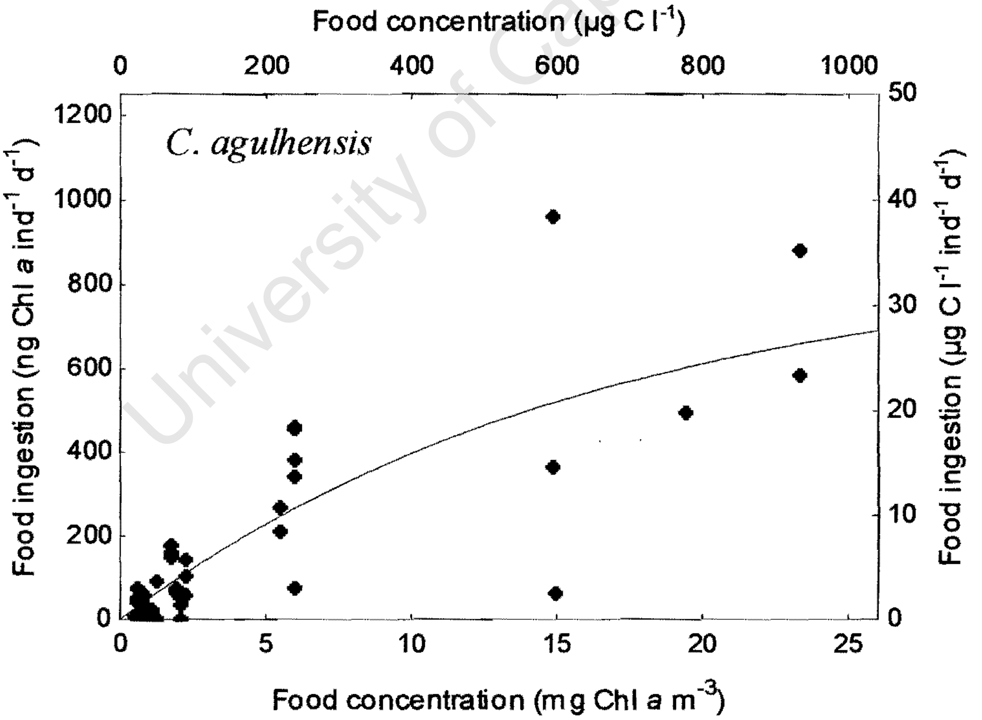
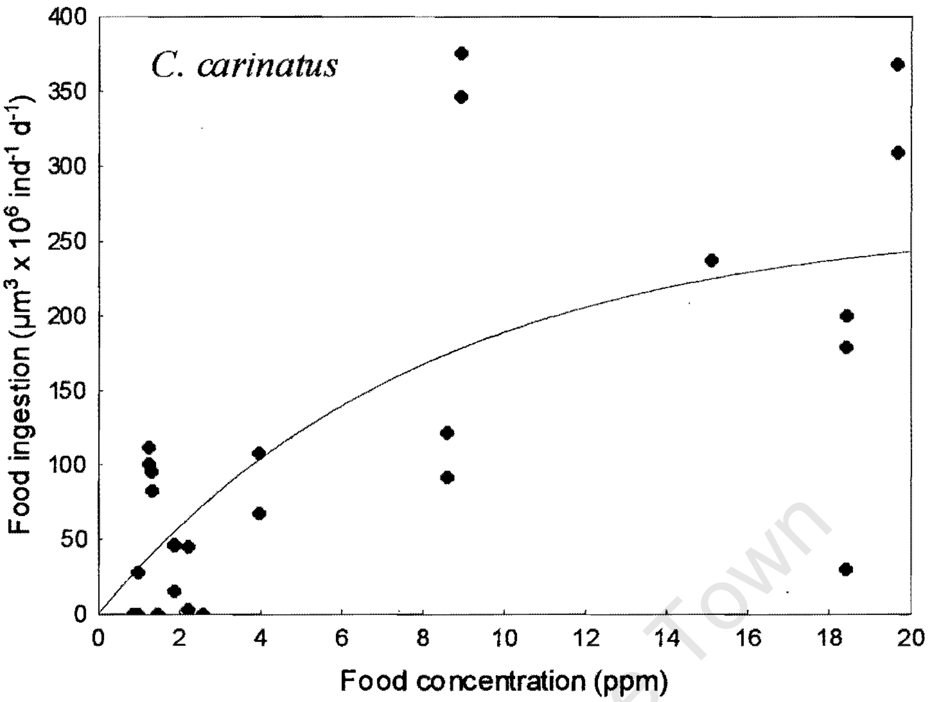


Figure 5.1. Ingestion rate (ng Chl *a* ind^{-1} d^{-1} and µg C ind^{-1} d^{-1}, assuming C:Chl = 40) in relation to total Chl *a* (mg m^{-3}) and carbon (µg C l^{-1}), by female (a) *C. carinatus* and (b) *C. agulhensis*. The fitted curves (in terms of Chl *a*) are $y = 359.8557 \times (1 - e^{-0.1882 \times x})$, $r^2 = 0.52$, $n = 25$ for *C. carinatus*, and $y = 868.0882 \times (1 - e^{-0.0612 \times x})$, $r^2 = 0.80$, $n = 50$ for *C. agulhensis*.

(a)



(b)

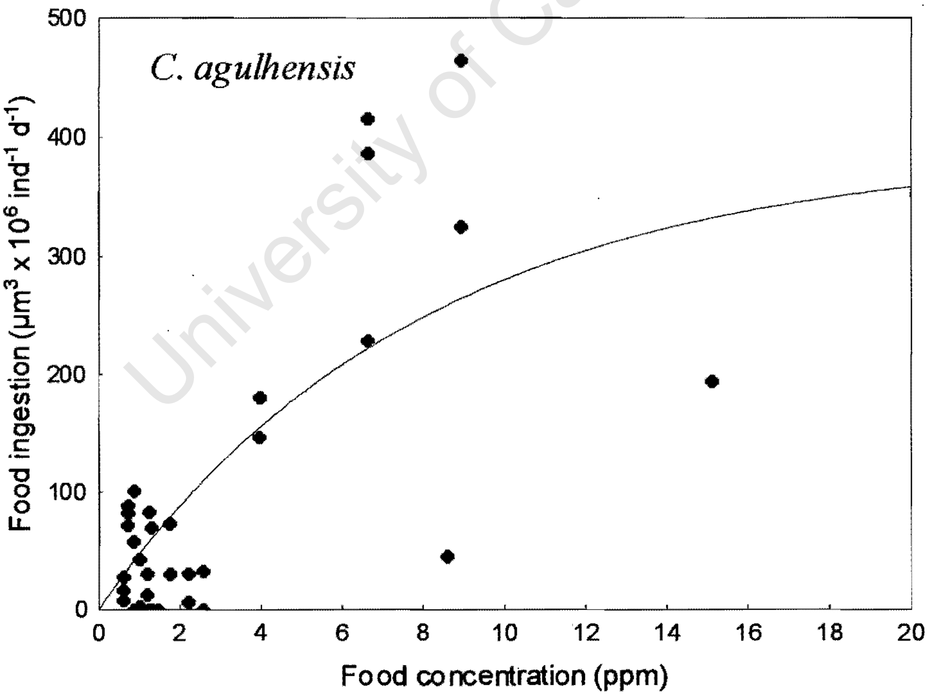


Figure 5.2. Ingestion rate ($\mu m^3 \times 10^6$ ♀$^{-1}$ d^{-1}) in relation to total particle volume (ppm) by (a) *C. carinatus* and (b) *C. agulhensis*. The fitted curves are $y = 265.1484 \times (1 - e^{-0.1250 \times x})$, $r^2 = 0.74$, $n = 28$ for *C. carinatus*, and $y = 388.2284 \times (1 - e^{-0.1282 \times x})$, $r^2 = 0.72$, $n = 35$ for *C. agulhensis*.

Maximum ingestion rates in terms of particle volume were observed at ~7-8 ppm for females of both species (Fig. 5.2). Maximum rates estimated by the Ivlev function, which explained 74 and 72% of the variance for *C. carinatus* and *C. agulhensis* respectively, were 265 $\mu m^3 \times 10^6$ ♀$^{-1}$ d^{-1} for *C. carinatus* and 388 $\mu m^3 \times 10^6$ ♀$^{-1}$ d^{-1} for *C. agulhensis*. As was observed for Chl *a*, these were somewhat lower than the observed maximum rates.

5.3.2 Particle size and species selection

A comparison of the volumetric size distribution of particles removed by copepods in the experimental bottles with that of the available food indicated similar ingestion curves for both species, with a preference for the larger particles that dominated the biomass (Fig. 5.3).Particles ingested were similar to, or slightly larger than, those that dominated the spectrum in terms of particle volume, whether small (~8 μm ESD; Fig. 5.3a), large (~45 μm ESD; Fig. 5.3b) or bimodal (~12 and 25 μm ESD; Fig. 5.3c) size distributions of food were encountered. Negative particle removal in the size classes smaller than those of peak biomass was observed during all three experiments, suggesting particle production.

In the small particle experiment (Fig. 5.3a), the phytoplankton was dominated by a small variety of the diatom *Thalassiosira* (mean cell volume 394 μm^3), and was ingested by both copepod species, although at faster rates by *C. agulhensis* (163 $\mu m^3 \times 10^6$ ♀$^{-1}$ d^{-1}) than by *C. carinatus* (88 $\mu m^3 \times 10^6$ ♀$^{-1}$ d^{-1}). In the large particle experiment (Fig. 5.3b), a variety of diatoms comprised 95% of the abundance of available food (Table 5.3), including a larger *Thalassiosira* sp. (>14 000 μm^3), which was usually found in chains of 2-3 cells, and which comprised 50% of the abundance, and the very large (>35 000 μm^3), usually solitary, *Coscinodiscus* sp. The ciliate *Mesodinium rubrum* (>8 000 μm^3) comprised the remaining 5%. *C. carinatus* displayed greatest preference for the small (1 000 μm^3) chain-forming pennate diatom *Pseudonitzschia pungens* and the small (424 μm^3) chain-forming centric diatom *Skeletonema costatum*, but avoided the larger *Thalassiosira* sp. and *M. rubrum*. In contrast, *C. agulhensis* displayed a strong preference for the ciliate, but fed randomly on *Thalassiosira* sp. and *P. pungens*. Selectivity coefficients for *Coscinodiscus* sp. were zero for both copepods, suggesting active avoidance of this large diatom. *S. costatum* also appeared to be completely avoided by *C. agulhensis*.

In the experiment with a bimodal distribution of particle volume (Fig. 5.3c), the phytoplankton biomass comprised seven diatom species (Table 5.4). Representative size counts of *Thalassiosira* spp. in the control water revealed a small (mean cell volume ~1037 μm^3) and large (mean cell volume ~6366 μm^3) variety to be present in a 60:40 ratio, but these were not differentiated in the cell counts from the experimental bottles. *C. carinatus* showed similar preferences for the chain-forming diatoms *P.*

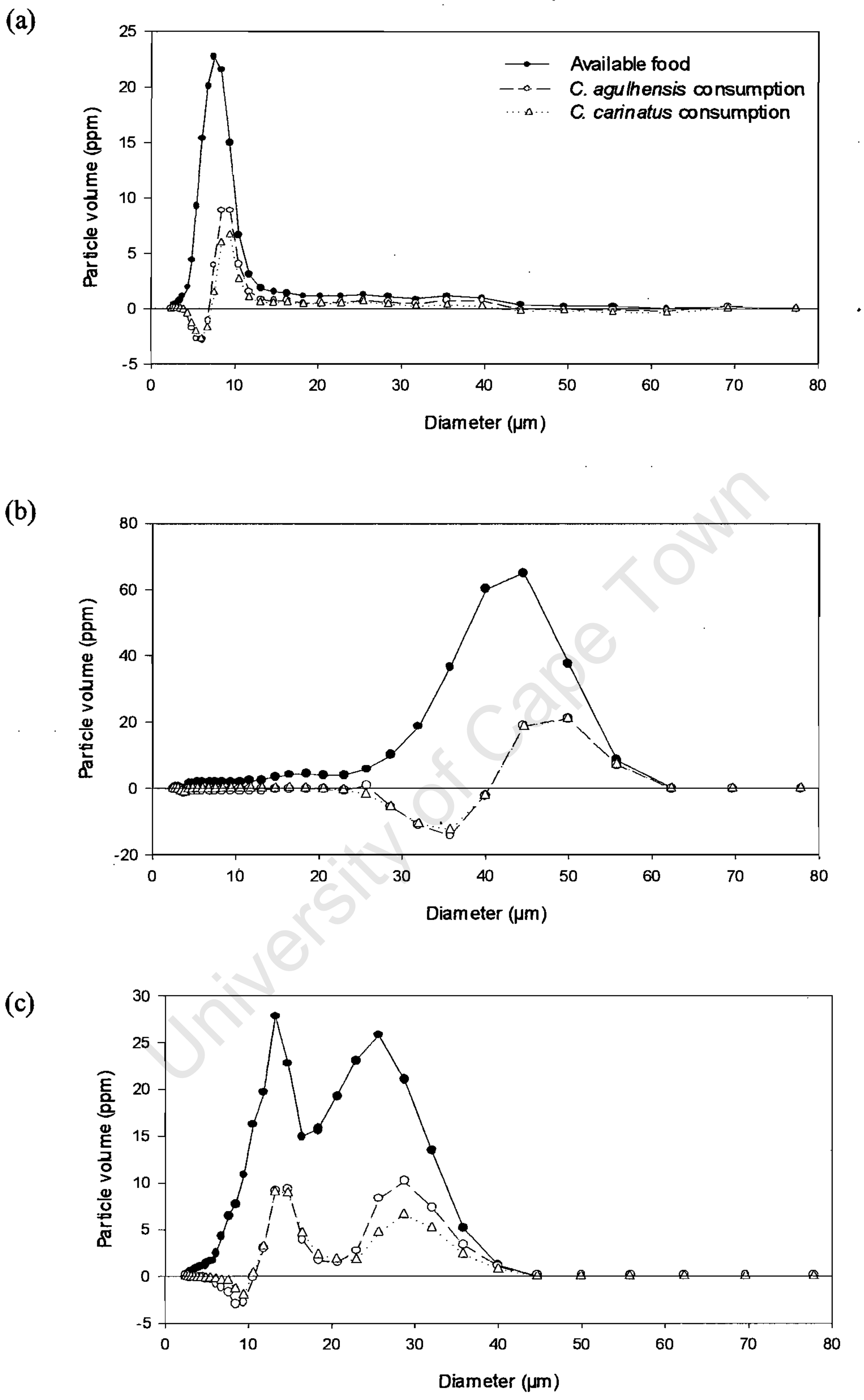


Figure 5.3. Comparative feeding (indicated by distribution of removed particles) by female *C. agulhensis* and *C. carinatus* fed ambient food characterized by (a) small, (b) large, and (c) bimodal size distributions of cell volume.

Table 5.3. Large cell experiment: abundance (*N*, cells ml^{-1}) and relative abundance of phytoplankton species in the ambient food environment (*p*) and diet (*r*) of *C. carinatus* and *C. agulhensis*. Dietary calculations were restricted to potential food species that comprised at least 5% of total food abundance. The selectivity coefficient (W_i, Vanderploeg and Scavia 1979) of these phytoplankton or microzooplankton species by both copepod species is also shown. For random feeding, W_i = 0.20. Preference for a species (W_i > 0.20) is indicated by bold text.

Species	Cell volume (μm^3)	Ambient food		*C. carinatus* diet			*C. agulhensis* diet		
		N	*p*	*N*	*r*	W_i	*N*	*r*	W_i
Thalassiosira sp.	14 168	430.5	0.50	156.9	0.49	0.14	104.8	0.68	0.20
Coscinodiscus sp.	35 555	182.6	0.21	0.0	0.00	0.00	0.0	0.00	0.00
Pseudonitzschia pungens	1 000	82.3	0.10	82.3	0.26	**0.39**	18.8	0.12	0.19
Skeletonema costatum	424	77.0	0.09	64.3	0.20	**0.33**	0.0	0.00	0.00
Mesodinium rubrum	8 479	40.1	0.05	14.7	0.05	0.14	30.2	0.20	**0.62**
Cylindrotheca closterium	121	32.7	0.04						
Pseudonitzschia seriata	2000	8.4	0.01						
Total		853.5	1.00	318.2	1.00	1.00	153.7	1.00	1.00

Table 5.4. Bimodal size experiment: abundance (N, cells ml^{-1}) and relative abundance of phytoplankton species in the ambient food environment (p) and diet (r) of *C. carinatus* and *C. agulhensis*. Dietary calculations were restricted to potential food species that comprised at least 5% of total food abundance. The selectivity coefficient (W_i, Vanderploeg and Scavia 1979) of each phytoplankton species by both copepod species is also shown. For random feeding, W_i = 0.20. Preference for a species (W_i > 0.20) is indicated by bold text.

Species	Cell volume (μm³)	Ambient food		*C. carinatus* diet			*C. agulhensis* diet		
		N	p	N	r	W_i	N	r	W_i
Pseudonitzschia pungens	1 000	354.0	0.35	154.0	0.45	**0.32**	194.5	0.74	**0.61**
Thalassiosira spp.	2 572	271.0	0.27	124.5	0.37	**0.34**	37.0	0.14	0.15
Pseudonitzschia seriata	2 000	173.5	0.17	0.5	0.00	0.00	0.0	0.00	0.00
Skeletonema costatum	424	138.0	0.14	60.5	0.18	**0.32**	30.5	0.12	**0.24**
Rhizosolenia fragillisima	4 040	45.5	0.05	1.5	0.00	0.02	0.0	0.00	0.00
Pennate diatom	2 000	8.5	0.01						
Rhizosolenia delicatula	2 670	8.0	0.01						
Total		998.5	1.00	341.0	1.00	1.00	262.0	1.00	1.00

pungens, *Thalassiosira* spp. and *S. costatum*, whereas *C. agulhensis* showed a strong preference for the dominant *P. pungens*, and a slight preference for *S. costatum*. Both copepods apparently avoided *P. seriata*, which comprised 17% of the total abundance, and the large (>4 000 µm^3) *R. fragillisima*, which comprised 5% of total abundance.

5.3.3 Diel feeding patterns

Diel patterns of gut pigment content (GPC) of various stages of *C. carinatus* and *C. agulhensis* collected near the surface on the West Coast during February 1995 (Fig. 5.4a) and on the Agulhas Bank during March 1994 (Fig. 5.4b) showed that both species appeared to feed throughout a 24-hr cycle. Although maximum values of GPC for each stage were usually observed at night, relatively high values were also observed during the day, particularly for female *C. carinatus* on the West Coast (Fig. 5.4a). There also appeared to be less diel variation in GPC of younger *C. agulhensis* stages (C1-C4) than in older stages (C5 and females) on the Agulhas Bank (Fig. 5.5b). The GPC of female *C. carinatus* was significantly related to the concentration of Chl *a* at both the surface and the f-max (Figs 5.5a and b), using data from both the West Coast and Agulhas Bank studies. There was a large amount of scatter to the data, however, and only 11% of the variance was explained by linear regressions. A maximum GPC of 16.8 ng pigment ♀$^{-1}$ was measured at an ambient food concentration of ~12 mg Chl *a* m^{-3}. There was no significant linear relationship between female *C. agulhensis* GPC and the concentration of Chl *a* at either the surface (Fig. 5.5c) or the f-max (Fig. 5.5d) during the Agulhas Bank study. Although much lower concentrations of Chl *a* were encountered during this study, GPC was still highly variable, with GPC ranging from 0 to >6 ng pigment ♀$^{-1}$ at <1 mg Chl *a* m^{-3}. A maximum GPC of 7.5 ng pigment ♀$^{-1}$ was measured at an ambient food concentration of ~2 mg Chl *a* m^{-3} (Fig. 5.5d).

Results from a GLM of *C. carinatus* GPC in relation to food concentration, time of day, and stage during the West Coast study indicated that there was no significant interaction between time of day and developmental stage (Table 5.5; Fig. 5.6a). However, *C. carinatus* GPC was significantly related to food concentration at the f-max (but not at the surface; results not shown) as well as to stage. GPC was generally greater at night than during the day (Fig. 5.6a), although not significantly so, and GPC of the females was slightly greater than that of the younger stages.

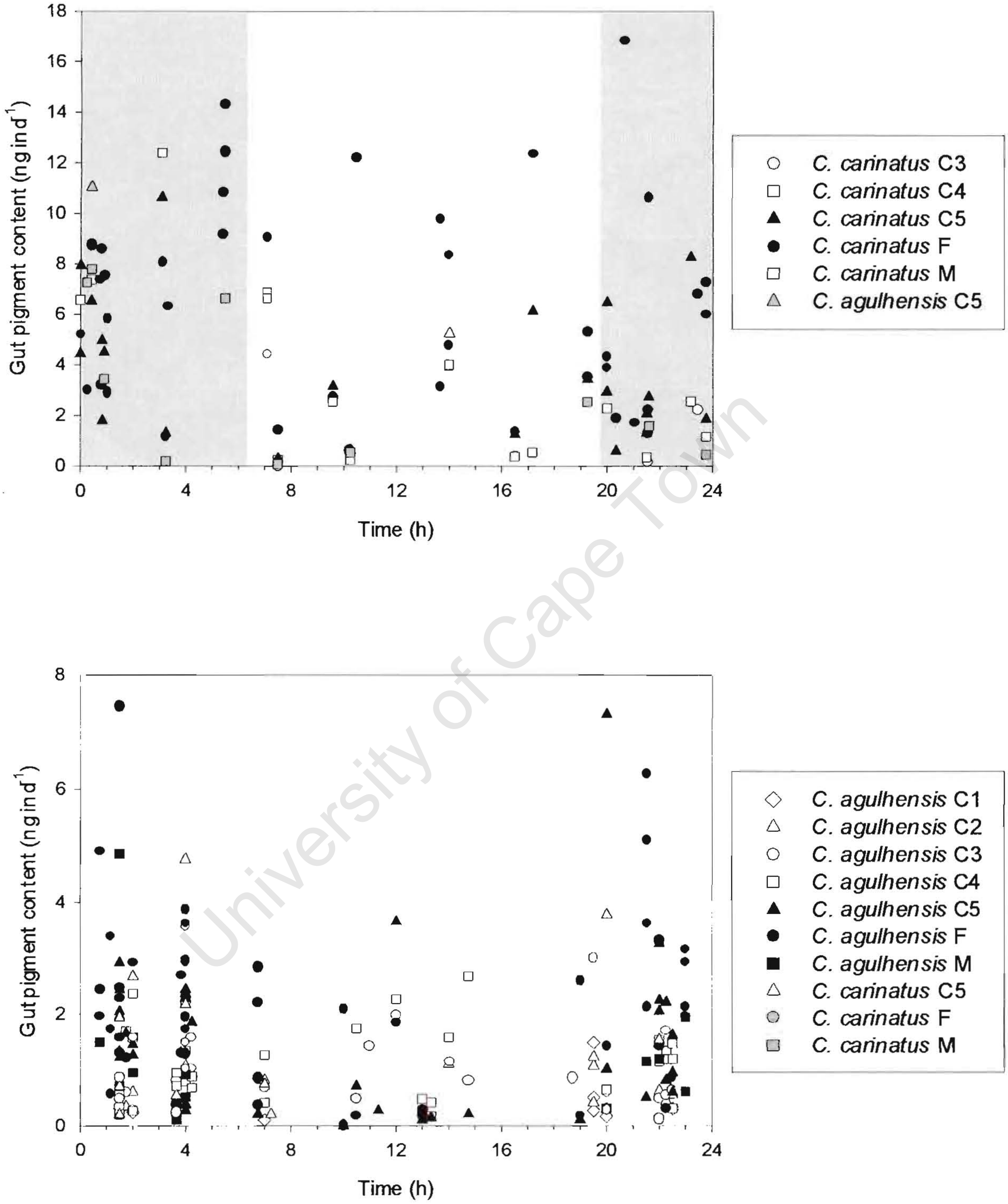
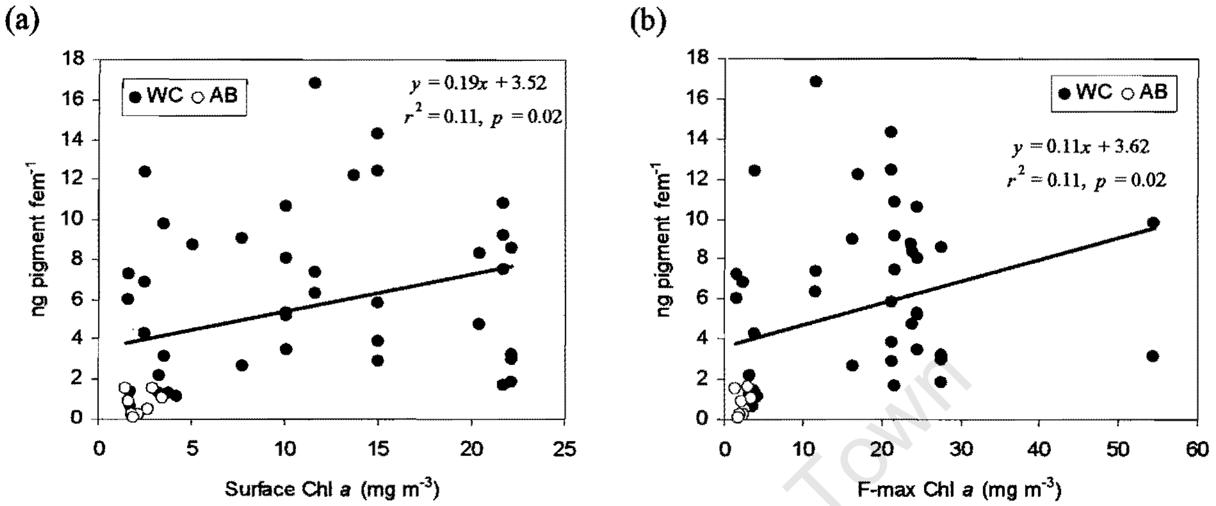


Figure 5.4. Diel variations in gut pigment content (ng pigment ind^{-1}) of different stages of *C. carinatus* and *C. agulhensis* (a) off the West Coast during February 1995, and (b) on the Agulhas Bank during March 1994. The shaded area indicates the period between sunset and sunrise.

C. carinatus



C. agulhensis

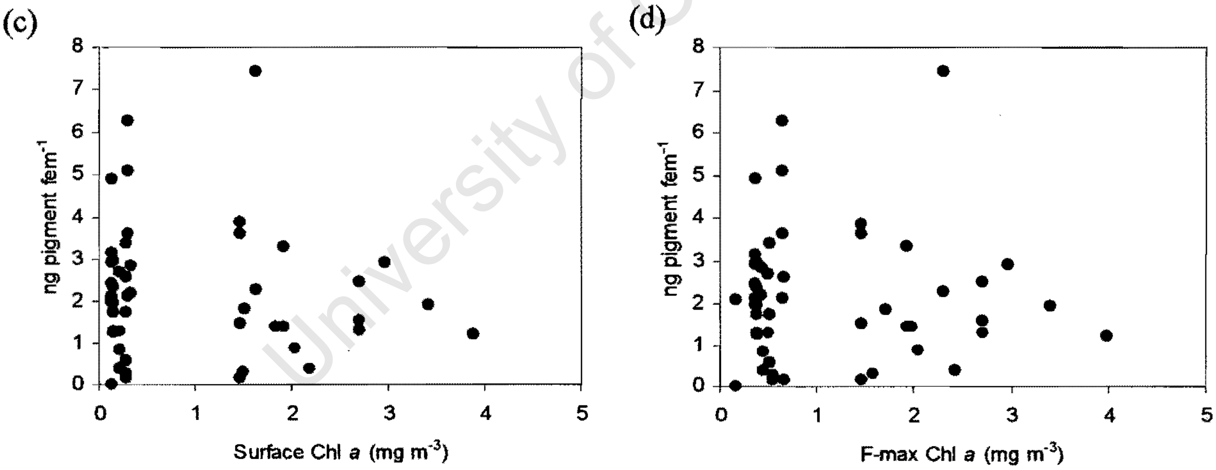
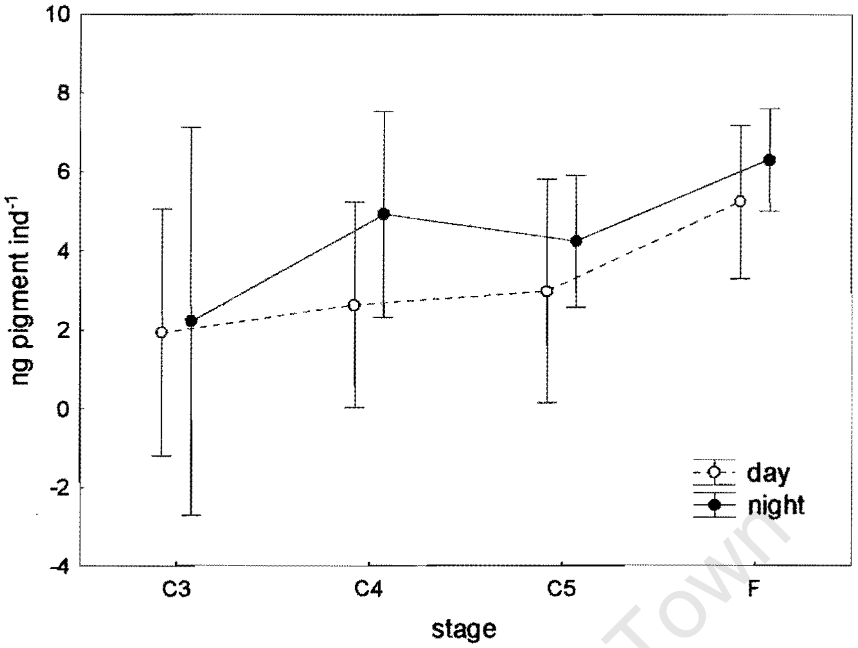


Figure 5.5. Scatterplots of gut pigment content (GPC, ng pigment ♀$^{-1}$) of female *C. carinatus* in relation to (a) surface Chl *a* (mg m^{-3}) and (b) Chl *a* at the fluorescence maximum on the West Coast during during February 1995, and of female *C. agulhensis* in relation to (c) surface Chl *a* and (d) Chl *a* at the fluorescence maximum on the Agulhas Bank during March 1994. Measurements of *C. carinatus* GPC from the latter study (AB) were combined with data from the West Coast (WC) in (a) and (b). Linear regressions are shown for (a) and (b), but were not significant for (c) and (d).

Table 5.5. *C. carinatus*: results of a general linear model used to test the effect of food concentration at the fluorescence maximum (mg Chl *a* m^{-3}), time of day (night or day) and stage (C3 and older, excluding males) on gut pigment content (ng pigment ind^{-1}). Significant effects ($p < 0.05$) are indicated in bold.

Effect	% variance explained	*SS*	*df*	*MS*	*F*	*p*
Intercept	13.65	172.99	1	172.99	14.60	**0.0000**
Food conc.	5.67	71.88	1	71.88	6.07	**0.0160**
Day/night	1.43	18.17	1	18.17	1.53	0.2193
Stage	7.75	98.27	3	32.76	2.76	**0.0476**
Day/night × Stage	0.43	5.41	3	1.80	0.15	0.9281
Error	71.06	900.46	76	11.85		

(a) *C. carinatus*



(b) *C. agulhensis*

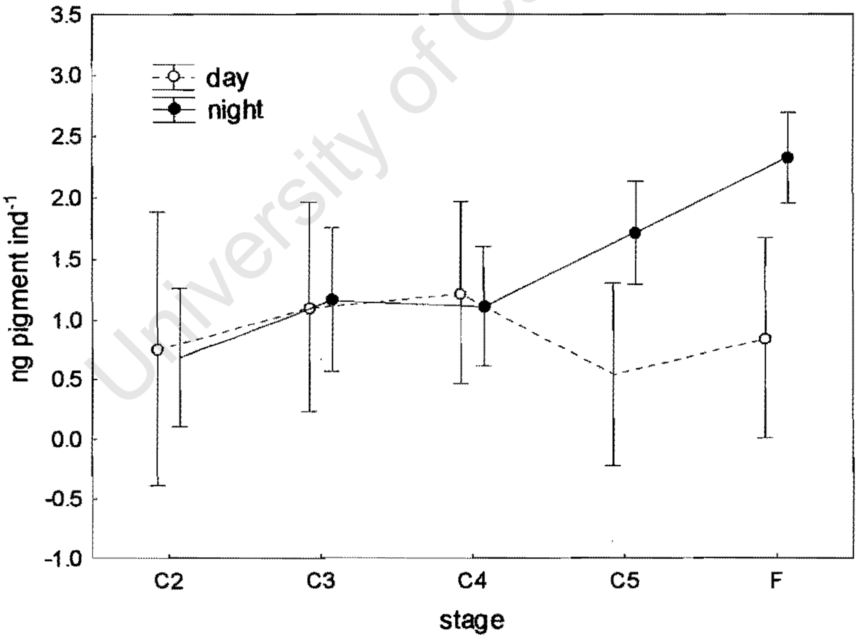


Figure 5.6. Results from GLM showing least square mean day-time and night-time gut pigment content (ng pigment ind^{-1}) of different stages of (a) *C. carinatus* and (b) *C. agulhensis* during studies off the West Coast (February 1995) and on the Agulhas Bank (March 1994) respectively. Error bars indicate 95% confidence intervals.

In contrast to *C. carinatus*, a GLM of GPC in relation to food concentration, time of day, and stage revealed a significant interaction between developmental stage and time of day for *C. agulhensis* during the Agulhas Bank study (Table 5.6). GPC of stages C2-C4 were similar during both day and night, but GPC of C5s and females were greater at night (Fig. 5.6b). GPC was not significantly related to the concentration of Chl *a* at either the f-max (Table 5.6) or the surface (results not shown).

5.4 DISCUSSION

5.4.1 Ingestion rates

Ingestion rates of *C. carinatus* and *C. agulhensis* showed considerable variability in relation to food concentration (Figs 5.1 and 5.2). During several experiments, low ingestion rates were observed despite high concentrations of Chl *a*, particularly for *C. carinatus*, suggesting poor food quality or poor female condition, or differences in feeding history. Nevertheless, both species displayed a similar functional response to food concentration overall, particularly with regard to particle volume, and appeared to attain maximum ingestion rates at ~15 mg Chl *a* m^{-3} (~600 μg C l^{-1}) and 7-8 ppm (Figs 5.1 and 5.2). These values could be overestimates of the critical concentration, however, as there were no measurements of ingestion rates for Chl *a* concentrations between 6 and 15 mg Chl *a* m^{-3} for either species (Fig. 5.1), or between 4 and ~9 ppm for *C. carinatus*, and between 4 and 7 ppm for *C. agulhensis* (Fig. 5.2).

Maximum rates of egg production by both species were achieved at food concentrations of approximately 10-15 mg Chl *a* m^{-3} and 3-4 ppm (Chapter 3), suggesting that a critical concentration of 7-8 ppm may be a little high. However, the hypothesis that *C. agulhensis* attains satiation at a lower food concentration than *C. carinatus* must be rejected based on the available data.

Similar functional relationships between ingestion rate and food concentration have been observed for other *Calanus* species, including *C. pacificus* (Frost 1972; Hassett and Landry 1983) and *C. finmarchicus* (Hansen *et al.* 1990; Båmstedt *et al.* 1999). Slightly lower satiated food concentrations than those estimated in this study for *C. carinatus* and *C. agulhensis* under natural food concentrations (~600 μg C l^{-1}) have been measured for several *Calanus* species fed on *Thalassiosira* monocultures in the laboratory, e.g. 300 μg C l^{-1} for *C. pacificus* (Runge 1980, 1984), 400 μg C l^{-1} for *C. finmarchicus* (Hirche 1990) and 450 μg C l^{-1} for *C. marshallae* (Peterson 1988). Parsons *et al.* (1967) reported that

Table 5.6. *C. agulhensis*: results of a general linear model used to test the effect of food concentration at the fluorescence maximum (mg Chl a m^{-3}), time of day (night or day) and stage (C2 and older, excluding males) on gut pigment content (ng pigment ind^{-1}). Significant effects (p < 0.05) are indicated in bold.

Effect	% variance explained	*SS*	*df*	*MS*	*F*	*p*
Intercept	16.23	43.47	1	43.47	33.20	**0.0000**
Food conc.	0.01	0.04	1	0.04	0.03	0.8693
Day/night	2.29	6.14	1	6.14	4.69	**0.0319**
Stage	2.75	7.37	4	1.84	1.41	0.2341
Day/night × Stage	4.89	13.08	4	3.27	2.50	**0.0451**
Error	73.82	197.71	151	1.31		

C. pacificus obtained a maximum ration at 7 ppm when feeding on natural phytoplankton blooms. In contrast, much higher concentrations (>800 μg C l^{-1}) were required for *C. finmarchicus* to achieve maximum ingestion rates on small cells such as *Rhodomonas baltica* (~8 μm diameter) and *Emiliania huxleyi* (~4 μm diameter; Båmstedt *et al.* 1999).

The maximum daily ration (% body carbon) observed for *C. carinatus* in this study (79%; Chl *a* = 23.4 mg m^{-3}) was less than that documented by Peterson *et al.* (1990a) under excess food conditions in the laboratory (126%; 8 000 cells *T. weissflogii* ml^{-1}), but greater than that observed by Timonin *et al.* (1992) under field conditions in the northern Benguela (58%; Chl *a* = 4.5 mg m^{-3}). Peterson *et al.* (1990b) reported a mean daily ration of 15-16% for *C. agulhensis* under conditions of high chlorophyll concentration (>3 mg Chl *a* m^{-3}), which was slightly lower than that observed under high Chl *a* concentrations during the present study (21%; Table 5.1).

5.4.2 Size and species selection

Similar particle-size selection was exhibited by *C. carinatus* and *C. agulhensis* females incubated in the same natural food assemblages. When food was abundant, both species appeared to select the larger particles that dominated the biomass, whether the ambient food was characterized by predominantly small-, large- or bimodal-sized particle spectra (Fig. 5.3). However, the ingestion rate by *C. carinatus* was approximately half that of *C. agulhensis* during the small particle experiment, suggesting that *C. carinatus* may feed less efficiently than *C. agulhensis* on small particles. The hypothesis that *C. carinatus* feeds inefficiently on small cells typical of the Agulhas Bank could therefore not be rejected.

Similar feeding behaviour was exhibited by *C. chilensis* females, which, at high food levels, selectively ingested particles with the greatest relative abundance, or particles slightly larger than those with greatest relative abundance (Cowles 1979). Disproportionate ingestion, or "preference" (Turner and Tester 1989), of large particles from natural assemblages has been observed for *C. pacificus* (Richman and Rogers 1969; Harris 1982) as well as for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* (Barthel 1988), although it has been proposed that this may be because *Calanus* handles large cells more efficiently than small cells (Frost 1977). The median diameter of particles ingested by *C. pacificus* was greater than that of available particles in 96% of the experiments conducted during a 72-day mesocosm study, during which a wide variety of phytoplankton were encountered (Harris 1982).

Other studies have documented non-selective feeding behaviour for *Calanus* species. Under non-saturated feeding conditions, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* removed particles in direct proportion to their abundance, with no apparent size-selective ingestion (Huntley 1981), and Turner and Tester (1989) proposed that copepods are primarily non-selective when suspension-feeding on natural phytoplankton assemblages. These differences in feeding behaviour may be related to differences in food availability. Cowles (1979) found that selectivity decreased with declining food abundance, as would be expected from optimal foraging theory. However, Barthel (1988) found that selectivity was independent of food abundance. Factors such as food quality, experimental methodology and the often-undetermined extent of omnivory further complicate the interpretation of feeding studies, and the issue of food selectivity is likely to remain the subject of much debate.

Negative particle removal observed during the experiments, suggesting particle production in the size classes smaller than the biomass peak, has been observed in other feeding studies, particularly those using natural particle assemblages (Gamble 1978; Deason 1980; Harris 1982; Roy *et al.* 1989). This may be attributable to inefficient ingestion of large cells, or the breakage of diatom chains (Paffenhöfer 1971), an effect commonly referred to as "sloppy feeding". This appears to be most pronounced when animals are feeding on large diatoms under conditions of excess food (Roy *et al.* 1989; Båmstedt *et al.* 2000). As chain-forming diatoms comprised 95 and 80% of the diets of *C. carinatus* and *C. agulhensis* respectively in the large-cell dominated experiment (Table 5.3), and 100% of their diets in the bimodal-sized experiment (Table 5.4), chain breakage by the feeding copepods provides a plausible explanation for the observed particle production. Certain "bottle effects" may also affect control and experimental bottle particle-size distributions differentially, including enhanced algal growth in the experimental bottles due to ammonium excretion by the grazers (Roman and Rublee 1980). Food chain effects may also be observed, such as selective predation upon microzooplankton by copepods in the experimental bottles, leading to a reduction in the comparatively greater grazing pressure by microzooplankton on the smaller phytoplankton size classes compared to the control bottles (Nejstgaard *et al.* 1997, 2001). However, such effects are difficult to quantify without parallel knowledge of the taxonomic composition and food selectivity of the microzooplankton (Båmstedt *et al.* 2000; Nejstgaard *et al.* 2001).

Although *C. carinatus* and *C. agulhensis* appear to have similar food-size preferences (Fig. 5.3), differing selectivity coefficients in each experiment indicated that they may have different preferences in terms of individual phytoplankton or microzooplankton species or types (Tables 5.3 and 5.4). *C. carinatus* displayed a broad preference for the smaller chain-forming diatoms in both the large- and bimodal-sized experiments, whereas *C. agulhensis* showed a strong preference for the ciliate *M. rubrum* in the large-cell experiment, and for the dominant diatom when only diatoms were present. It is difficult to make generalizations based on these limited results, but it is noteworthy that the ciliate *M.*

rubrum was eaten disproportionately by *C. agulhensis*. A number of studies have shown ciliates to be favoured food items for *Calanus* species (Kleppel 1993; Fessenden and Cowles 1994; Atkinson 1996; Nejstgaard *et al.* 1997), and algal ingestion alone may often be insufficient to meet the metabolic requirements of copepods in the ocean (Stoecker and Capuzzo 1990; Kleppel 1993; Ohman and Runge 1994; Peterson and Dam 1996; Nejstgaard *et al.* 2001). Omnivorous feeding has previously been inferred for *C. agulhensis* (Peterson *et al.* 1990b), and it thus seems likely that feeding on microzooplankton may play an important role in supplementing the nutrition of *C. agulhensis* on the Agulhas Bank, where phytoplankton abundance is generally low (Brown 1992). The preference shown by *C. carinatus* for small diatom chains is consistent with the dominance of this type of phytoplankton in upwelling areas.

5.4.3 Diel feeding

Diel variations in feeding activity have been observed for many copepod species (Haney 1988), including *C. carinatus* in the northern Benguela (Timonin *et al.* 1992), *C. agulhensis* in the southern Benguela (Peterson *et al.* 1990b), and many other *Calanus* species such as *C. chilensis* (Castro *et al.* 1991), *C. finmarchicus* (Daro 1985; Kiørboe *et al.* 1985), *C. helgolandicus* (Harris 1988; Harris and Malej 1986), and *C. pacificus* (Ohman 1988; Dagg *et al.* 1989; Landry *et al.* 1994; Dagg *et al.* 1998), as well as the boreal species *C. cristatus* and *C. plumchrus* (Ishii 1990), and *C. propinquus* and *C. simillimus* (Atkinson *et al.* 1992a, 1992b, 1996). These feeding rhythms are sometimes bimodal (Ishii 1990), with increased crepuscular feeding rates. Durbin *et al.* (1990) suggested that diel feeding rhythms are endogenous and controlled separately from diel vertical migration patterns, if present, although some studies have demonstrated tight coupling between diel migratory and feeding rhythms, with suppressed feeding rhythms when food is limiting (Mackas and Bohrer 1976; Boyd *et al.* 1980; Huntley and Brooks 1982).

As GPC measurements were restricted to animals collected within the upper 10 m of the water column in this study, indications of diel feeding are confounded by diel vertical migratory behaviour. Significant diel variations in feeding were only found for *C. agulhensis* on the Agulhas Bank (Table 5.5), and were restricted to the older stages (C5s and females, Fig. 5.6b). These results suggest two possible scenarios: either (1) younger stages did not descend during the day but remained near the surface where they continued to feed, whereas those older stages collected near the surface during the day represented a minority that either were unable to descend or chose not to, or (2) all stages remained near the surface during the day but only the younger stages continued to feed at rates comparable to those measured at night.

Food levels were frequently low during the Agulhas Bank study (mean Chl *a* = 1.82 mg m^{-3} at the surface; 2.04 mg m^{-3} in the food-rich layer), which combines data from three separate 24-hr stations. Many of the younger stages remained in the upper 20 m of the water column during the day, and the older stages tended to delay their daytime descent under low concentrations of Chl *a* (this is explored further in Chapter 6). The first scenario thus appears to be the most likely, with older stages collected near the surface during the day comprising individuals that had not descended, and that either did not feed or did so at slow rates. Some studies have concluded that copepods descend only when satiated (Huntley and Brooks 1982; Atkinson *et al.* 1992a), and that circadian periodicity only operates under conditions of high food availability, when the copepods are able to satisfy their nutritional requirements by nocturnal migration alone (Roman *et al.* 1988; Atkinson *et al.* 1992a). Furthermore, Dagg *et al.* (1989) observed that although some *C. pacificus* appeared in the surface layer up to 2.5 h before sunset, feeding increased substantially only well after sunset. This observation is thought to be linked to predator avoidance, as the food-packed guts of copepods feeding during daylight may attract visual predators (Stearns 1986; Dagg *et al.* 1989; Bollens and Stearns 1992). As predation risk increases with size (Tande 1988; Fiksen and Giske 1995), larger copepods that remain near the surface during the day would be less likely to continue feeding than the smaller stages, in order to minimize their daytime visibility. Diel vertical migration (DVM) may vary amongst individuals (Hays *et al.* 2001), and is not necessarily synchronous, thus the combination of patchy food and individual variability (e.g. due to age, feeding history or genetic variability) may result in some members of a certain stage attaining sufficient food and energy reserves at night to descend, and others not.

The results observed for *C. agulhensis* on the Agulhas Bank contrast with those of Peterson *et al.* (1990b), who found that *C. agulhensis* exhibited a diel feeding rhythm off the West Coast, independent of whether or not they were vertically migrating. This apparent contradiction may be a consequence of different ambient food concentrations during the two studies; mean concentration of Chl *a* was much greater (17.2 mg m^{-3}) during the West coast study (Peterson *et al.* 1990b), suggesting that all stages of *C. agulhensis* would be able to achieve satiation through nocturnal feeding alone, without needing to "risk" daytime feeding.

The absence of a significant diel feeding rhythm by *C. carinatus* during the West Coast study is harder to explain, as there is no supplementary information on DVM. Concentrations of Chl *a* were much higher compared to the Agulhas Bank study, which may have resulted in the significant relationship observed between *C. carinatus* GPC and Chl *a* (Table 5.4). Although mean Chl *a* concentrations (9.3 mg m^{-3} at the surface; 15.4 mg m^{-3} at the f-max) appeared to be sufficient for *C. carinatus* to achieve satiation at night, feeding clearly continued during the daytime, although at slightly lower rates (Fig.

5.6a). Daytime feeding under high food conditions suggests that there was a low risk of predation near the surface, either due to the predation risk being at depth, or else to the increased turbidity caused by the high food concentration masking the visibility of the copepods, as suggested by dynamic optimization theory (Fiksen and Giske 1985).

In summary, the hypothesis that *C. carinatus* and *C. agulhensis* have different diel feeding patterns cannot be rejected based on the available data, but it is likely that they both have very plastic feeding behaviour that varies in response to both food availability and predation risk. Further studies of diel feeding rhythms when both species are abundant will be required to gain more insight into any possible differences.

5.5 CONCLUSIONS

C. agulhensis and *C. carinatus* displayed a similar functional response to food concentration in terms of ingestion rate, with maximum ingestion rates observed at Chl *a* concentrations of ~15 mg m^{-3} and 7-8 ppm. Both species also displayed similar feeding behaviour in terms of particle size selection, and generally appeared to prefer the larger particles that dominated the food biomass, although slower ingestion rates on small (<10 μm) particles by *C. carinatus* compared to *C. agulhensis* suggests that *C. carinatus* may feed less efficiently on small cells. Differing selectivity coefficients suggests a preference for different food species, and the possibility of resource partitioning. Whereas *C. carinatus* appeared to prefer small chain-forming diatom species, *C. agulhensis* ingested the ciliate *M. rubrum* disproportionately to its abundance, suggesting that microzooplankton may supplement nutritional requirements of this copepod species when phytoplankton abundance is low. The limited data available on diel feeding suggests plasticity of feeding behaviour by both species, which may be moderated in response to food availability and predation risk. In terms of feeding ecology, however, the two species are very similar.

CHAPTER 6

Diel vertical migration of *Calanoides carinatus* and *Calanus agulhensis* in relation to food availability

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6.1. INTRODUCTION

Many zooplankton species are able to migrate vertically over large distances each day. The most common pattern of diel vertical migration (DVM) is where the population lives at some distance below the surface during the day, but swims upwards towards the surface around sunset ("evening ascent"), where the animals remain during the hours of darkness. Prior to sunrise, the animals begin to swim downwards to return to their daytime depths ("dawn descent"). This is sometimes referred to as "normal" or "nocturnal migration". Variations of this diel pattern have also been observed, such as "reverse migration", in which animals occur close to the surface by day and descend to deeper water at night, and "twilight migration", in which ascents occur at both sunset and sunrise, with "midnight sinking" in between (Huntley 1985; Hays *et al.* 1996; Mauchline 1998). Light, or relative change in light intensity, is considered to be the prime environmental cue for ascent and descent (Ringelberg 1995; Mauchline 1998), but descent may also be triggered by the presence of visual predators (Bollens and Frost 1989a, b; Neill 1990) or by satiation (Mackas and Bohrer 1976; Atkinson *et al.* 1992a).

The relative importance of food and predation as selective mechanisms for DVM has been hotly debated. Huntley and Brooks (1982) demonstrated that hungry copepods (*Calanus pacificus*) behaved differently to well-fed copepods in a predator-free mesocosm. They proposed that hunger is the primary factor controlling vertical migration behaviour, and may override other stimuli such as avoidance of predation; their colloquialism for this is "better dead than unfed". In contrast, Frost (1988) concluded that predator avoidance was the major selective advantage of DVM in this same species, based on observations in a temperate fjord as well as a model of population growth. Many other studies consider the adaptive significance of DVM to be best explained by predator evasion, whether as normal DVM in response to visual predators or as reverse DVM in response to invertebrate predators (Zaret and Suffern 1976; Gliwicz 1986; Bollens and Frost 1989a, b; Hays *et al.* 1996; Neill 1992; Pearre 1973). Predation can be both an evolutionary and a proximal ("inducing") agent for variation in DVM (Neill 1992), in other words through selective predation as well as behavioural plasticity (Hays *et al.* 1996). Kiørboe (1998) argues that population growth rates are much more sensitive to variations in mortality than to variations in fecundity, and that population dynamics in planktonic copepods are thus strongly controlled by top-down processes. This could translate as "better unfed than dead".

Dagg *et al.* (1998) concluded that after many years of debate, it should be accepted that the downward diel migration of copepods during daytime is a response to visually orienting predators. However, there are many examples where vertical migratory behaviour is mediated by food availability or feeding, and DVM can generally be regarded as a balance or trade-off primarily between predation risk and nutritional reward (Kerfoot 1985; Dagg 1985; Dagg *et al.* 1997), but possibly other factors too (Haney 1988; Falkenhaug *et al.* 1997). A simple model developed by Iwasa (1982) demonstrated that DVM is one of the options open to plankton to resolve the conflicting needs to feed and to survive in an environment in which there are complementary gradients in food availability and visual predation pressure, particularly if these gradients vary in time (e.g. daily or seasonally).

Other hypotheses that have been proposed to account for DVM include bioenergetic advantages, horizontal dispersion and transport, breeding migrations, and avoidance of photo-damage (Longhurst 1976; Angel 1985; Kerfoot 1985). The bioenergetic advantage hypothesis (McLaren 1963, 1974) has been largely discredited, however, and DVM is now considered to carry an energetic or fitness cost as opposed to a benefit (Ohman 1990). In addition to facilitating horizontal dispersion, DVM may also provide an important population retention mechanism in habitats characterized by strong advection, such as upwelling environments, where animals are able to exploit differential current shears at different depths (Wroblewski 1982; Verheye *et al.* 1991; Etiane *et al.* 1998), and in tidal estuaries (Kimmerer and McKinnon 1987).

Ohman (1990) concludes that DVM is a dynamic rather than a fixed, invariant trait within a population. An animal will migrate to feed, breed, avoid visual predators or obtain a net gain in energy; it will suspend migration to exploit food patches, avoid predators, conserve energy or overwinter at depth. The priorities will vary according to species, individuals, age, season and environment. Comparative studies of vertical migration of different species under the same environmental conditions therefore provide a valuable tool for investigating hypotheses regarding plasticity of behaviour, such as the interplay between hunger and predation risk, and population retention mechanisms.

The diel vertical migratory behaviour of copepodite and adult *C. carinatus* in the southern Benguela upwelling system has been well documented (Verheye 1991; Verheye and Field 1992). Ontogenetic layering of *C. carinatus* was observed during both day and night at a relatively shallow (50 m) anchor station on the West Coast, with deeper distributions at night, and increasing amplitude of DVM with increasing age. The amplitude of stage-specific DVM was linked to food availability, which varied according to the phase of upwelling. DVM was pronounced when food was plentiful near the surface (following the advection of newly upwelled water), but suppressed when surface chlorophyll levels were low (during relaxation of upwelling).

In contrast, little information is available for *C. agulhensis*. During an investigation into diel feeding and vertical migration of the copepod community along a transect off the Olifants River on the West Coast, Peterson *et al.* (1990b) found that most *C. agulhensis* copepodites (C1-C4) remained within the upper 20 m at a shallow (80 m), Chl *a*-rich (17.2 mg m^{-3}) inshore station. Farther offshore (195 m; 3.8 mg Chl *a* m^{-3}), older copepodites (C4, C5 and females) displayed normal DVM, although many young stages (C1-C3) remained in the upper 20 m both day and night offshore. Interestingly, all *C. carinatus* copepodites (C1-C5) at this offshore station displayed reverse DVM, suggesting different stage-specific behaviour to *C. agulhensis* under the same conditions.

The aims of this study were firstly to provide a comprehensive study of the DVM of *C. agulhensis* on the Agulhas Bank, in order to match similar knowledge for *C. carinatus* in the southern Benguela upwelling system, and secondly to test the hypothesis that these two copepod species exhibit different vertical migratory behaviour under the same environmental conditions. To achieve these aims, the vertical distribution of both species was investigated in relation to ambient food availability during a field study on the Agulhas Bank.

6.2. MATERIAL AND METHODS

Three stations on the Agulhas Bank were sampled regularly over separate 48-h periods during early March 1994 (Fig. 6.1). Temperature, depth and fluorescence profiles were obtained using a temperature-depth recorder in conjunction with a Chelsea Instruments Aquatracka submersible fluorometer mounted on a Magnum rosette, and water samples were collected at the surface and depth of maximum fluorescence (f-max) for determination of chlorophyll *a* and particle spectra. Chlorophyll samples were analysed on board the ship according to the method of Parsons *et al.* (1984), whilst the particle-size spectra were measured using a Coulter Multisizer. Current strength at 30 m was measured using a vessel-mounted Acoustic Doppler Current Profiler (ADCP).

Zooplankton were collected every 2-6 h using a 200-µm mesh, 1-m^2, multiple opening-closing rectangular midwater trawl (RMT 1×6), which was towed obliquely at 2 kt (3-7 km h^{-1}) over five

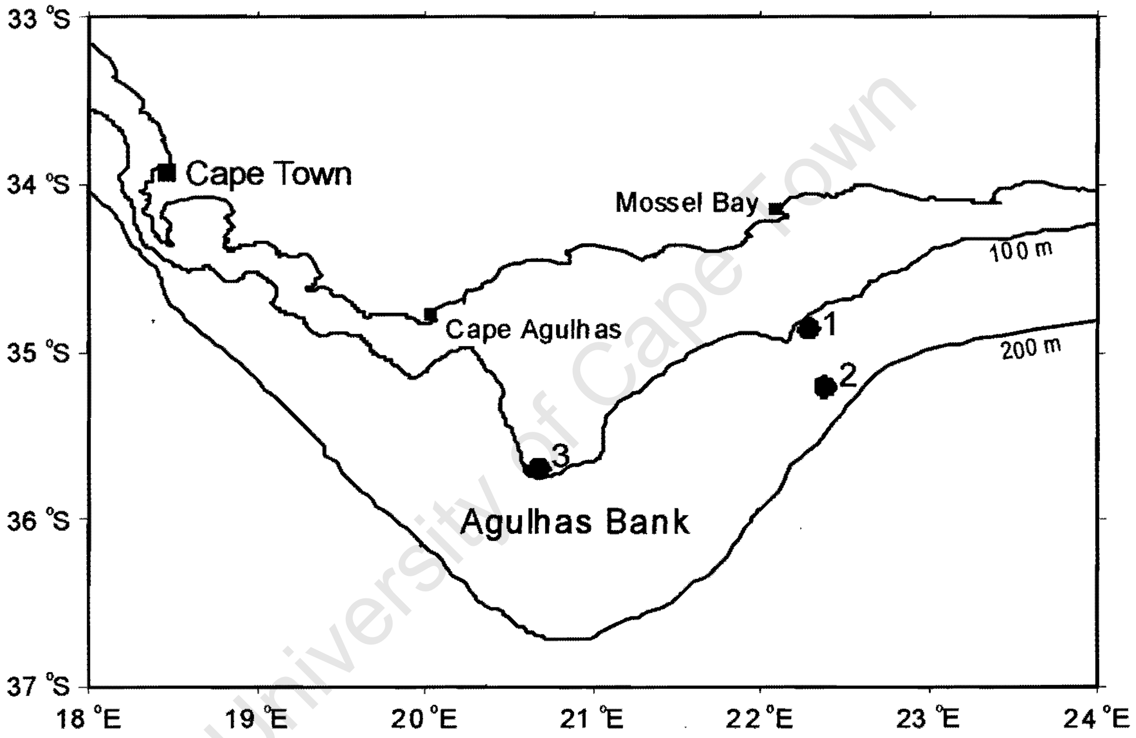


Figure 6.1. Map showing location of three 48-hr stations occupied on the Agulhas Bank during March 1994.

depth strata at Stations 1 and 2, and four depth strata at Station 3, from just above the bottom to the surface. These strata were ~100-80 m, 80-60 m, 60-40 m, 40-20 m, and 20-0 m at Station 1; ~125-100 m, 100-75 m, 75-50 m, 50-25 m, and 25-0 m at Station 2; and ~80-50 m, 50-35 m, 35-25 m and 25-0 m at Station 3. Flow rate was estimated using a flowmeter mounted above the mouth of the net, and 100% efficiency was assumed for the tows, which were of approximately equal, short duration. As a consequence of gear failure towards the end of Station 2, zooplankton samples were subsequently collected using a Bongo net of 200-µm mesh and 0.57-m^2 mouth area. These nets were hauled vertically over three depth strata: from 125-0 m, 100-0 m and 75-0 m. Zooplankton collected in the latter haul (equivalent to the three upper RMT depth strata) were assumed to be evenly distributed throughout this depth stratum.

Upon retrieval, the contents of each net were preserved in 4% buffered formalin for later analysis. In the laboratory, the contents of each jar were allowed to settle, and the settled volume was diluted 10 times. All copepods in a 2-ml subsample were counted, and standardized to numbers per m^3 using flowmeter data. The mean vertical position (weighted mean depth, WMD) of copepods in the water column was calculated using the method of Pearre (1973):

$$d = \frac{\sum n_i d_i}{\sum n_i}$$

where n_i is the number of individuals per m^3 at that depth range and time, and d_i is the mid-point of the depth-range. By calculating the weighted mean depth of each copepodite stage at each station, vertical movement of the population could then be tracked through time.

The amplitude of DVM each day at each station was estimated by comparing the WMD of each stage at midnight (00h00) with the WMD at 10h00 the following morning. The 10h00 samples were chosen because there were more data available at this time compared to the midday (13h00) samples (five night/day data pairs for 10h00 as opposed to three for 13h00). Furthermore, several developmental stages displayed a bimodal depth distribution at 13h00 at Station 1 (Appendix 2), and the WMD method assumes that animals are distributed unimodally in the water column (Pearre 1973).

An index of food availability each night was obtained by averaging the particle volume (ppm) at the depth of maximum fluorescence for all samples collected between 21h00 and 03h00. The "food-rich layer" was defined as the depth range where the concentration of Chl *a* was greater than 0.5 mg m^{-3}, as indicated by the fluorescence profiles. A general linear model (GLM) was used to relate DVM to mean night-time particle volume (ppm) at the f-max (*Food concentration*, used as a continuous variable), as well as the categorical variables *Species* (*C. agulhensis* vs *C. carinatus*) and *Stage* (C2 and older, including males).

6.3. RESULTS

6.3.1. Environmental conditions

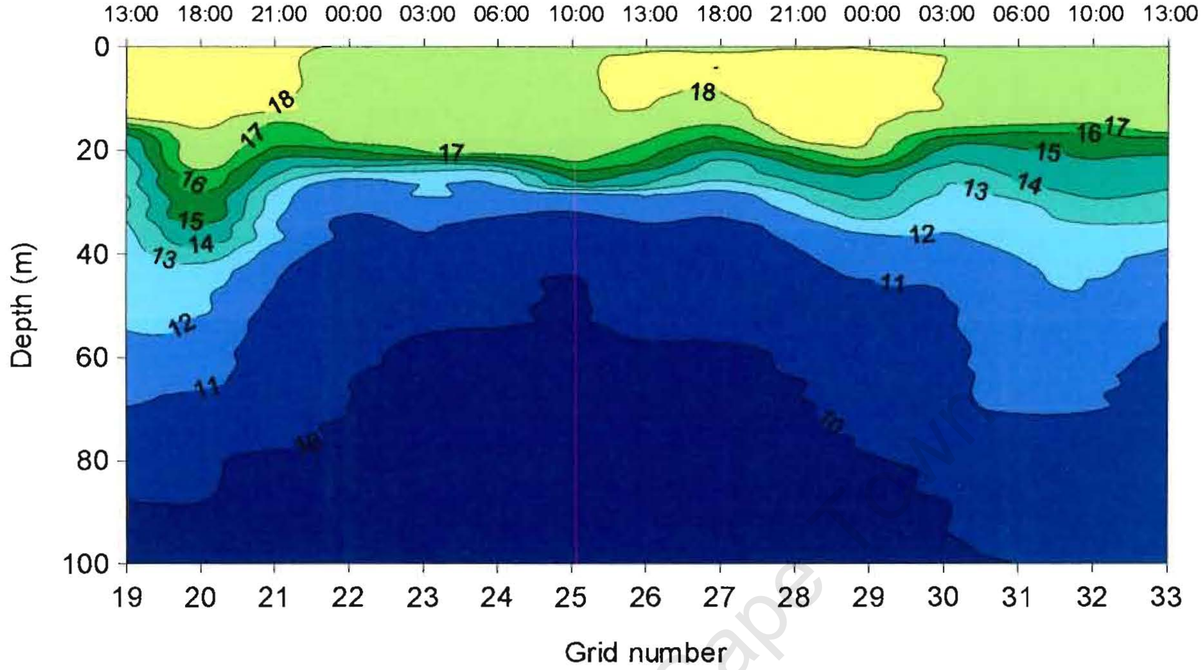
Station 1 (100 m depth) was characterized by a strong thermocline at 20-25 m, beneath a well-mixed upper layer of relatively warm (17-19°C) and chlorophyll-rich (>1 mg m^{-3}) water (Fig. 6.2). The 17°C isotherm coincided with the thermocline, indicating the presence of the cool ridge often observed on the central Agulhas Bank (Chapter 2). The concentration of Chl *a* in the upper mixed layer was greater during the first day of the time-series, ranging from 2 to >3 mg m^{-3}, but declined to <2 mg m^{-3} over much of the second day. Beneath the thermocline the water column was characterized by cold (9-12°C), chlorophyll-poor (<0.5 mg m^{-3}) water, and temperature profiles indicated a doming of the isotherms from approximately midnight of the first day to midnight of the second day of sampling. This doming may have resulted in the slightly elevated Chl *a* concentrations (>3 mg m^{-3}) observed near the surface towards the middle of the sampling period. Currents at 30 m were moderate and to the southwest, averaging 44.4 ± 0.9 cm s^{-1} (± SE).

Station 2 (140 m depth) was characterized by a much weaker thermocline at 20-30 m, and generally warmer temperatures (>12°C) above 100 m (Fig. 6.3). Concentration of Chl *a* was again greatest above the thermocline in the upper mixed layer, and was insignificant (<0.5 mg m^{-3}) below the thermocline. Chl *a* was initially relatively low (<2 mg m^{-3}) but increased to >4 mg m^{-3} near the surface on the second day. Currents at 30 m were moderate to slow, and to the southwest, averaging 20.8 ± 2.3 cm s^{-1}.

Station 3 (80 m depth) was characterized by very warm (>20°C) oligotrophic (<0.5 mg Chl *a* m^{-3}) water in the upper mixed layer above a strong thermocline at ~30 m (Fig. 6.4). Very low subsurface concentrations of Chl *a* (<1 mg m^{-3}) were restricted to a narrow stratum of water (approximately 20 m deep) below the thermocline. Temperature and Chl *a* profiles indicated an internal oscillation with a period of ~20 h (Alan Boyd, MCM, pers. comm.), resulting in alternate rising and falling of the isotherms, and synchronized movement of the Chl *a*-rich layer below the thermocline. Currents at 30 m

Station 1 (100 m)

(a) Temperature (°C)



(b) Chlorophyll a (mg m^{-3})

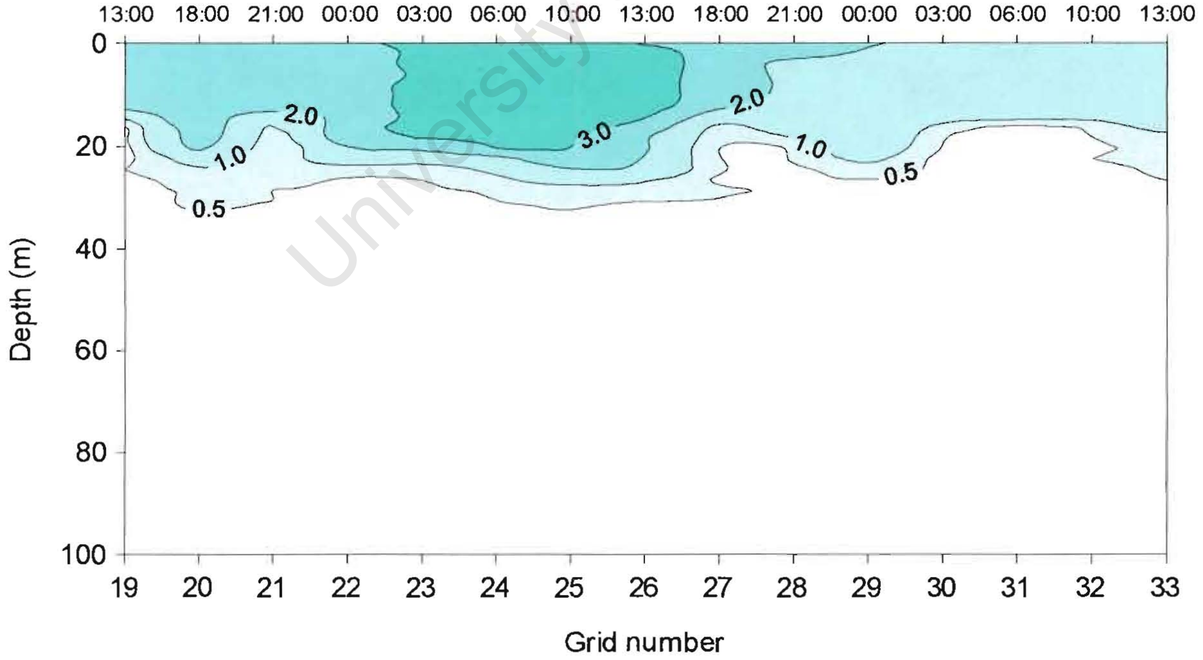
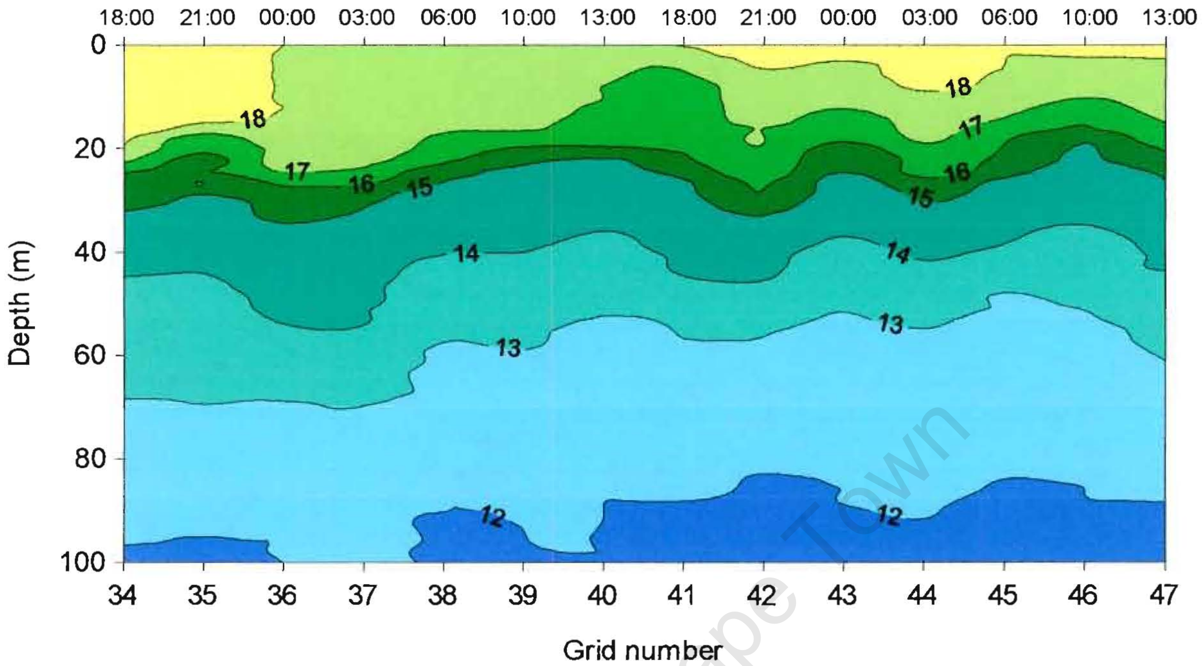


Figure 6.2. Vertical distribution of (a) temperature (°C) and (b) chlorophyll a (mg m^{-3}) within the upper 100 m over a 48-hr period at Station 1. Sampling time is shown at the top of the graphs, and the sequential grid reference number at the bottom.

Station 2 (125 m)

(a) Temperature (°C)



(b) Chlorophyll *a* (mg m^{-3})

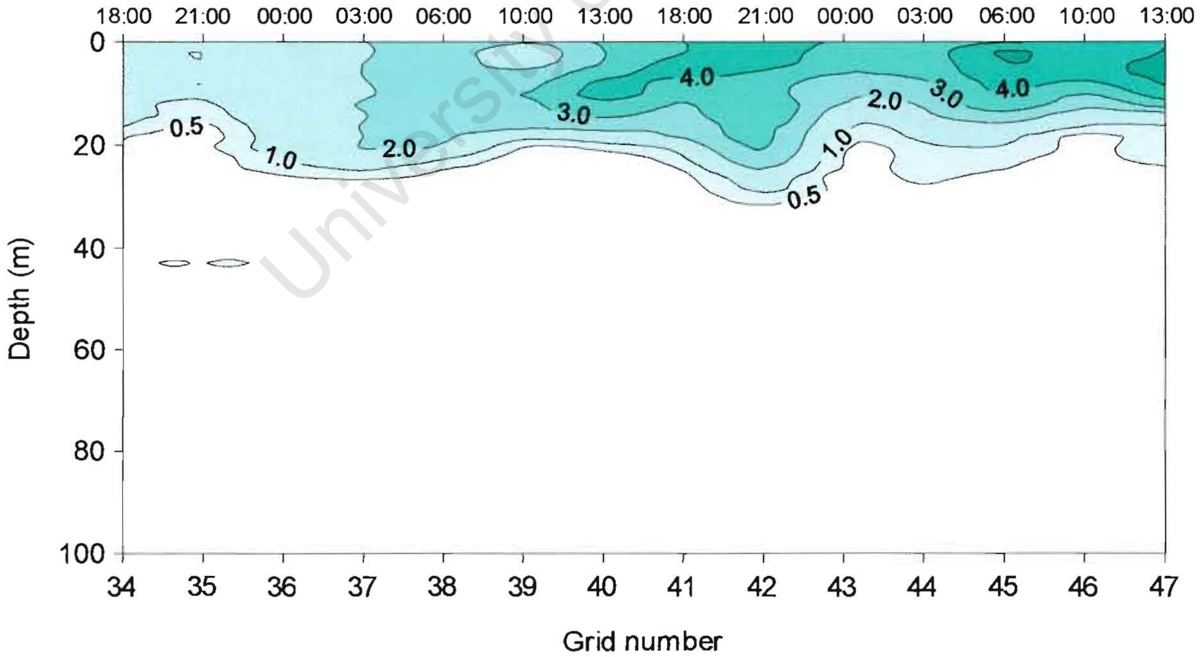
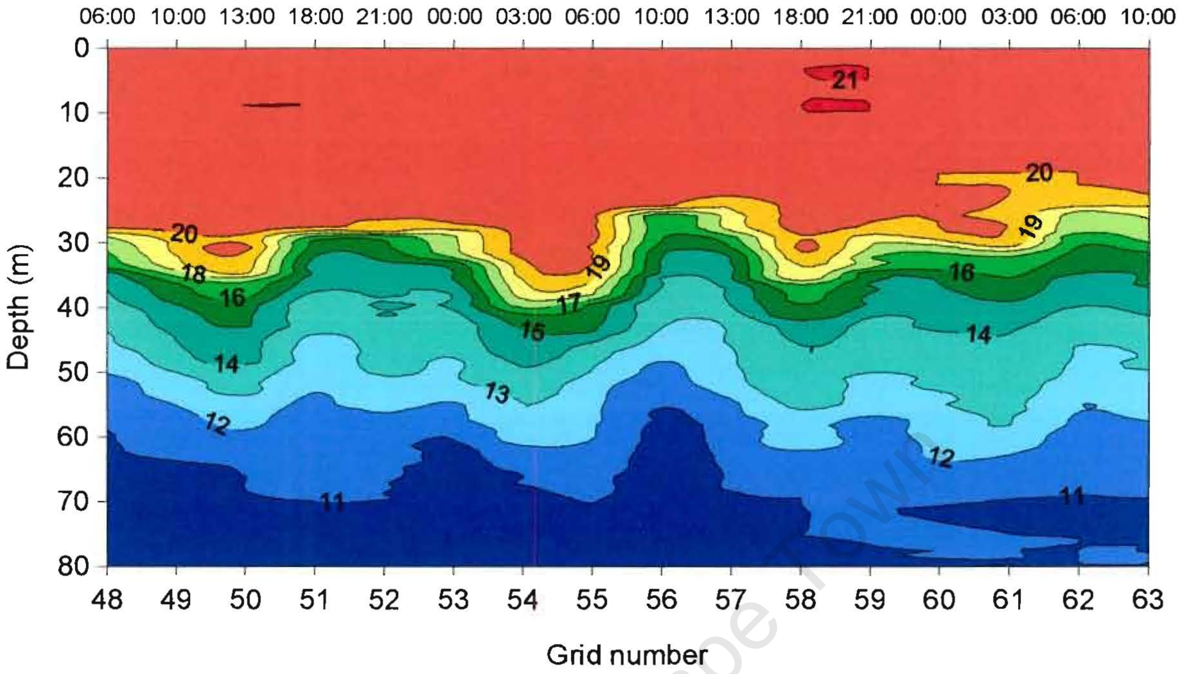


Figure 6.3. Vertical distribution of (a) temperature (°C) and (b) chlorophyll *a* (mg m^{-3}) within the upper 100 m over a 48-hr period at Station 2. Sampling time is shown at the top of the graphs, and the sequential grid reference number at the bottom.

Station 3 (80 m)

(a) Temperature (°C)



(b) Chlorophyll *a* (mg m^{-3})

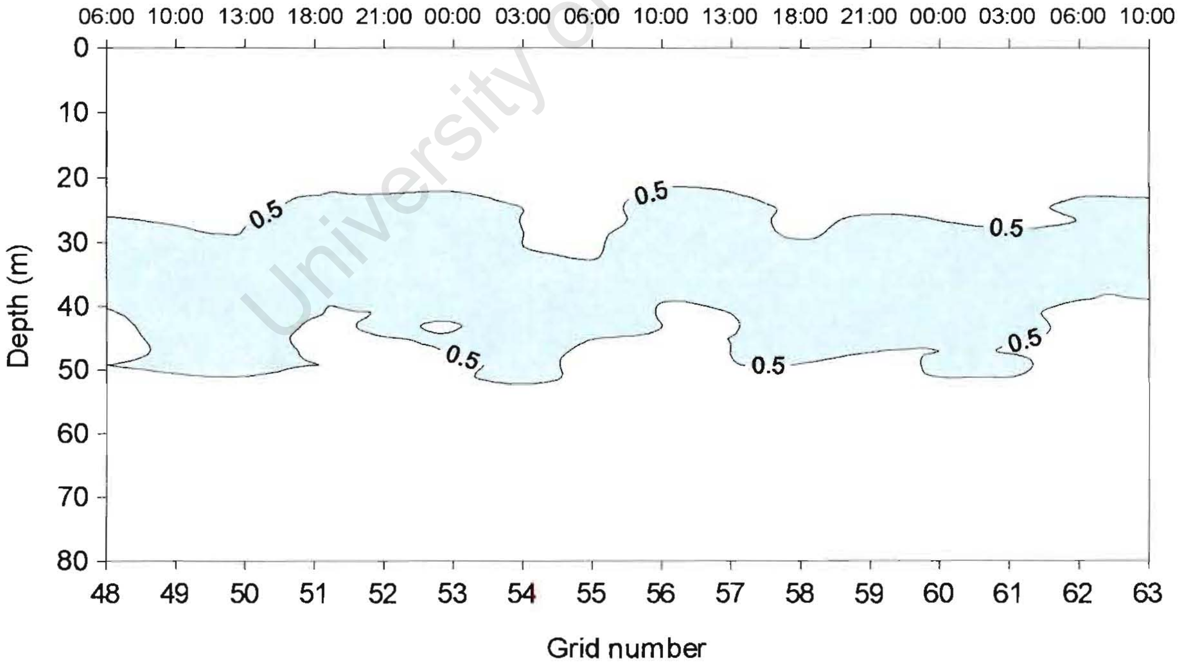


Figure 6.4. Vertical distribution of (a) temperature (°C) and (b) chlorophyll *a* (mg m^{-3}) within the upper 80 m over a 48-hr period at Station 3. Sampling time is shown at the top of the graphs, and the sequential grid reference number at the bottom.

at this station were of variable speed and direction due to the inertial oscillation, but generally slow (10.8 ± 1.0 cm s^{-1}) and to the north-north-west.

Particle-size spectra from the depth of maximum fluorescence (f-max) at midnight indicated a prominent peak (3.5 ppm) of large cells (~20 μm diameter) on Day 1 at Station 1, and a smaller peak (~1 ppm) of cells ~40 μm in diameter (Fig. 6.5a). By Day 2, the 20 μm peak had diminished substantially to <1 ppm, coincident with the lower concentration of Chl *a* above the thermocline compared to Day 1 (Fig. 6.2). Station 2 was characterised by a small peak of 20 μm cells on Day 1 (~1 ppm; Fig. 6.5b), when Chl *a* concentration was relatively low (<2 mg m^{-3}, Fig. 6.3), but a much greater peak of these cells was apparent on Day 2 (3.5 ppm) when Chl *a* concentration above the thermocline was high (3.0-4.5 mg m^{-3}). Station 3 was characterized by extremely low particle volumes, with no clear size peaks (Fig. 6.5c).

6.3.2. Diel Vertical Migration

Abundance of each stage (No. m^{-3}) collected in each depth stratum by the RMT nets is shown in Appendix 2. *C. agulhensis* was generally more abundant than *C. carinatus*, particularly at Station 3. Both species were most abundant at Station 1, in the vicinity of the cool upwelling ridge. Abundances at Stations 1 and 2 were generally much lower during mid-morning compared to the previous night.

C. agulhensis exhibited typical DVM at Station 1 on Day 1, ascending to the near-surface, food-rich layer (~5 ppm at the f-max; Fig. 6.6c) after sunset, where the copepods remained throughout the night, and then descending before sunrise (Fig. 6.6a). By late morning (10h00), all stages except for the C1s and late-stage nauplii had returned to deeper water. Ontogenetic layering was evident during the day, with older stages occurring progressively deeper. On Day 2, which was characterized by diminished food levels in terms of particle volume in the food-rich layer (~2 ppm), the dawn descent appeared to be retarded compared to the previous day. No copepod samples were collected at dawn (06h00) due to a malfunction of the RMT, but by 10h00 the youngest copepodites (C1-C3) were still concentrated within the near-surface layer, and the WMDs of the older copepodite stages were shallower compared to 10h00 the previous morning (Day 1).

Although the vertical distribution of the copepodites was predominantly unimodal, stages C2 to female were bimodally distributed just before sunrise on Day 1 (06h00; Appendix 2), with generally greater abundance in the upper water column (0-20 m) and a secondary node of abundance near the bottom (80-100 m). The vertical distribution at 10h00 was somewhat uncertain due to malfunctioning of two of

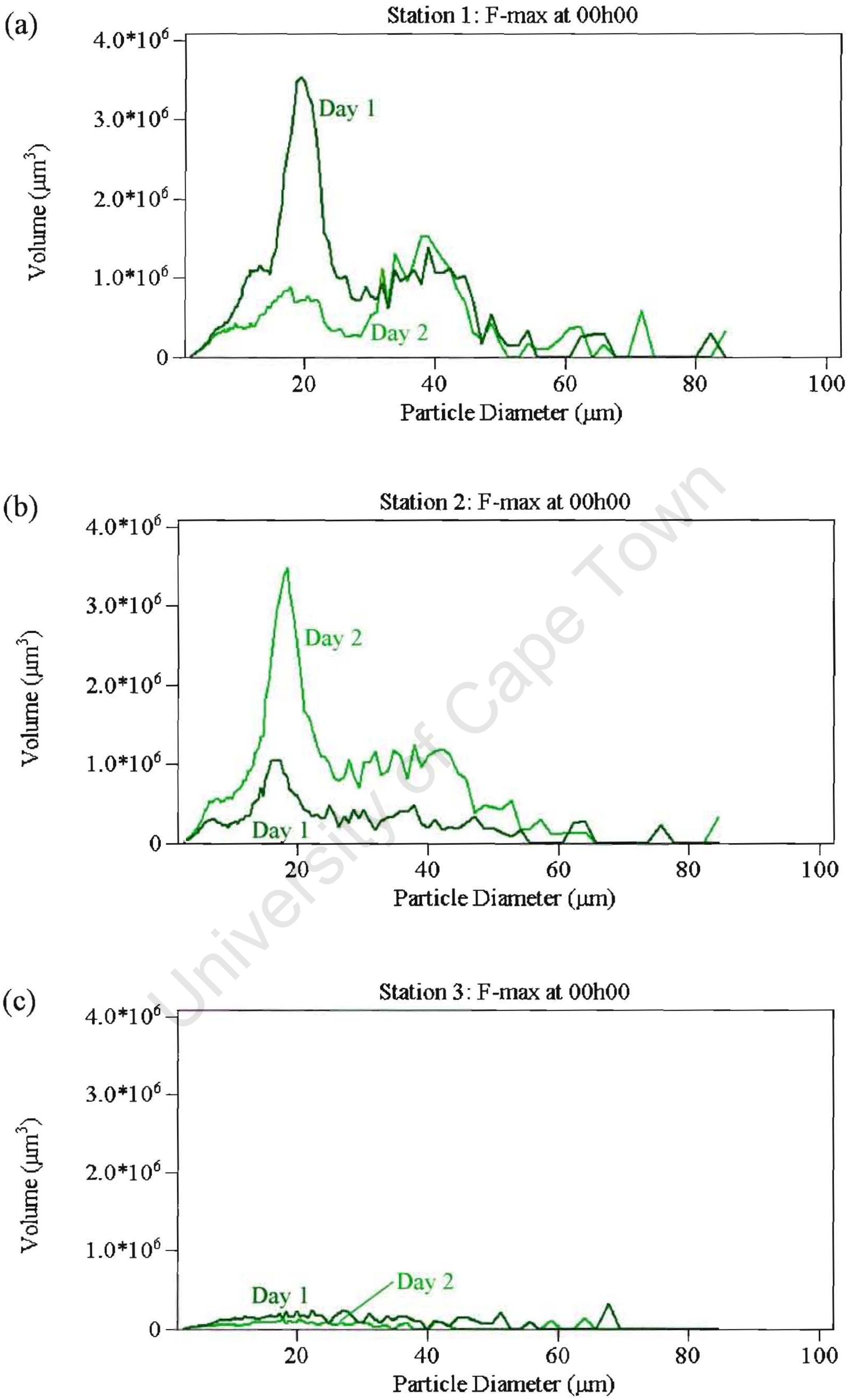


Figure 6.5. Particle volume spectra ($\mu m^3 \times 10^6\ ml^{-1}$ = ppm) at midnight at the depth of maximum fluorescence on each day of sampling at (a) Station 1, (b) Station 2 and (c) Station 3.

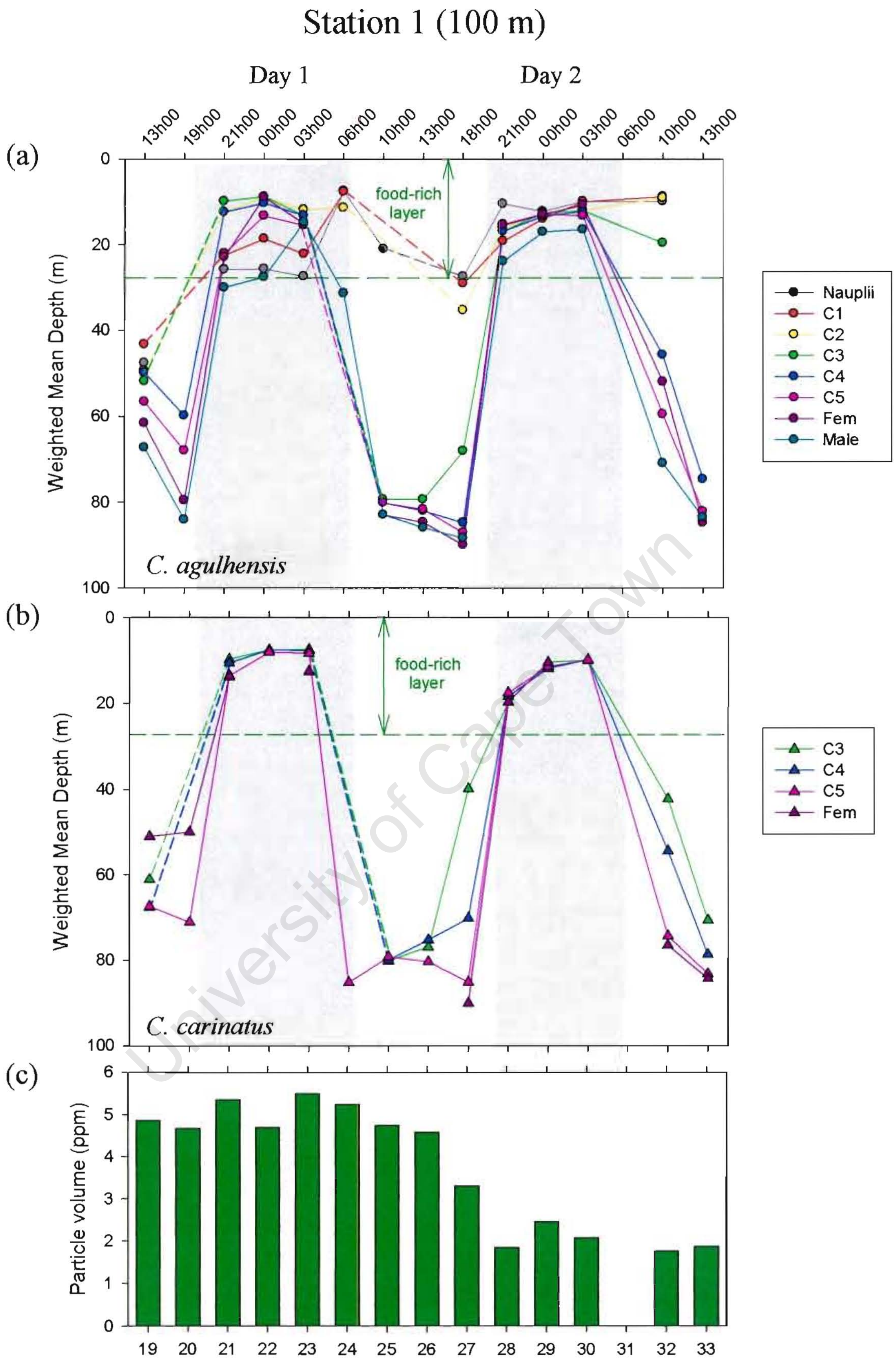


Figure 6.6. Station 1: weighted mean depths (m) of different stages of (a) *C. agulhensis* and (b) *C. carinatus*, and (c) particle volume (ppm) in the food-rich layer, representing phytoplankton biomass. Sampling time is shown at the top of the figure, and the sequential grid reference number below. Dotted lines indicate bimodal distribution. Shaded area represents period of darkness, from sunset to sunrise.

the nets, but clearly indicated greater abundance in the deepest stratum (80-100 m) compared to the upper layers (0-40 m). Just after midday (13h00) following the first night of sampling there was a greater abundance of nauplii and C1s in the 20-40 m depth stratum compared to the deepest stratum (80-100 m), and relatively high abundance of C2s between 20 and 60 m as well as from 80 to 100 m. This bimodal distribution was also observed at 13h00 after the second night of sampling, but not at the very beginning of Station 1, when all stages were evenly distributed over several depth strata (Appendix 2).

Abundance of *C. carinatus* copepodites was variable and often much lower than those of *C. agulhensis* at Station 1, particularly for the younger stages (C1-C2) and adults. However, the older copepodites (C3-C5) displayed similar DVM patterns to those of *C. agulhensis*, including a delayed descent after the second day of sampling (Fig. 6.6b). The descent of *C. carinatus* at 06h00, just before sunrise on Day 1, appeared to be ontogenetically staggered (Appendix 2), with most C3s in the upper depth stratum (0-20m), the C4s bimodally distributed between the surface (0-20 m) and the deeper layers (60-100 m), and the C5s predominantly in the bottom depth stratum (80-100 m).

At Station 2 the near-surface presence of all *C. agulhensis* copepodite stages prior to sunset (18h00) on Day 1 suggested either an early ascent or lack of descent the previous day (Fig. 6.7a). This near-surface concentration coincided with low food abundance of ~1 ppm at the f-max in the food-rich layer (Fig. 6.7c). At 06h00 the older stages (C4-female) had begun to descend, but were still relatively shallow compared to the same time at Station 1, and the younger stages (C1-C4) were still concentrated near the surface. This pattern had not changed significantly by 10h00, although most stages (except for the females) had moved slightly deeper in the water column; the females had shifted to a slightly shallower depth. As food levels increased during the day, from ~2 to 5 ppm at the f-max, the copepods resumed their downward migration, although the younger stages (C1-C3) remained within the upper food-rich layer. By 18h00 only the C5s and females were concentrated in deeper water (~100 m), but all stages returned to the upper food-rich layer by 21h00. This indicated an ascent of ~80 m within 3 hours for the C5s and females, and ~30 m for the C4s and males. Shortly before sunrise (06h00) on Day 2, all stages appeared to have begun their downward migration, and by 10h00 the older stages (C5 and adults) were concentrated below 80 m whereas the WMD of the younger copepodites (C1-C4) ranged from 40 to 50 m. Daytime ontogenetic layering was again evident, with a greater WMD with increasing age. There was no indication of bimodal distribution at Station 2; all stages displayed a unimodal depth preference or were relatively evenly distributed through the water column (Appendix 2).

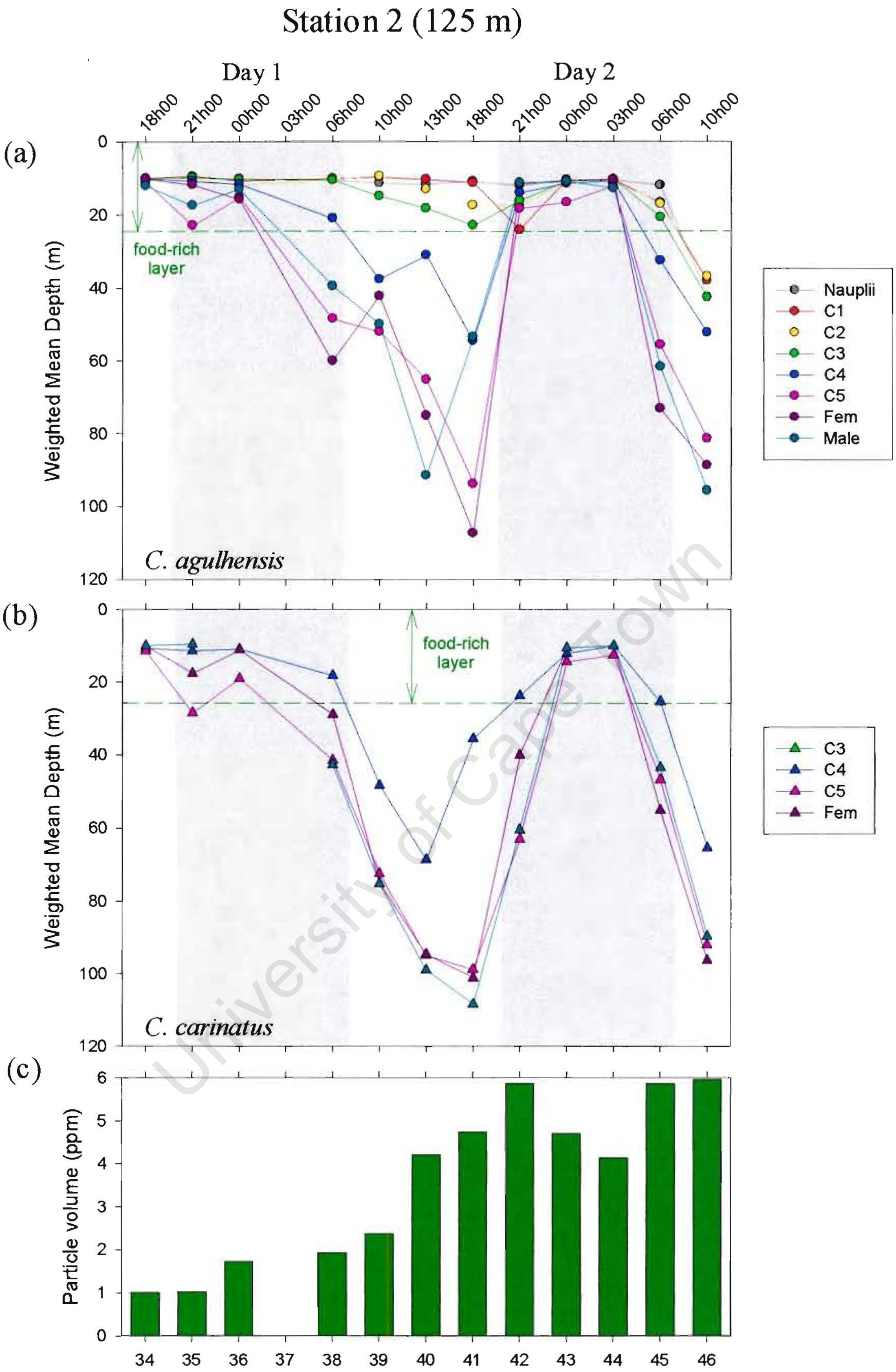


Figure 6.7. Station 2: weighted mean depths (m) of different stages of (a) *C. agulhensis* and (b) *C. carinatus*, and (c) particle volume (ppm) in the food-rich layer, representing phytoplankton biomass. Sampling time is shown at the top of the figure, and the sequential grid reference number below. Shaded area represents period of darkness, from sunset to sunrise.

Abundance of younger *C. carinatus* copepodites (C1-C3) at Station 2 was generally low, as was observed at Station 1, but the older copepodites displayed similar DVM to *C. agulhensis,* and were also concentrated near the surface at the beginning of sampling when food concentration was relatively low (Fig. 6.7b). However, the older *C. carinatus* copepodites (C4-adult) descended to deeper water earlier than those of *C. agulhensis* once food abundance began to increase, although their ascent the following evening appeared to be slower; by 21h00 only the C4s had returned to the upper food-rich layer.

At Station 3 the thermocline, which was characterized by very low food levels (<0.5 ppm; Fig. 6.8c), formed the upper limit of both species' nocturnal distribution (Fig. 6.8a,b), except for *C. carinatus* females which appeared to "overshoot" this layer slightly at 22h00 and dropped back to the food-rich layer by midnight. Subsequent daytime (10h00) WMDs were similar to those of the previous night.

Figure 6.9 provides a summary of the amplitude of DVM for all stages of both species where a night/day comparison was possible. Both species exhibited ontogenetic layering during the daytime, although the actual depth occupied by each stage varied according to the conditions at the time of sampling. Whereas *C. agulhensis* and *C. carinatus* showed broadly similar patterns of DVM under the same environmental conditions, there were also some differences. Although data on the youngest copepodite stages of *C. carinatus* (C1-C3) were rare, they indicated a tendency for deeper daytime descent compared to *C. agulhensis* (Figs 6.9a and b). *C. carinatus* also appeared to descend deeper than *C. agulhensis* under relatively poor food conditions (Figs 6.9b and c), particularly the females.

6.3.3. The effect of food concentration, species and stage on DVM

Results from a GLM of the amplitude of DVM in relation to *Food concentration, Species* and *Stage* during this study showed that the interaction between *Species* and *Stage* was not significant, explaining only 2% of the variance (Table 6.1). However, the amplitude of DVM was significantly related to *Food concentration, Species* and *Stage* as main effects. *Food concentration* was the most important predictor of DVM, explaining 58% of the variance, followed by *Stage* (19%) and *Species* (7%).

The mean amplitude of DVM (m) between 00h00 and 10h00 the following morning was significantly greater for *C. carinatus* compared to *C. agulhensis* (Fig. 6.10a), and also increased with age (Fig. 6.10b) for both species, although the mean amplitude of DVM by males was similar to that by C5s. Although the interaction between *Species* and *Stage* was not significant, a plot of this interaction (Fig. 6.10c) provides a useful summary of stage- and species-specific DVM at a mean food concentration of ~3 ppm.

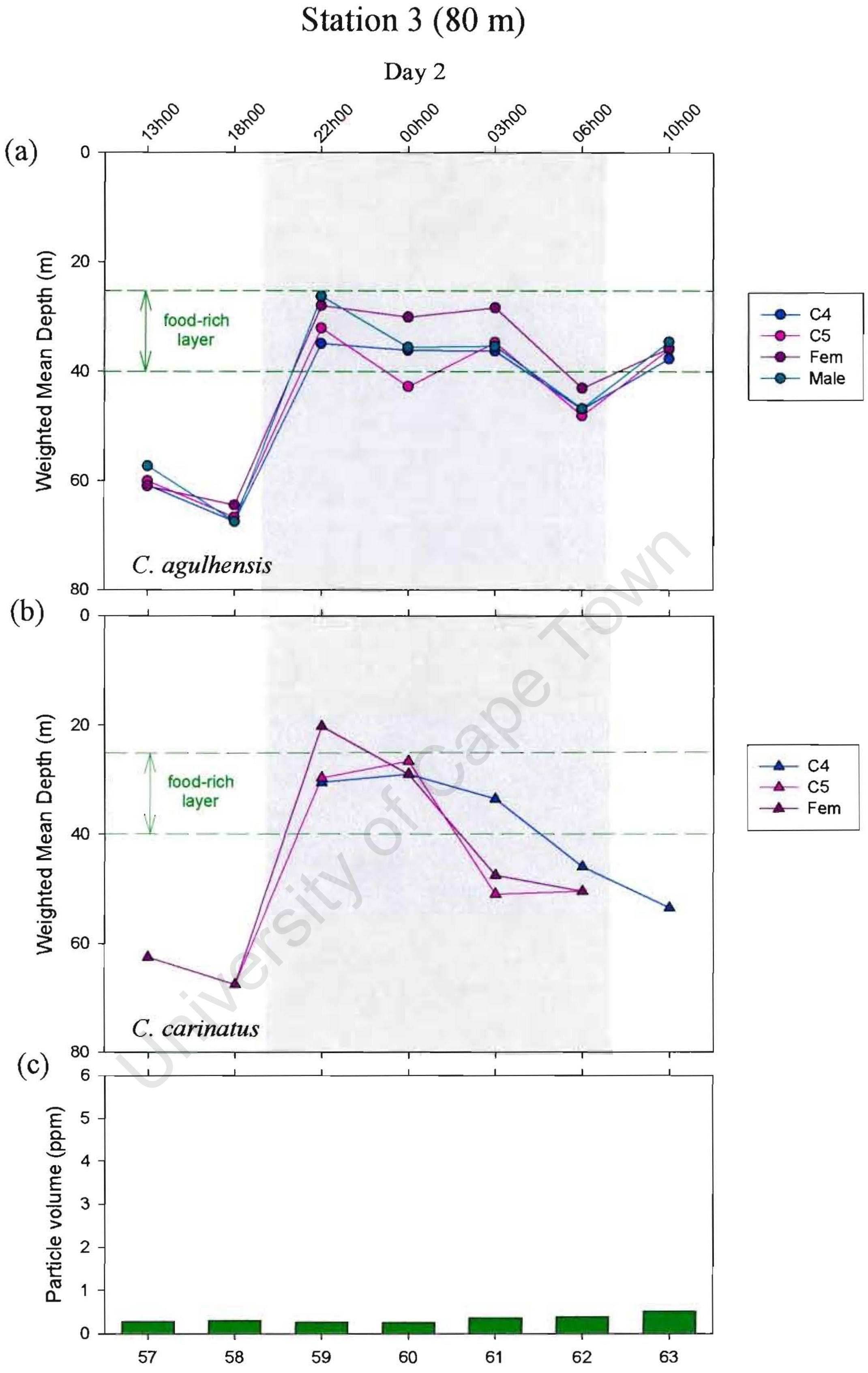


Figure 6.8. Station 3: weighted mean depths (m) of different stages of (a) *C. agulhensis* and (b) *C. carinatus*, and (c) particle volume (ppm) in the food-rich layer, representing phytoplankton biomass. Sampling time is shown at the top of the figure and the sequential grid reference number below. Shaded area represents period of darkness, from sunset to sunrise.

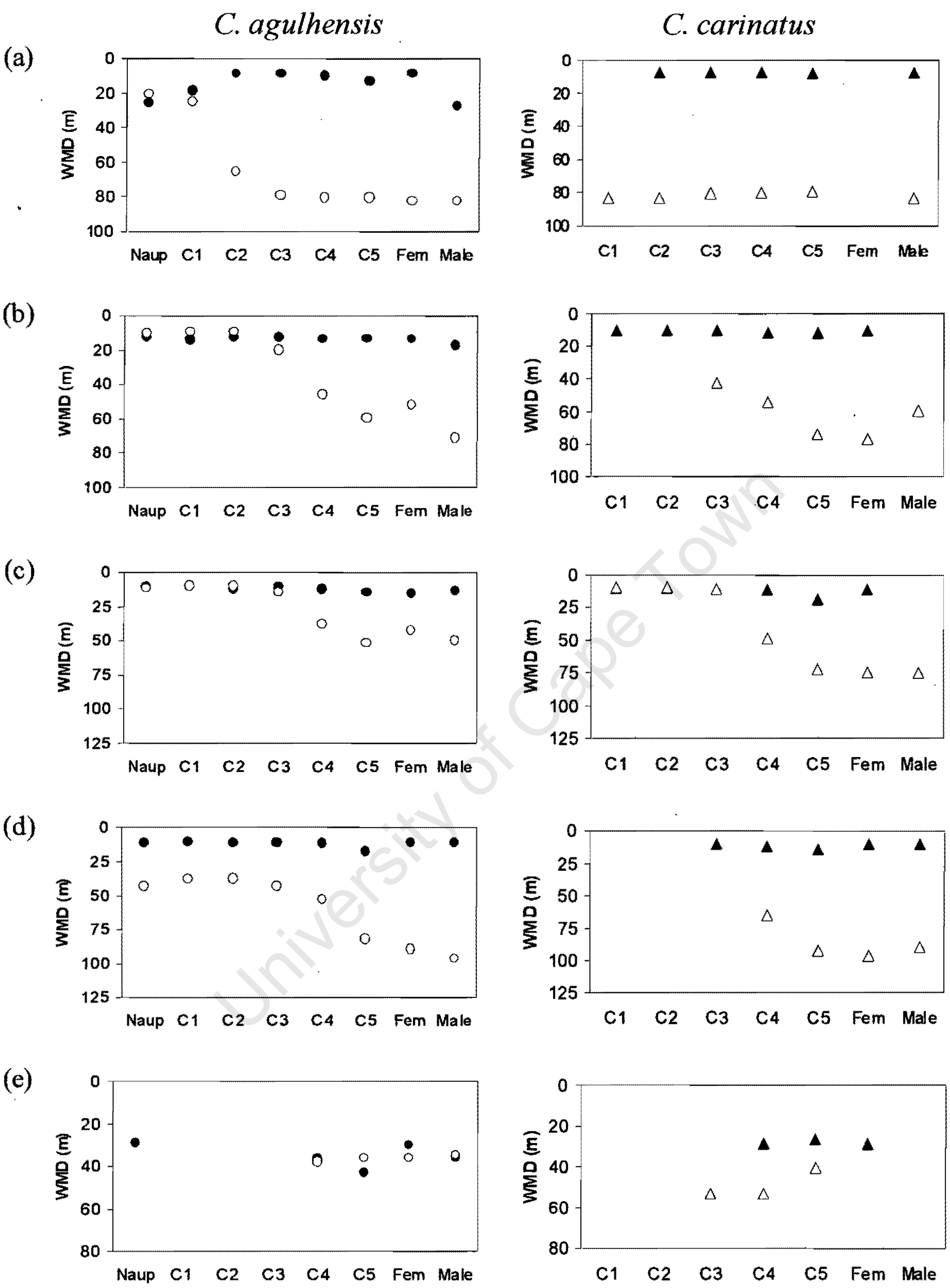


Figure 6.9. Midnight (00h00, black symbols) and late morning (10h00, white symbols) WMDs of late nauplius and copepodite stages of *C. agulhensis* and *C. carinatus* at (a) Station 1, Day 1; (b) Station 1, Day 2; (c) Station 2, Day 1; (d) Station 2, Day 2; and (e) Station 3, Day 2.

Table 6.1. Results of a general linear model used to test the effect of mean night-time food concentration at the f-max (ppm), species (*C. carinatus* or *C. agulhensis*) and stage (C2 and older) on diel vertical migration (m). Significant effects ($p < 0.05$) are indicated in bold.

Effect	% variance explained	*SS*	*df*	*MS*	*F*	*p*
Intercept	1.13	385.64	1	385.64	2.53	0.1211
Food conc.	57.69	19775.40	1	19775.40	129.82	**0.0000**
Species	6.51	2232.89	1	2232.89	14.66	**0.0005**
Stage	18.76	6430.69	5	1286.14	8.44	**0.0000**
Species × Stage	1.24	425.21	5	85.04	0.56	0.7310
Error	14.67	5026.78	33	152.33		

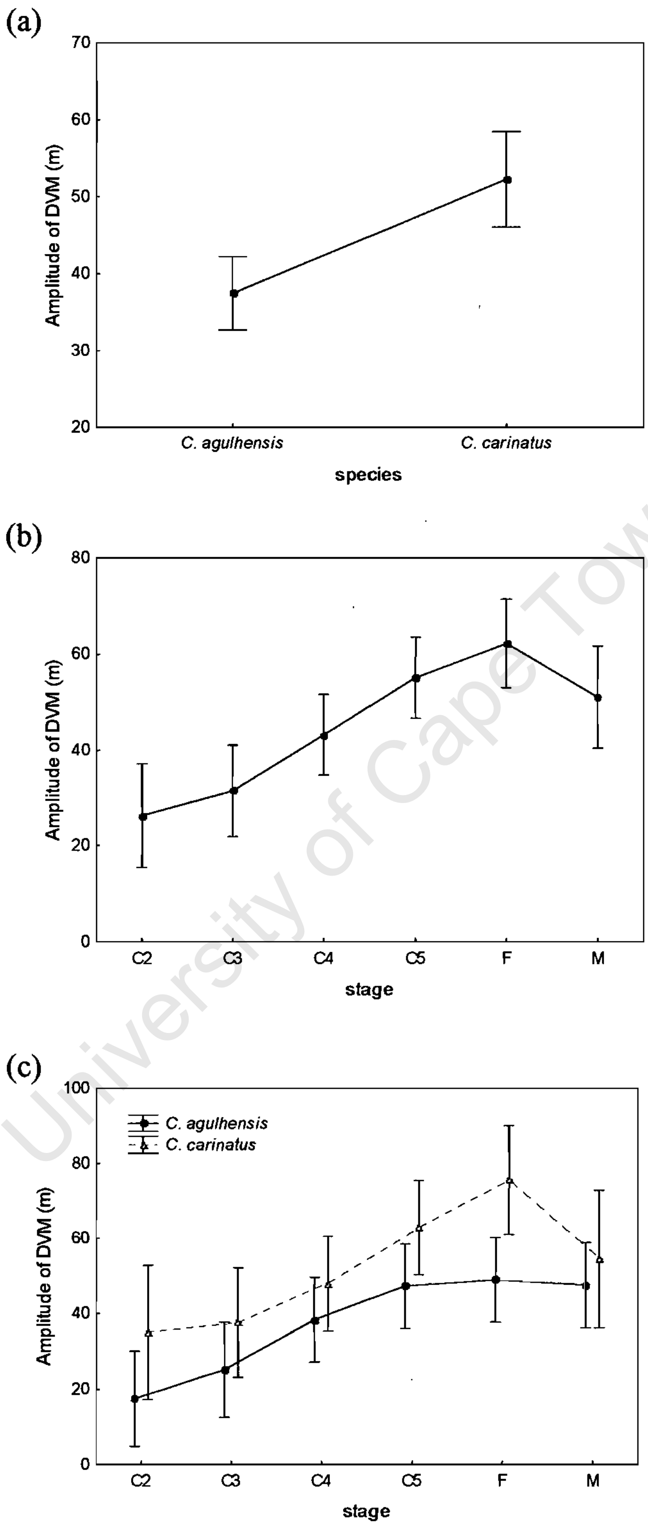


Figure 6.10. Results of GLM showing mean DVM amplitude (± 95% CI, m) of copepodite stages C2 and older of *C. carinatus* and *C. agulhensis* in relation to (a) species, (b) stage and (c) the interaction between species and stage. The covariate mean food concentration was 3.18 ppm.

The amplitude of DVM of the larger stages (C4s, C5s and females) of both species was significantly positively correlated with food concentration ($p < 0.001$; Fig. 6.11). No attempt was made to correlate DVM of the smaller stages with food concentration, owing to (1) low abundance or absence of some of these stages at Stations 2 and 3, and (2) bimodal distributions at Station 1 (Appendix 2).

6.4. DISCUSSION

At night during the present study, all sampled stages of both *C. agulhensis* and *C. carinatus* were concentrated in the region of greatest abundance of Chl *a*, which varied from a near-surface layer of ~25 m at Stations 1 and 2 to a subsurface layer ~15 m deep (from 25 to 40 m) at Station 3. Similarly, Bohrer (1980) found that the night distributions of late stages of *Pseudocalanus minutus* and *Calanus finmarchicus* were determined by the location of phytoplankton food in the water column – at night the copepods "sought out" that region of the water column where phytoplankton food was most concentrated. Huntley and Brooks (1982) observed that all feeding stages of *C. pacificus* were concentrated in the relatively phytoplankton-rich surface waters at night.

During the day, however, the different copepodite stages descended to depths that varied according to developmental stage, food availability and the time of day. Under conditions of abundant food on the Agulhas Bank, both *C. agulhensis* and *C. carinatus* displayed strong DVM, ascending to the food-rich layer around sunset, and descending before sunrise (between 03h00 and 06h00). By 10h00 the whole population, except for the smallest copepodite stages (nauplii and C1s), had returned to deeper water. The amplitude of migration was related to body size (Fig. 6.10b), with females migrating deepest. Ontogenetic layering has been observed for many other *Calanus* species, including *C. finmarchicus* (Tande 1988; Unstad and Tande 1991; Dale and Kaartvedt 1999), *C. glacialis* (Hansen *et al.* 1990; Unstad and Tande 1991), *C. helgolandicus* (Williams and Conway 1980), *C. pacificus* (Huntley and Brooks 1982; Osgood and Frost 1994) and *C. sinicus* (Uye *et al.* 1990; Huang *et al.* 1992), as well as for *C. carinatus* in the southern Benguela upwelling system (Verheye *et al.* 1991; Verheye and Field 1992) and off Ivory Coast (Binet and Suisse de Sainte Claire 1975; Binet 1977). This is thought to be a consequence of stage-specific feeding behaviour and swimming ability, as well as size-related susceptibility to predation, and may be important in reducing competition between different life-cycle stages (Tande 1988). A dynamic optimization model of vertical migration indicated that older stages should descend deeper than younger stages, and furthermore leave the night-time habitat earlier and ascend back later in the day (Fiksen and Giske 1995). Ontogenetic layering is also recognized as a

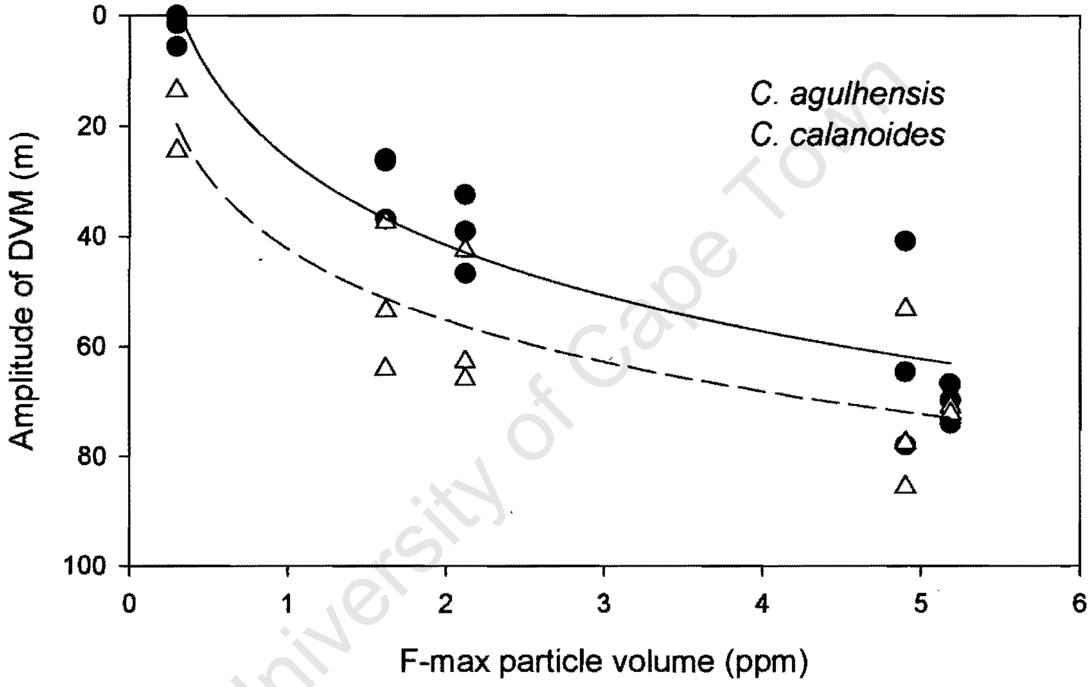


Figure 6.11. Semi-logarithmic regressions between amplitude of DVM (m) and mean night-time particle volume (ppm) at the fluorescence maximum for the larger copepodite stages (C4, C5 and female) of *C. carinatus* and *C. agulhensis*. The fitted curves are: $y = 18.70 \text{ Ln } (x) + 42.28$, $r^2 = 0.75$, $n = 13$, $p < 0.001$, and $y = 22.65 \text{ Ln } (x) + 25.84$, $r^2 = 0.86$, $n = 15$, $p < 0.001$, respectively.

mechanism for population retention in regions subject to strong advection such as upwelling areas (Wroblewski 1982; Verheye *et al.* 1991; Peterson 1998).

When food became less abundant, the copepods extended the time spent in the upper water column. They either remained in the food-rich layer for longer, or descended more slowly, so that by 10h00 the population had not yet completed its descent. Furthermore, the near-surface distribution of the population at 18h00 on Day 1 at Station 2, when food concentration was relatively low, suggests that the copepods may ascend early or even remain near the surface during daylight if low food abundance persists. Variable DVM in relation to food concentration has also been observed for *C. carinatus* off the West Coast. Both juveniles and adults migrated extensively when Chl *a* near the surface was plentiful, but displayed suppressed DVM when Chl *a* near the surface was low (Verheye and Field 1992). Similar behaviour was noted for *C. pacificus* during a mesocosm study (Huntley and Brooks 1982). *C. pacificus* copepodites performed high-amplitude migrations when phytoplankton was abundant, but as food availability declined, migration amplitudes decreased and eventually ceased, such that copepodites remained in the relatively food-rich surface waters at all times.

The significant relationship between food concentration at the f-max at night and the amplitude of DVM (Table 6.1; Fig. 6.11) suggests that the vertical migratory behaviour of both *C. agulhensis* and *C. carinatus* is strongly linked to food abundance, with the copepods possibly attempting to obtain a minimum food ration before descending to deeper water. The reward of this minimum ration, presumably to maximise growth in juveniles and egg production in females, seems therefore to outweigh the concomitant higher risk of predation near the surface. What is perceived by the copepods as a minimum ration is uncertain; there may be a minimum required threshold of food concentration before organisms react to predation pressure, and this threshold may vary for different species (Han and Straškraba 1998). Mackas and Bohrer (1976) and Atkinson *et al.* (1992a) found evidence that the downward movement of herbivorous copepods is triggered by satiation. Huntley and Brooks (1982) also suggested that, when food availability is low, *C. pacificus* remains in the relatively food-rich layer to feed until satiated. They further proposed that circadian periodicity only operates under conditions of high food availability, when the copepods are able to satisfy their nutritional requirements by nocturnal migration alone.

The greater amplitude of DVM of *C. carinatus* compared to *C. agulhensis* (Figs 6.10a, 6.11) under the same food conditions could be a consequence of (1) different nutritional requirements or feeding behaviour, (2) differential swimming ability, or (3) differential predation risk. If descent is indeed triggered by satiation, this suggests that *C. carinatus* may feed more efficiently at low food concentrations compared to *C. agulhensis*, particularly since there appeared to be a greater difference in DVM between the two species at the lowest food concentrations (Fig. 6.11). The limited data available on comparative feeding of C5s and females during this study (Chapter 5) indicated no significant difference in gut pigment content between the two species at night, thus there is at present no evidence to support the hypothesis of differential feeding efficiency. Differential swimming ability may well be a contributing factor, since older stages of *C. carinatus* ascended more rapidly than those of *C. agulhensis* (Appendix 2). Furthermore, personal observation has shown *C. carinatus* to be more difficult to capture with a handheld pipette than *C. agulhensis*, indicating a faster escape response. Differential visual predation risk has not been tested for these species. DVM tends to be most pronounced in larger and/or more highly pigmented species, i.e. those that are more visible and hence susceptible to visual predation (Hays *et al.* 1994; Hays 1995). Stage-specific body length and width are slightly greater for *C. agulhensis* compared to *C. carinatus* (see Table 1.2 in Chapter 1), whereas *C. carinatus* often tends to be more brightly pigmented compared to *C. agulhensis* (pers. obs.), partly due to its greater lipid content (Borchers and Hutchings 1986; W. Hagen and H. Verheye, unpublished data), although this diminishes with poor feeding conditions. With the limited information available, differential swimming ability thus appears to be a likely cause of the differential response to food concentration, but differential predation risk cannot be ruled out.

The relationship between DVM of the younger stages (N/C1-C3) of both species and food availability is uncertain, mainly due to fewer data being available. Furthermore, the vertical distribution of the younger stages was often bimodal, particularly at Station 1. Bimodal distributions may be a sampling artefact of asynchronous migration combined with a long stationary time relative to transit time (time spent changing depths; Pearre 1979), but this is more likely to occur for older, faster swimming stages than younger, slower animals. It could also be a result of different cohorts originating from eggs laid at different depths or in different water masses. Whatever the cause, younger stages are less likely to be food-limited under poor food conditions than older stages, as advocated by Richardson and Verheye (1999), Weber and Roff (1995) and Hirst and Sheader (1997). Rey and Hansen (2000) found nearly maximal growth rates of *C. finmarchicus* nauplii at relatively low food levels (~50 g C l^{-1}), suggesting that nauplii exhibit far less dependence on food supply than copepodite stages do.

In non-advective environments, DVM by predominantly herbivorous marine copepods seems to be largely a trade-off between feeding and avoiding being eaten. DVM is arguably a direct consequence of eating, since non-feeding *Calanus* nauplii do not migrate vertically, whereas first-feeding nauplii do (Huntley and Brooks 1982; Huang *et al.* 1992; Durbin *et al.* 2000). Feeding creates an associated risk of predation by increasing the visibility of a relatively transparent individual due to the accumulation of pigmented stomach contents (Stearns 1986; Dagg *et al.* 1989; Bollens and Stearns 1992). In shallower water there is a greater abundance of food, but also a greater chance of being spotted by visual predators, hence the need to find a trade-off between the survival/growth/egg production benefit of food and the mortality risk due to predation. The level of predation risk an organism "accepts" varies according to its genetic make-up, its life-cycle stage and its nutritional state (Angel 1985). Whereas some studies conclude that nutritional state, or hunger, has a greater influence than predation on DVM (Huntley and Brooks 1982), others advocate predation as the more important factor (Frost 1988; Bollens and Frost 1989a, b).

The present study was conducted under conditions of moderate to weak currents. This contrasts with studies on DVM of *C. carinatus* in the West Coast upwelling region (Verheye *et al.* 1991; Verheye and Field 1992), where strong advection resulted in significant changes in abundance of animals over the time-series as well as rapid changes in the food environment. Changes in DVM in the present study should therefore be mainly attributable to fluctuations in food availability or predation risk. Potential vertebrate predators include anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and roundherring *Etrumeus whiteheadi* (James 1987; James and Findlay 1989; van der Lingen 1994; Wallace-Fincham 1987). Most information on the distribution of pelagic fish on the Agulhas Bank is obtained from surveys conducted during November, during peak spawning by anchovy, thus the abundance and distribution of these fish during March is uncertain. During November, abundance of these fish is generally low on the central Agulhas Bank (Barange *et al.* 1999), but dense concentrations are found on the outer edge of the cool ridge, and appear to shift shorewards as warm water from the Agulhas Current moves onshore as summer progresses (Hutchings 1994). Other potential predators are Cape horse mackerel *Trachurus trachurus capensis*, which are widespread over much of the Agulhas Bank (Badenhorst and Smale 1991; Kerstan and Leslie 1994). Stomach content analyses indicate extensive predation by these fish on large *C. agulhensis* (pers. obs.) amongst other planktonic crustaceans. The impact of invertebrate predation on zooplankton in the Agulhas Bank is considered to be low compared to the West Coast (Hutchings *et al.* 1991; Verheye *et al.* 1994).

The reverse DVM of *C. carinatus* copepodites (C1-C5) observed by Peterson *et al.* (1990b) at an offshore site off the West Coast, in contrast to normal DVM by late-stage *C. agulhensis* (C4-female) is intriguing, although copepod DVM in their study was inferred from comparative day/night abundances in just the upper 20 m. Peterson *et al.* (1990b) did not propose an explanation for the observed differences in migratory patterns, but reverse DVM is frequently considered to be a response to invertebrate predators (Ohman *et al.* 1983; Ohman 1990; Frost and Bollens 1992; Neill 1992). It is possible that reverse DVM of *C. carinatus* could have been prompted by the high abundance of the euphausiid *Euphausia lucens* at this site, which exhibited a high degree of carnivory even during the day (78.5%, and 100% by 19h30; Gibbons *et al*. 1991) and contained large numbers of copepod mandibles in their stomachs. Although the evidence for reverse DVM in this study is an isolated example, and may be debated, the possibility exists that *C. carinatus,* evidently a faster migrator than *C. agulhensis,* may also be capable of more plastic behaviour than *C. agulhensis* in conditions of high risk of invertebrate predation, and this poses a potentially fruitful area for future investigations.

6.5. CONCLUSIONS

Ontogenetic migration by *C. carinatus* and *C. agulhensis* was demonstrated by an increase in amplitude of DVM with age. Both species appear to adapt their vertical migratory behaviour in response to changing food conditions, and displayed a significant positive relationship between DVM and food concentration. The lower the food availability, the more time the copepods spent in the region of greatest food concentration, either delaying their descent or ascending prematurely to maximize their food intake. The benefit of a minimum (possibly satiation-linked) food ration, presumably to maximize growth and egg production, may thus outweigh the higher risk of predation near the surface for both species. *C. carinatus* displayed a significantly greater amplitude of DVM compared to *C. agulhensis* under the same food conditions, which may be related to its faster swimming ability, but differential predation risk based on visibility (in terms of pigmentation and lipid content) cannot be excluded.

CHAPTER 7- Synthesis

C. carinatus is a characteristic species of many tropical and temperate upwelling systems, colonizing recently upwelled water at copepodite stage 5 (C5), and reproducing rapidly after moulting to adult. Data collected during 28 cruises off the South African coast between 1988 and 2000 indicate that *C. carinatus* is abundant during both spring/summer and autumn/winter in the highly productive southern Benguela system, with greatest abundance on the central West Coast, downstream from the Cape Columbine upwelling cell. It is also found on the Agulhas Bank, mainly on the outer shelf of the central and eastern bank between the 100- and 200-m depth contours, but at relatively low abundance compared to the West Coast. Its presence on the Agulhas Bank is most likely the result of transport from upwelling centres on the East Coast, along the narrow shelf inshore of the core Agulhas Current as it flows south-west wards along the shelf edge towards the Agulhas Bank, where shelf-edge upwelling and local retention through ontogenetically-based diel vertical migration enhance moderate levels of abundance.

C. agulhensis has a centre of abundance closely associated with the cool ridge of upwelled water (the Agulhas Ridge) on the central Agulhas Bank, which is characterized by enhanced primary production and a quasi-permanent retention mechanism. Dispersion of copepodite stages from this centre allows *C. agulhensis* to dominate over the whole Agulhas Bank, although its centre of abundance is displaced westwards when the Agulhas Ridge is absent. Dispersion to the west and north, combined with convergent northwest flow on the WAB, results in considerable advection of this species by the shelf-edge jet current to the West Coast during spring and summer.

Despite the fact that the biannual surveys can best be regarded as "snapshots" in time, with little or no prior knowledge of environmental history, data collected from these surveys indicate a considerable level of population stability of both species in their core areas, but greater variability in non-core areas. High interannual variability in abundance of *C. carinatus* during summer probably reflects the inherent variability of the dynamic Benguela upwelling system, in contrast to more consistent productivity and greater population stability of *C. agulhensis* on the Agulhas Bank.

There is considerable spatial overlap in the distribution of the two copepod species, yet the separation of their core areas suggests that there are fundamental differences between the two species that make them better suited to their respective areas of dominance, and allow them to maintain life-cycle closure there. Physical and environmental differences between their core habitats present a number of hypotheses to be tested in order to explain the differences in distribution and abundance of the two species. The principal hypotheses are that *C. carinatus* and *C. agulhensis* have different thermal preferences or tolerances, have different dietary requirements in terms of food abundance, size and/or type, are adapted to different scales of temporal variability of food availability, and have different vertical migratory behaviour and/or population retention mechanisms.

H1: *C. carinatus* egg production is inhibited by warm temperatures typical of the Agulhas Bank; conversely, *C. agulhensis* egg production is reduced at cooler temperatures characteristic of the Benguela upwelling region

Laboratory experiments showed that food-satiated rates of egg production were similar for both species across a broad temperature range (9-18°C), increasing linearly with temperature, but that *C. carinatus* had significantly faster rates of egg production than *C. agulhensis* at the warmest temperature investigated (21°C). The hypothesis that *C. carinatus* egg production is inhibited by warm temperatures typical of the Agulhas Bank, and conversely that *C. agulhensis* egg production is reduced at cooler temperatures characteristic of the Benguela upwelling region, is therefore rejected. Furthermore, the faster egg production by *C. carinatus* at 21°C is likely to be mitigated by significantly greater natural mortality of females at this temperature, which may result in a lower net production compared to *C. agulhensis*.

Generalized additive models indicated that temperature had a significant effect on egg production by both species in the field, but that the effects of food concentration and food size were considerably more important. As a result, the roughly dome-shaped relationship observed between egg production and temperature in the field, which appears to be a consequence of low phytoplankton abundance at extreme temperatures, was largely obscured when food abundance and food size were accounted for. An additional source of temperature-related variance in field experiments may be the considerable thermal variability experienced by migrating copepods during their diel cycle, resulting in a varied thermal history.

H2: *C. agulhensis* can attain satiation (and maximum rates of egg production) at a lower food concentration than *C. carinatus*.

Ingestion rates of *C. carinatus* and *C. agulhensis* showed considerable variability in relation to food concentration in the field, but both species displayed a similar functional response to food concentration in terms of ingestion rate, with maximum ingestion rates observed at Chl *a* concentrations of ~15 mg m^{-3} and 7-8 ppm. Mean daily ingestion rates of bulk phytoplankton by females and late stage copepodites of the two species were not significantly different. Maximum rates of egg production by both species were achieved at food concentrations of approximately 10-15 mg Chl *a* m^{-3} and 3-4 ppm, suggesting that a particle volume of 7-8 ppm may overestimate the critical concentration. However, the hypothesis that *C. agulhensis* attains satiation at a lower food concentration than *C. carinatus* is rejected.

In situ egg production by both species was significantly greater on the West Coast compared to the South Coast, which is consistent with significantly greater mean concentrations of both Chl *a* and particle volume at the depth of maximum fluorescence on the West Coast compared to the South Coast

H3: *C. carinatus* feeds less efficiently than *C. agulhensis* on small cells typical of low food concentrations associated with the Agulhas Bank.

Generalized additive models indicate that particle size may be of greater importance to *C. carinatus* than *C. agulhensis* in terms of egg production, yet both species displayed similar feeding behaviour in terms of particle size selection, and generally appeared to prefer the larger particles that dominated the food biomass, whether small- (~8 μm ESD), large- (~45 μm ESD) or bimodal (~12 and 25 μm ESD) size-distributions of food were encountered. However, the ingestion rate by *C. carinatus* was approximately half that of *C. agulhensis* during the small particle experiment, suggesting that *C. carinatus* may feed less efficiently than *C. agulhensis* on small cells. The hypothesis that *C. carinatus* feeds less efficiently on small cells typical of the Agulhas Bank can therefore not be rejected.

The proportion of Chl *a* greater than 10 μm on the West Coast was not significantly different from that on the South Coast, although the proportion of particle volume greater than 10 μm was significantly greater on the West Coast (69.6%) compared to the South Coast (61.4%). This significant but small difference suggests that food sizes in the two areas may not be as disparate as traditionally perceived. However, differing selectivity coefficients when incubated in identical natural food assemblages suggest that the two copepods prefer different food species, presenting the possibility of resource partitioning under diverse food conditions. Although diatoms comprised the bulk of the diet of both copepods, *C. carinatus* preferentially selected small chain-forming diatom species, whereas *C. agulhensis* ingested the ciliate *M. rubrum* disproportionately to its abundance. This suggests that *C. agulhensis* may have a greater tendency towards omnivory than *C. carinatus*, and that microzooplankton may have an important role in supplementing nutritional requirements of *C. agulhensis* when phytoplankton abundance is low.

H4: *C. carinatus* is better adapted to the pulsed food environment characteristic of the southern Benguela upwelling region; conversely, *C. agulhensis* is better adapted to more consistent food availability typical of the Agulhas Bank

Laboratory experiments indicated that *C. agulhensis* recovered faster than *C. carinatus* from short (1-3 day) periods of starvation, but that *C. carinatus* recovered more rapidly than *C. agulhensis* from long (7-9 day) periods of starvation. Some *C. agulhensis* did not recover at all from 9 days without food. Rapid recovery from short periods without food by *C. agulhensis* was probably facilitated by continued egg production when food was absent, albeit at a slower rate. This may be an efficient strategy in a system where food availability is relatively constant. In contrast, *C. carinatus* terminated egg production much sooner than *C. agulhensis* when food was absent, but was able to regain maximum reproductive output faster than *C. agulhensis* following longer periods without food, most likely due to greater lipid reserves. The hypothesis that *C. carinatus* is better adapted to intermittent food availability, whereas *C. agulhensis* is better adapted to more consistent food availability, is therefore not rejected.

H5: *C. agulhensis* does not display ontogenetically-based diel vertical migratory behaviour (DVM) on the Agulhas Bank.

An investigation of vertical distribution and migratory behaviour of *C. agulhensis* and *C. carinatus* at three 48-hr stations on the Agulhas Bank revealed that both species displayed similar patterns of ontogenetically-based diel vertical migration under the same environmental conditions. The amplitude of DVM was significantly related to food concentration, with both species spending more time in the relatively food-rich upper layer when mean food abundance was low, presumably in order to obtain a minimum food ration before descending to the relative safety of deeper water. *C. carinatus* had a significantly greater amplitude of DVM compared to *C. agulhensis* under the same food conditions, which may be related to its faster swimming ability, although differential predation risk could not be excluded. The hypothesis that *C. agulhensis* does not display ontogenetic or diel vertical migration on the Agulhas Bank is rejected; the two species instead appear to have very similar vertical migratory behaviour under the same environmental conditions. The limited data available on diel feeding suggests plasticity of feeding behaviour by both species, which may be moderated in response to food availability and predation risk.

Conclusions

C. carinatus and *C. agulhensis* had similar functional responses to temperature and food concentration in terms of egg production and ingestion rate. Both species displayed similar patterns of ontogenetically-based diel vertical migration under the same environmental conditions on the Agulhas Bank, delaying their daytime descent when food abundance was relatively poor. *C. carinatus* had a significantly greater amplitude of DVM compared to *C. agulhensis* under the same food conditions, which may be related to its faster swimming ability. Although both species appeared to select the larger particles that dominate the food biomass, *C. carinatus* may feed less efficiently on small (<10 μm) food items compared to *C. agulhensis*. The two copepods may also have different preferences in terms of food species, with *C. carinatus* preferring chains of small diatoms, whereas *C. agulhensis* showed greater omnivorous tendencies, with a preference for ciliates over diatoms. Perhaps the most important difference between the two species was that *C. agulhensis* recovered faster than *C. carinatus* from short periods of starvation, whereas *C. carinatus* recovered more rapidly than *C. agulhensis* from long periods of starvation. This is probably because *C. carinatus* is able to accumulate greater lipid reserves than *C. agulhensis*, and can thus withstand longer periods without feeding. Preliminary results from lipid analyses suggest that, in contrast to *C. agulhensis*, the lipid content of which is dominated by structural phospholipids, a high proportion of the lipid content of *C. carinatus* is comprised of wax esters, which allow efficient energy storage by marine herbivorous copepods, and are particularly vital in ecosystems with a periodically limited food supply (Hagen 2000).

C. carinatus is able to opportunistically exploit localized upwelling events and the associated rapid food growth, because of its relatively high rates of egg production, rapid development, and early feeding by its nauplii. However, it is also able to withstand long periods without food, or with poor food abundance, and can recover rapidly when conditions improve. These characteristics enable it to thrive in an unpredictable and variable food environment such as that in the southern Benguela upwelling region. In contrast, *C. agulhensis* appears to be less opportunistic, and is limited by slightly slower rates of egg production, slower development rates and delayed first-feeding. Since food size appears to be less important, it may feed more efficiently on small cells, as has been shown for other *Calanus* congeners, and may depend more on omnivory to supplement its nutritional requirements. When food abundance declines it does not completely halt reproduction, but continues to produce eggs at slow rates, and is able to resume moderate rates of egg production fairly quickly when food again becomes abundant. It is thus well suited to an environment where food abundance is generally low but relatively consistent. However, it does not accumulate large energy reserves, and thus females cannot withstand long periods without food, which are more likely on the variable West Coast.

The abundance of *C. carinatus* on the shelf of the west coast upwelling region is enhanced by seeding from resting stages, local retention through ontogenetically-based vertical migratory behaviour, and adaptation to the variable food environment, including rapid development and the accumulation of lipid reserves. The abundance of *C. agulhensis* on the Agulhas Bank is favoured by enhanced growth rates, production and retention associated with the Agulhas Ridge, and adaptation to low but consistent food availability. These characteristics result in the two copepods being less suited to their non-core areas, and at a competitive disadvantage if they are transported to these regions. However, they are at an additional disadvantage in their non-core areas because they tend to occur at the margins of these regions. *C. carinatus* was mostly transported to the outer Agulhas Bank, along the shelf-edge, where temperatures are warmest, food conditions are generally poor (apart from sporadic shelf-edge upwelling), and advection to the retentive inner Agulhas Bank is unlikely. Furthermore, there may be considerable predation risk from spawning clupeoid fish along the shelf-edge during spring and summer, and also the risk of offshore advection with meanders of the Agulhas Current. Likewise, *C. agulhensis* tended to be transported quite far offshore along the West Coast by the jet current, where food abundance is low, temperatures are warm, and the likelihood of reaching the food-rich inshore area through advection or relaxation of upwelling is relatively poor. Transport to the West Coast is greatest during spring and summer, when the jet current is strongest, but also when transport of clupeoid eggs and larvae is greatest, which is likely to result in relatively high rates of predation on copepod eggs and nauplii by hungry fish larvae. There is also a concomitant risk of offshore advection from the outer shelf. The combination of these factors results in the perennial occurrence of high abundances of *C. carinatus* off the West Coast, and of *C. agulhensis* on the Agulhas Bank.

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APPENDIX 1

Contour maps of SST and the temperature at 30 m (°C), mean or maximum chlorophyll *a* in the upper 30 m (mg m^{-3}), and abundance of the different copepodite stages of *Calanoides carinatus* and *Calanus agulhensis* (No. m^{-2}) around the coast of South Africa between July 1988 and November 2000. Place names on the maps are abbreviated as follows: OR – Orange River mouth, HB – Hondeklipbaai, CC – Cape Columbine, CT – Cape Town, CA – Cape Agulhas, MB – Mossel Bay, CF – Cape St Francis, PE – Port Elizabeth, EL – East London.

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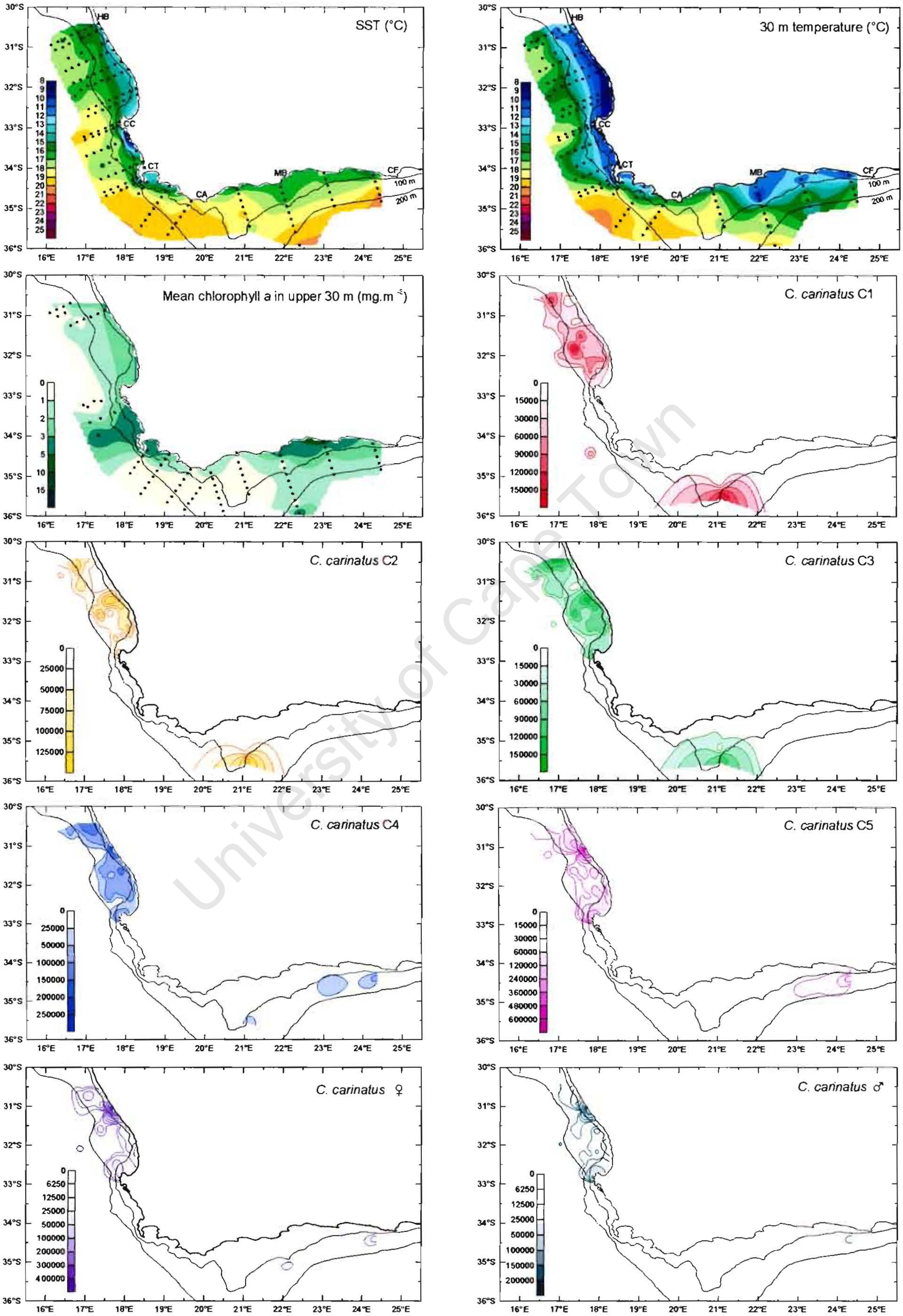

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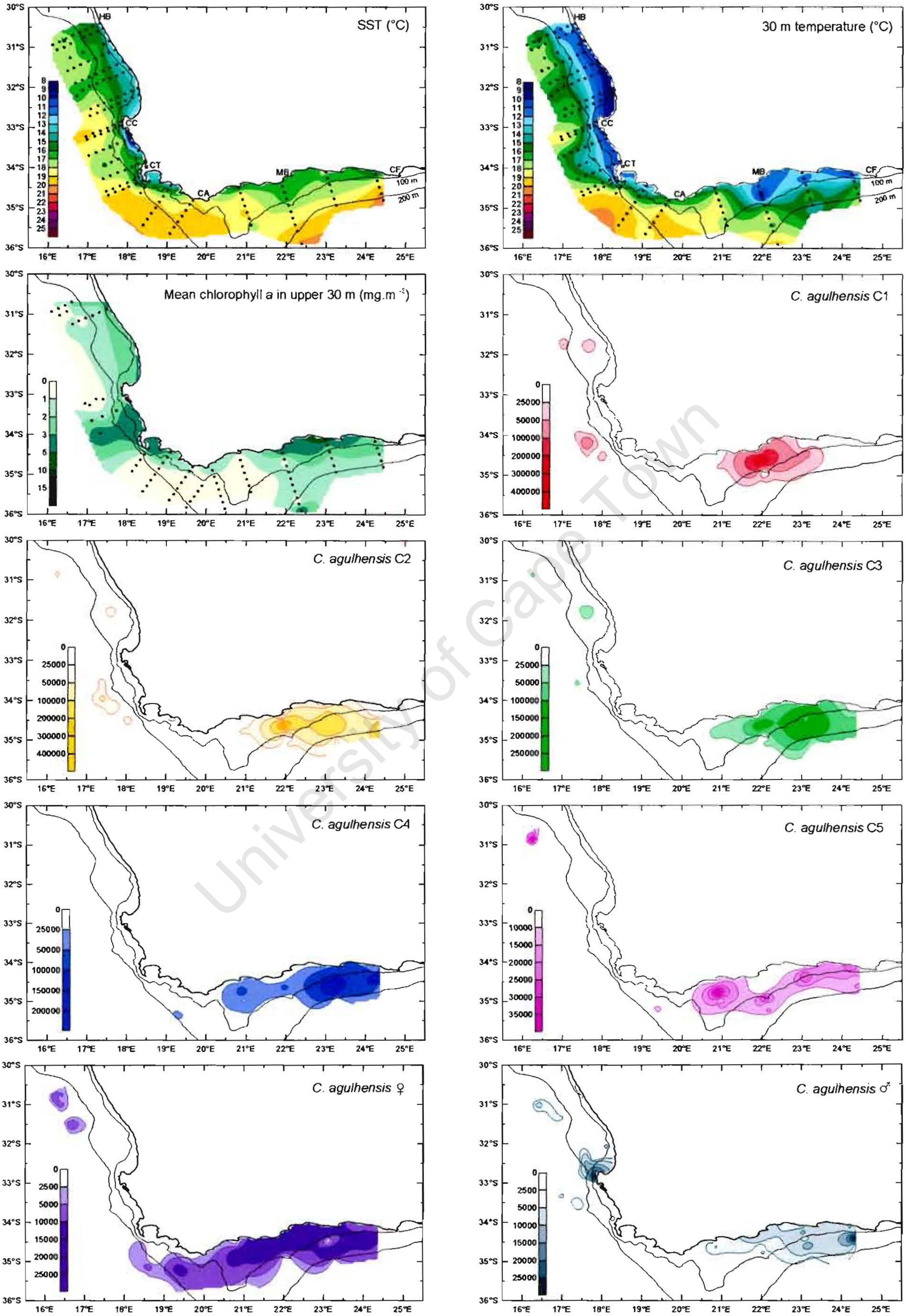

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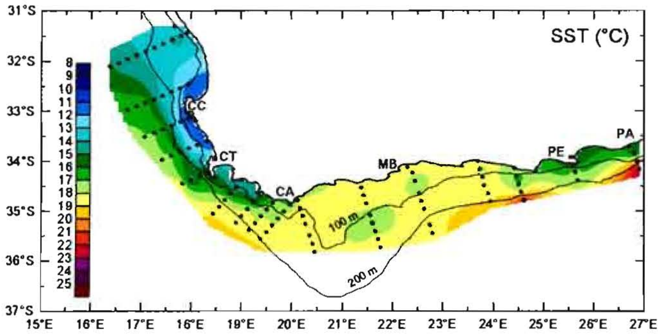

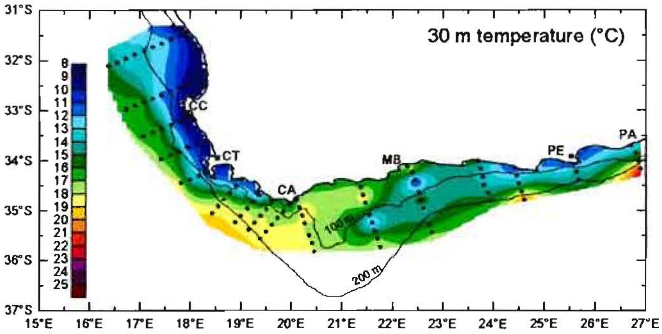

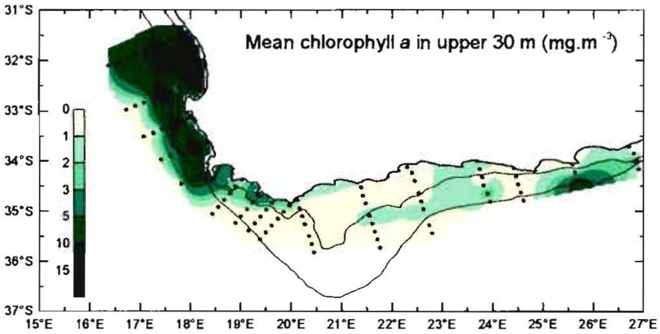

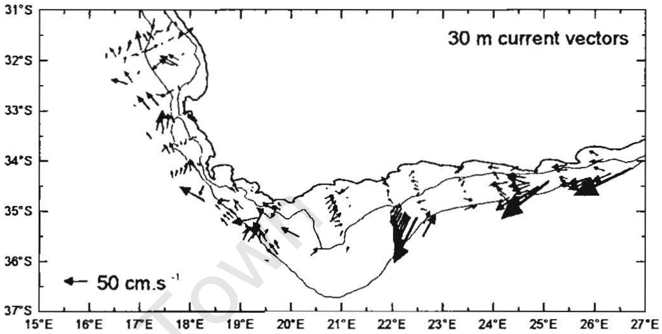

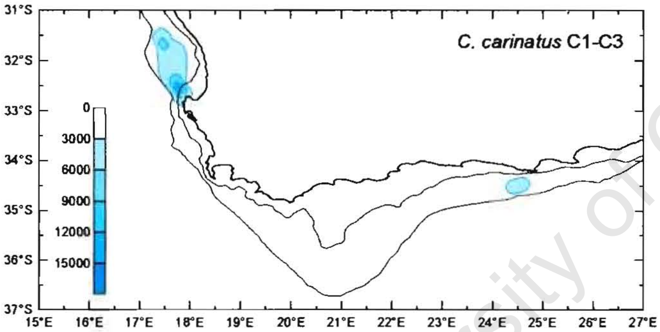

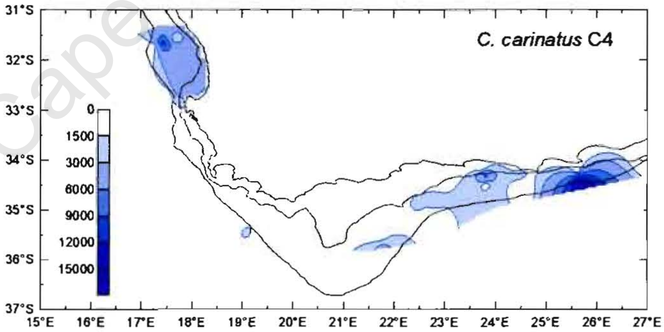

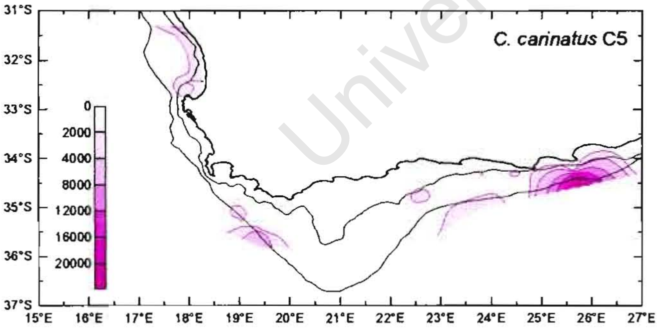

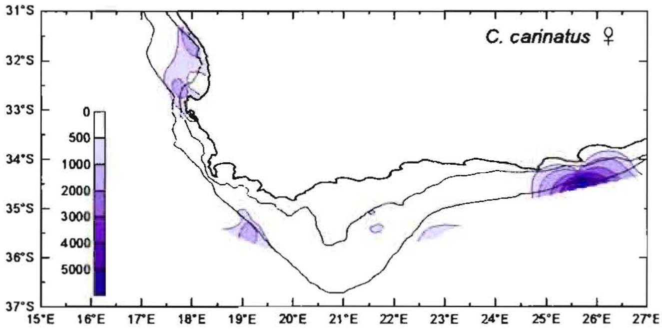

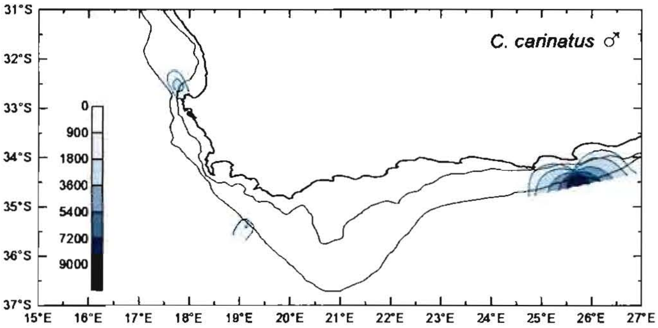

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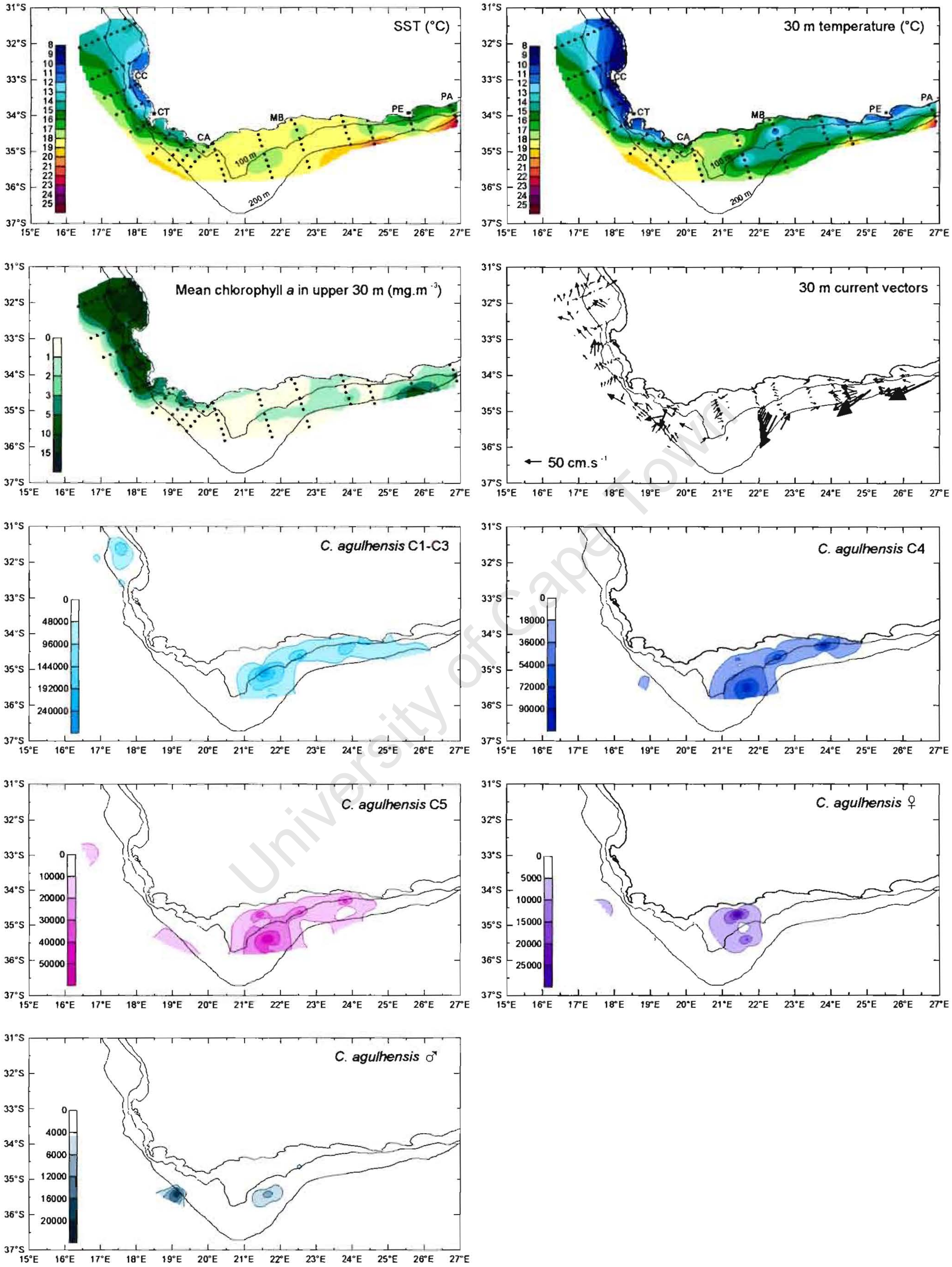

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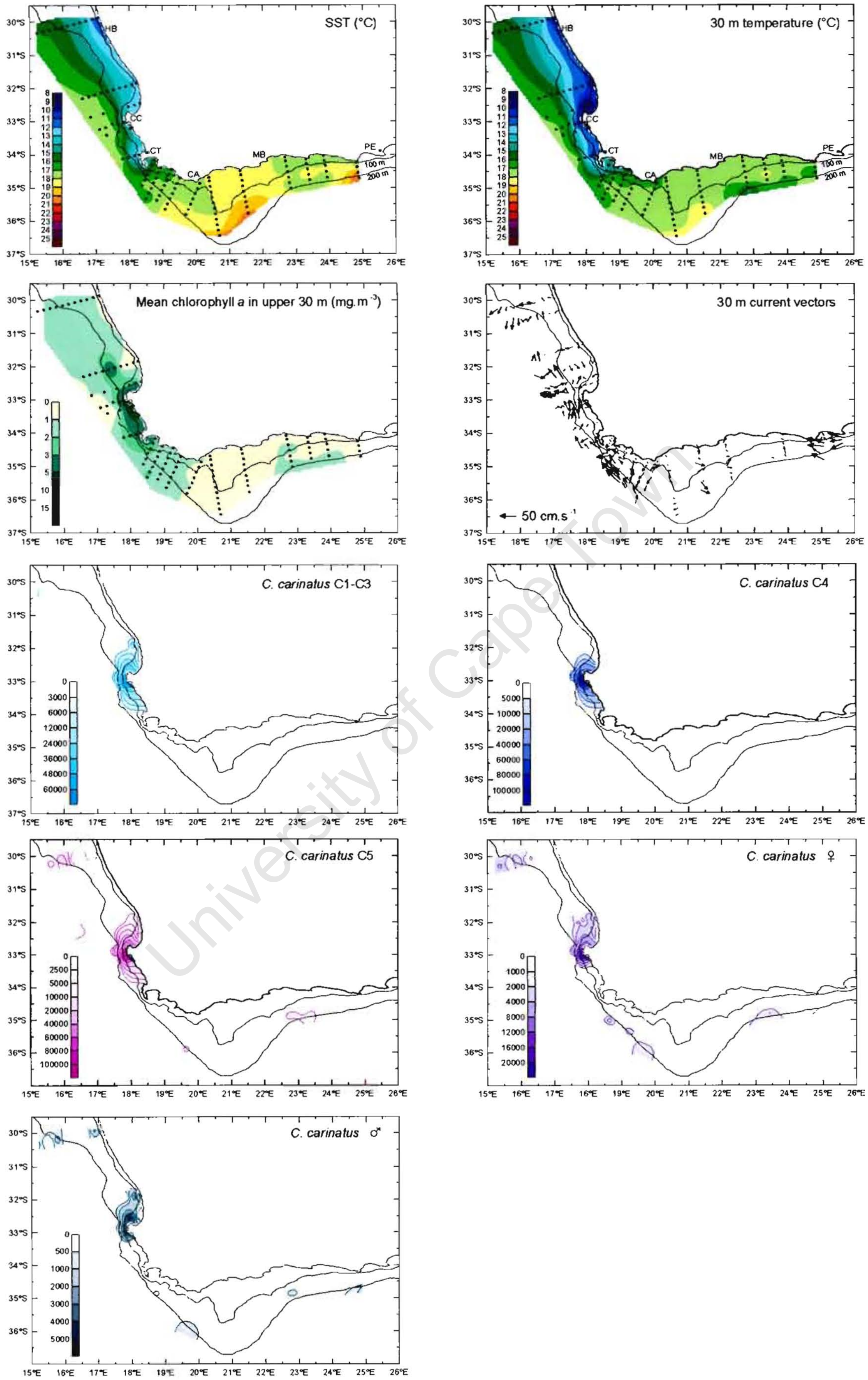
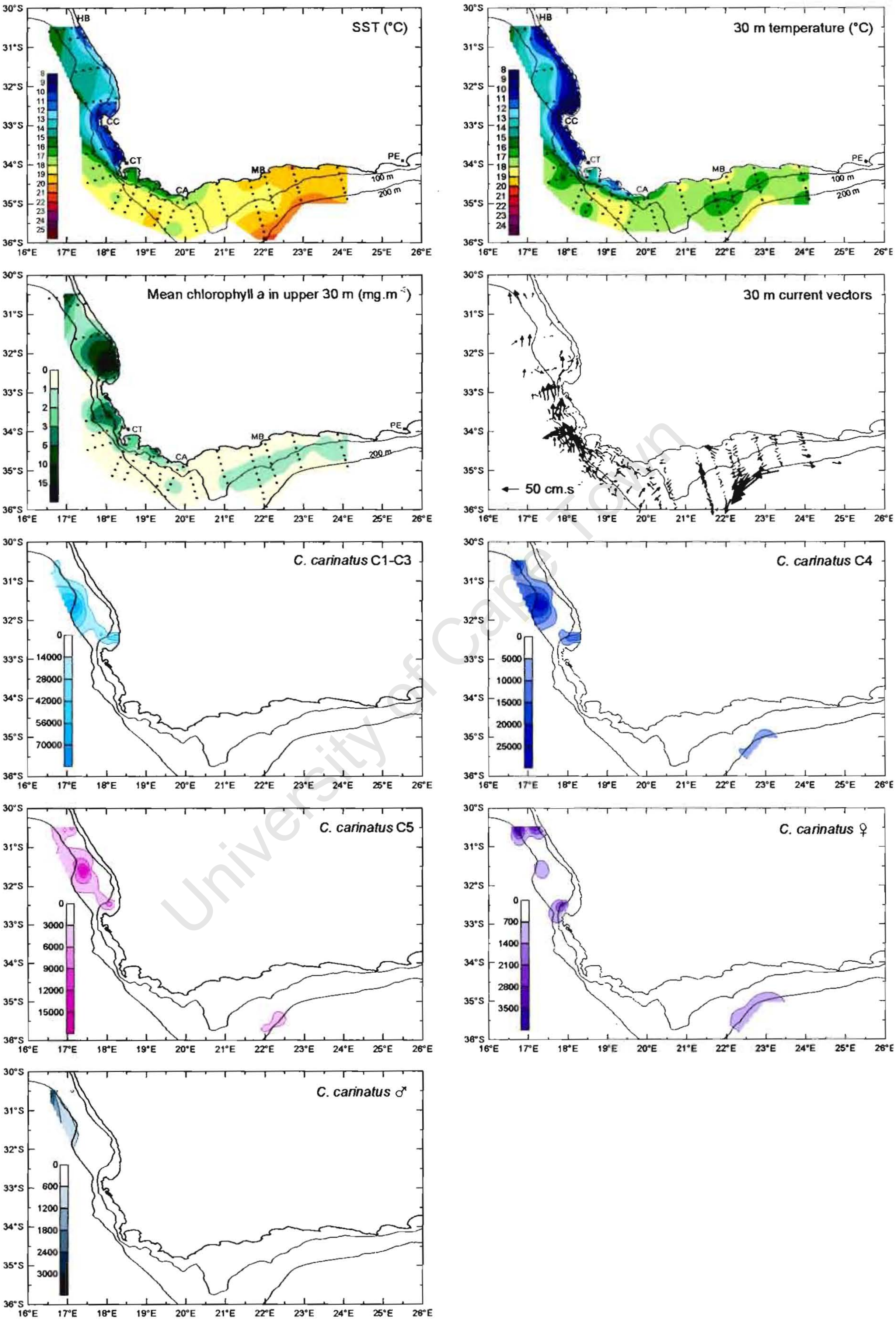
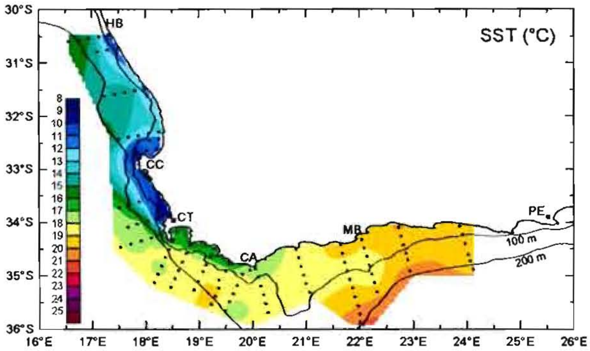
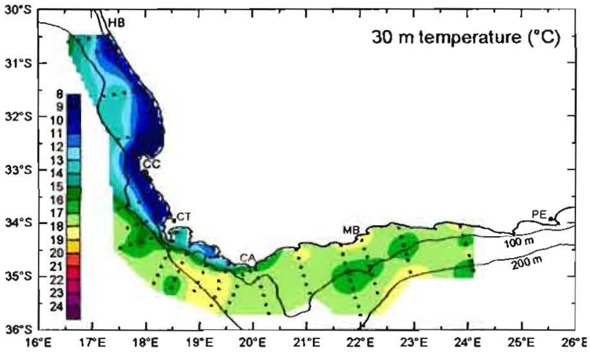


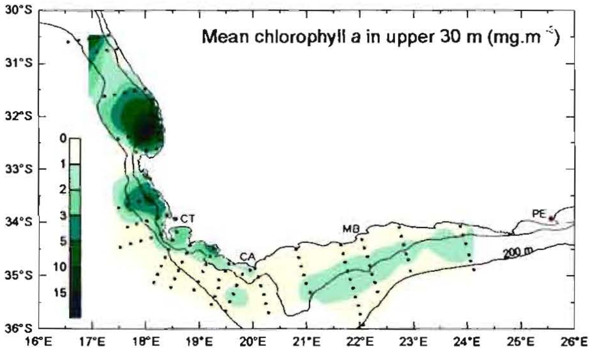
NOVEMBER 1991 – *C. carinatus*

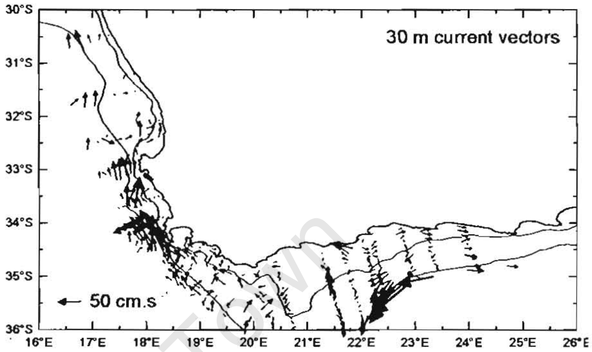


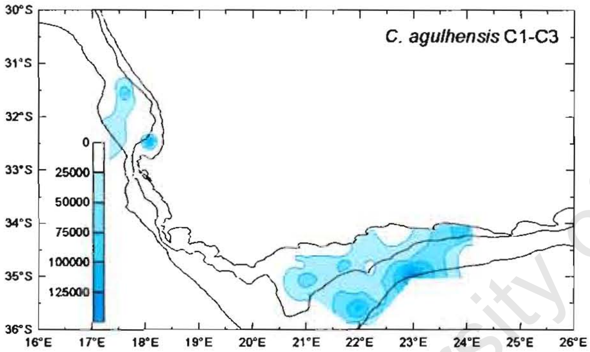
NOVEMBER 1991 – *C. agulhensis*

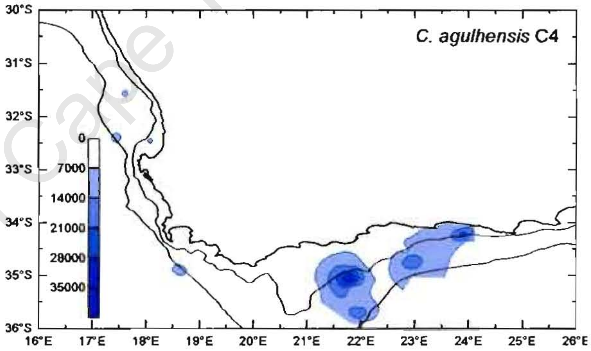

SST (°C)

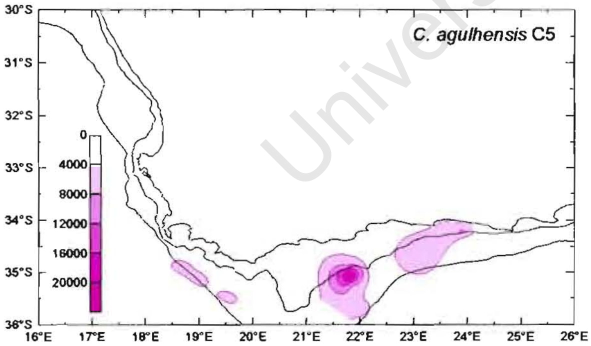

30 m temperature (°C)

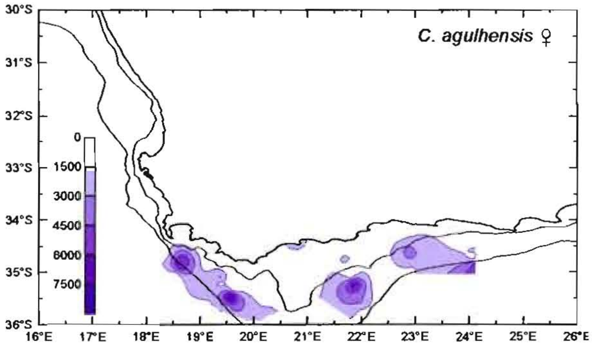

Mean chlorophyll *a* in upper 30 m (mg.m⁻³)

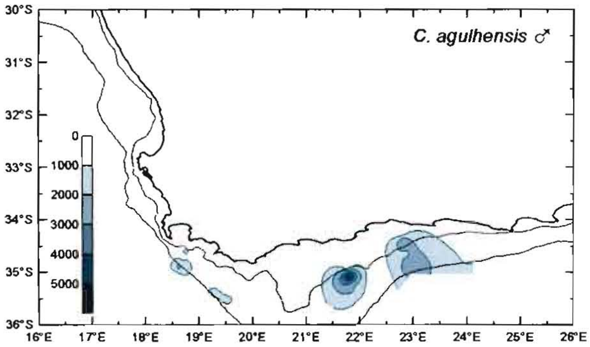

30 m current vectors


C. agulhensis C1-C3

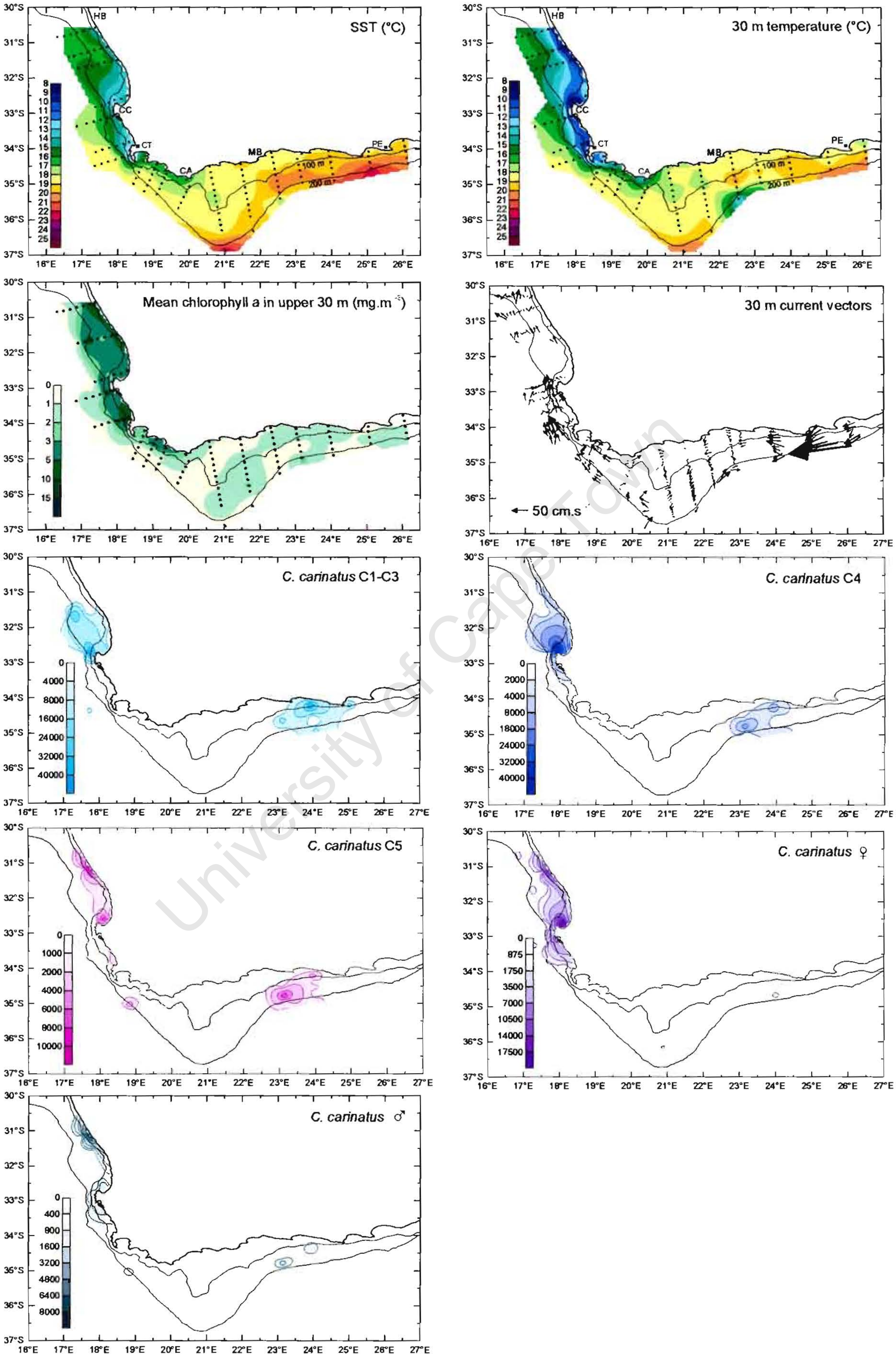

C. agulhensis C4


C. agulhensis C5


C. agulhensis ♀


C. agulhensis ♂

NOVEMBER 1992 – *C. carinatus*



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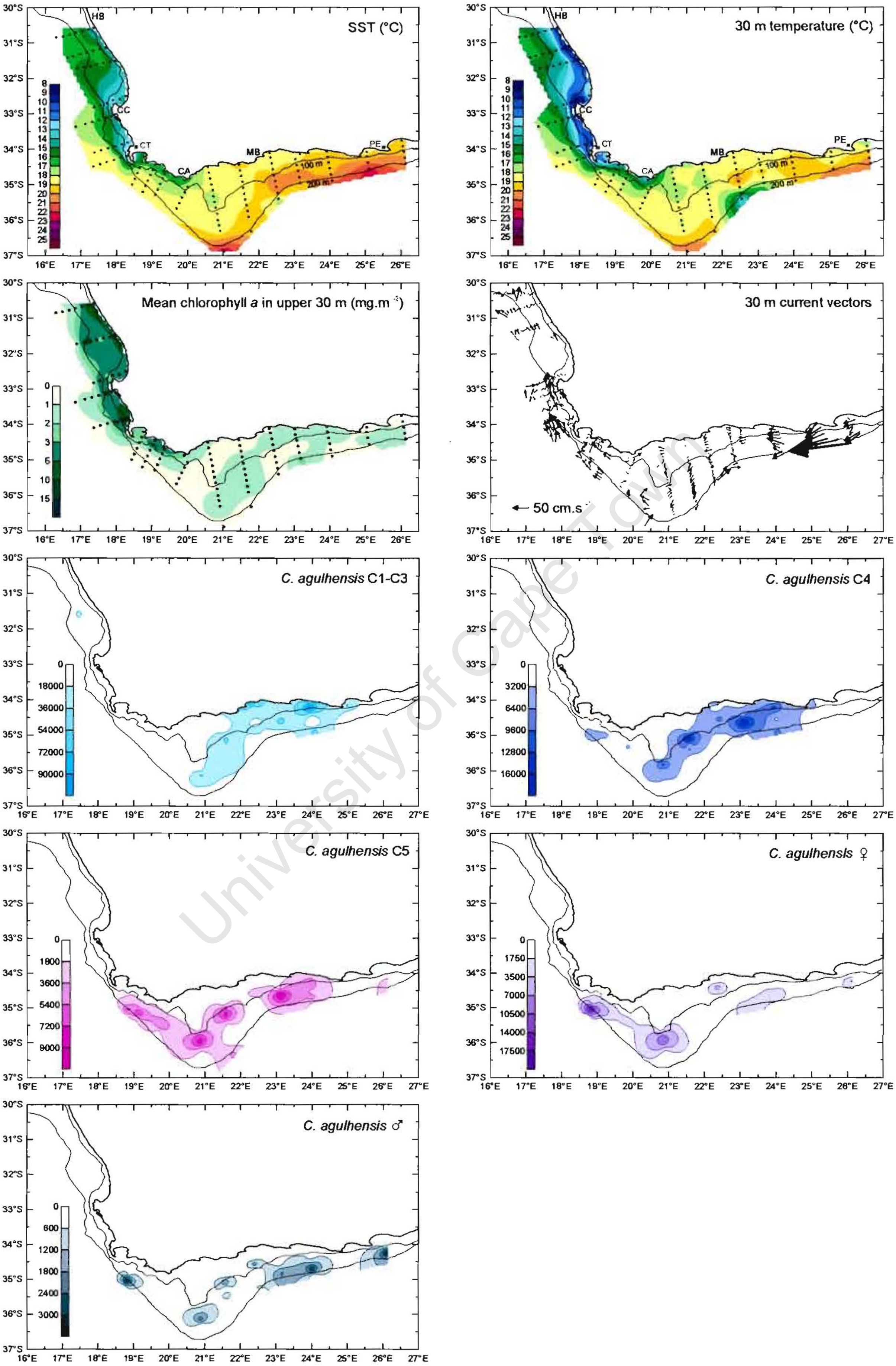

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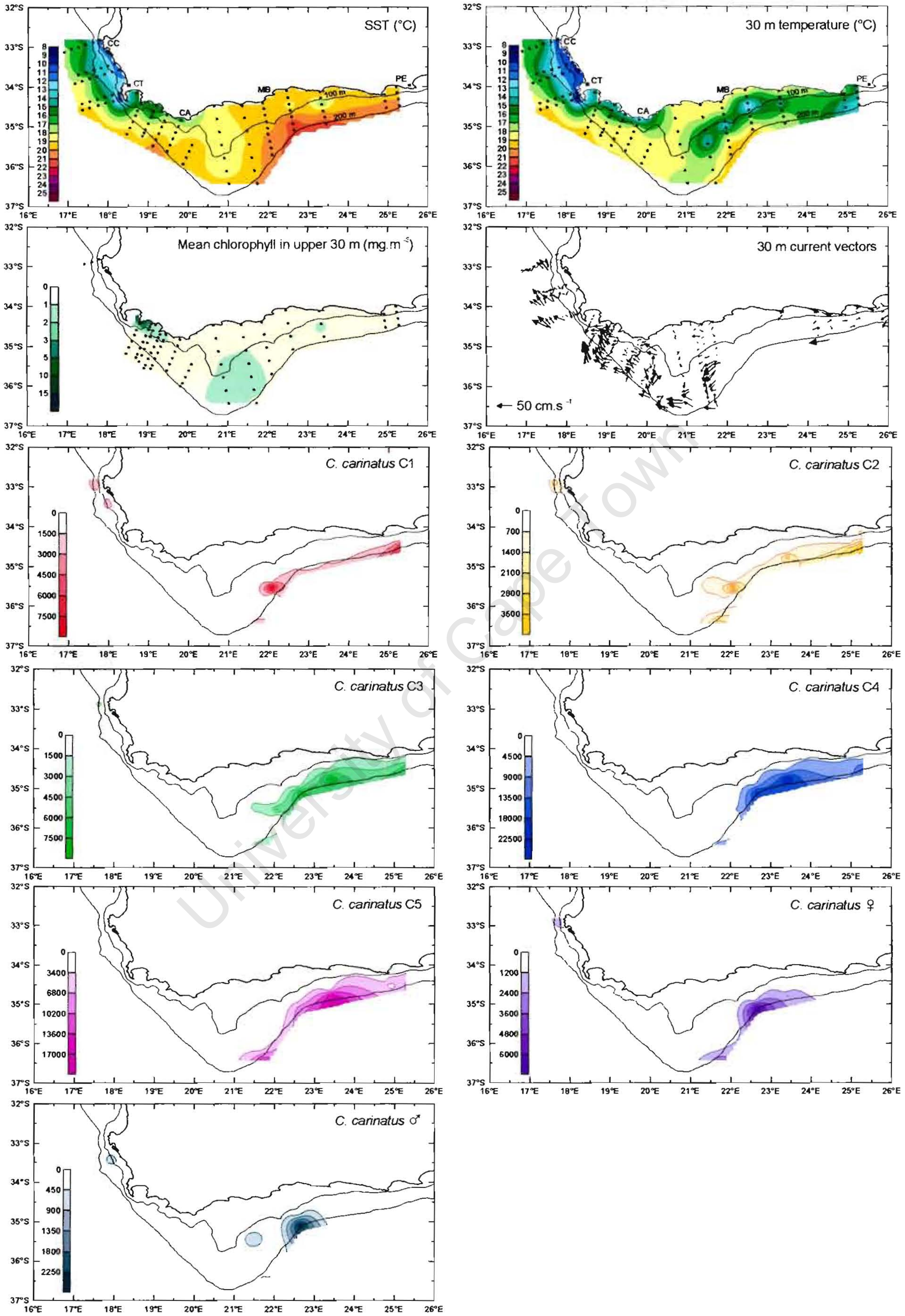

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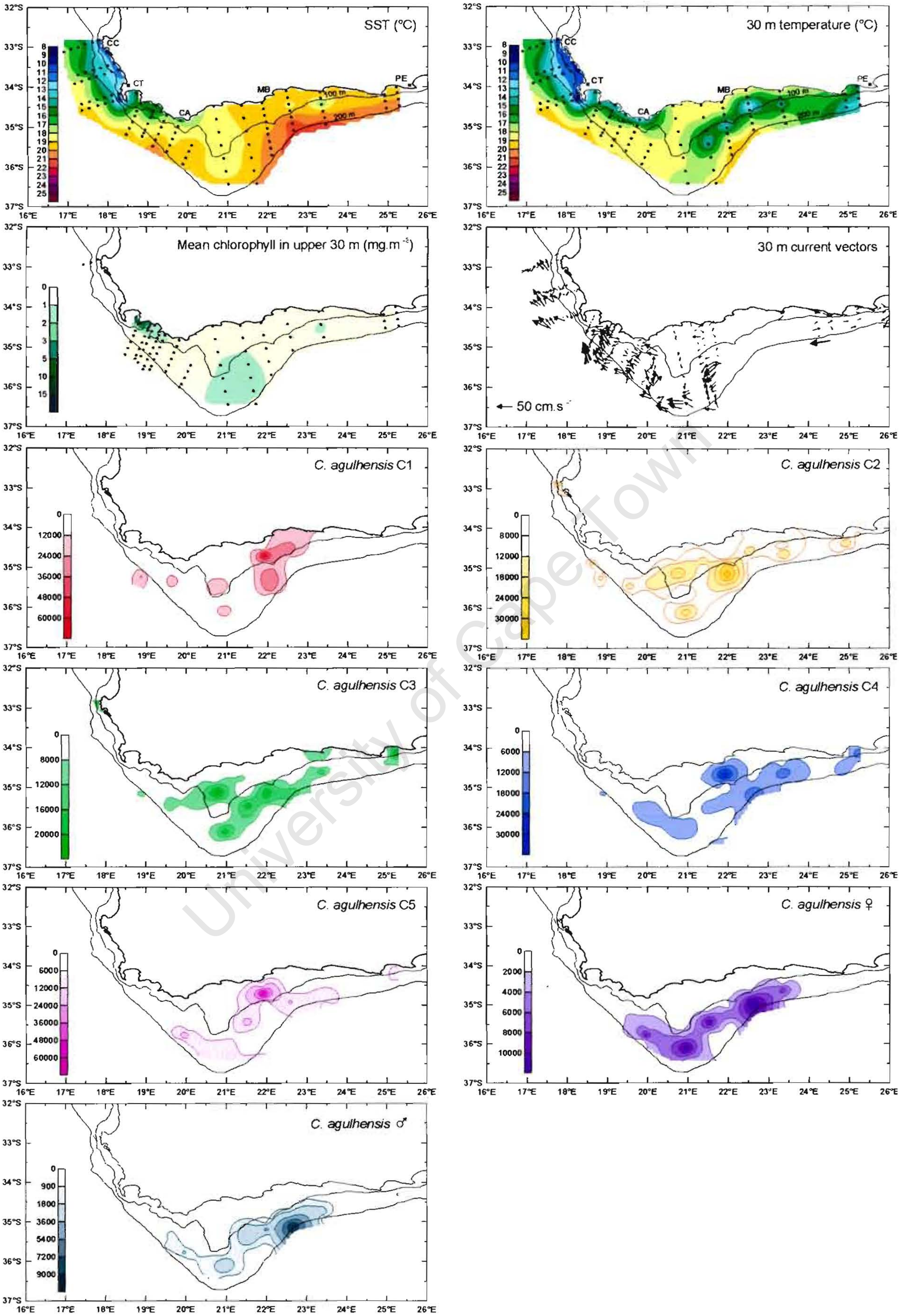

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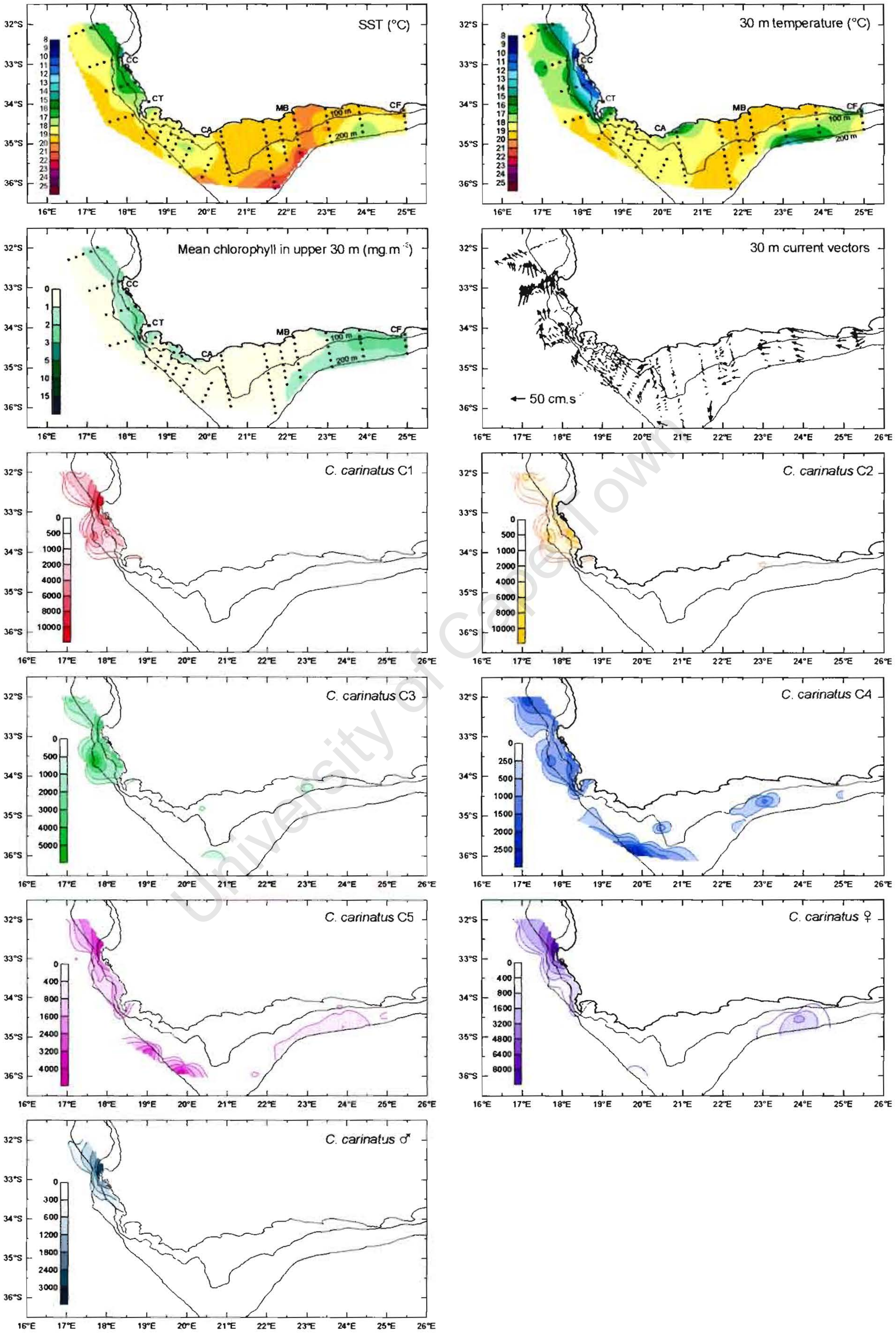

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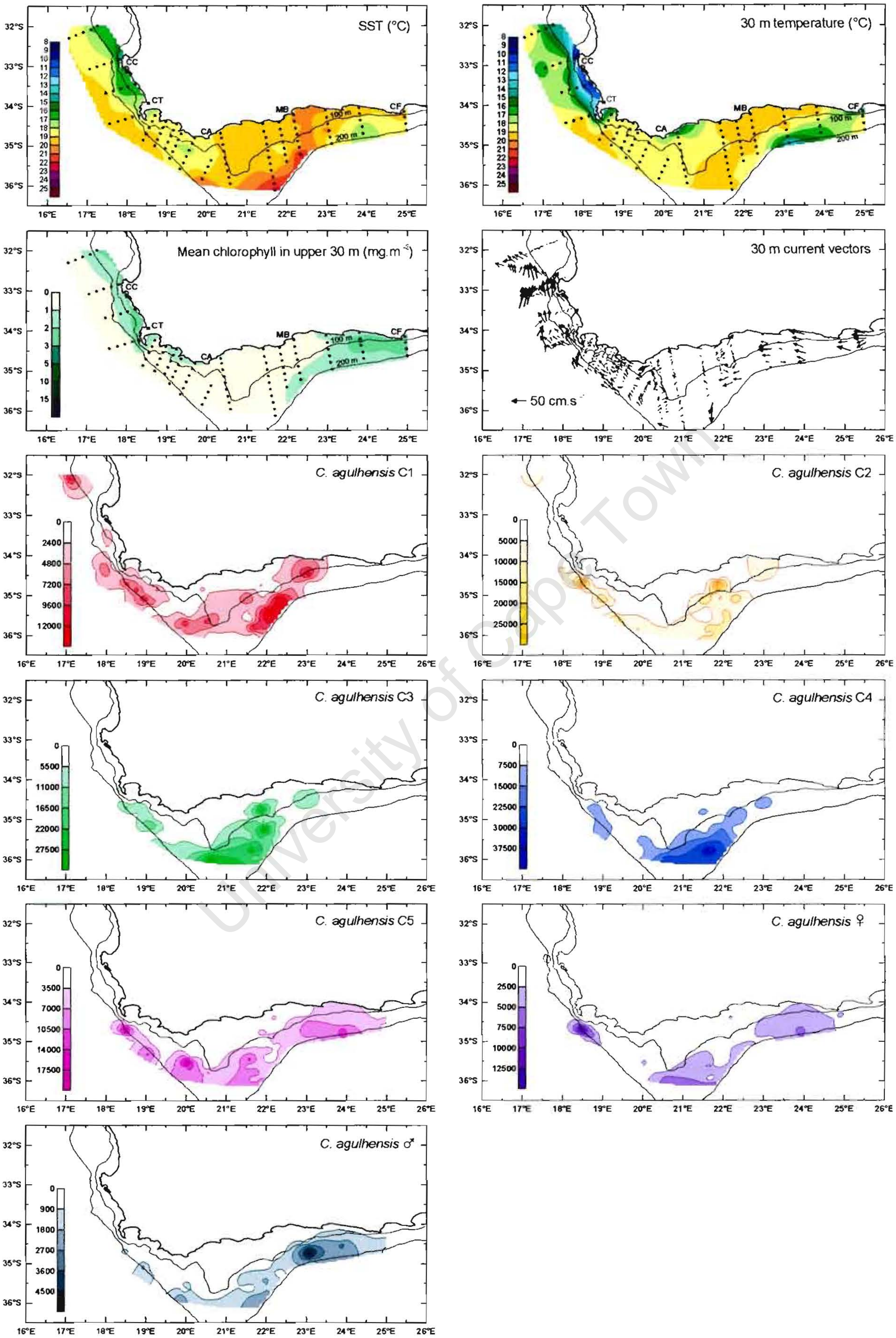

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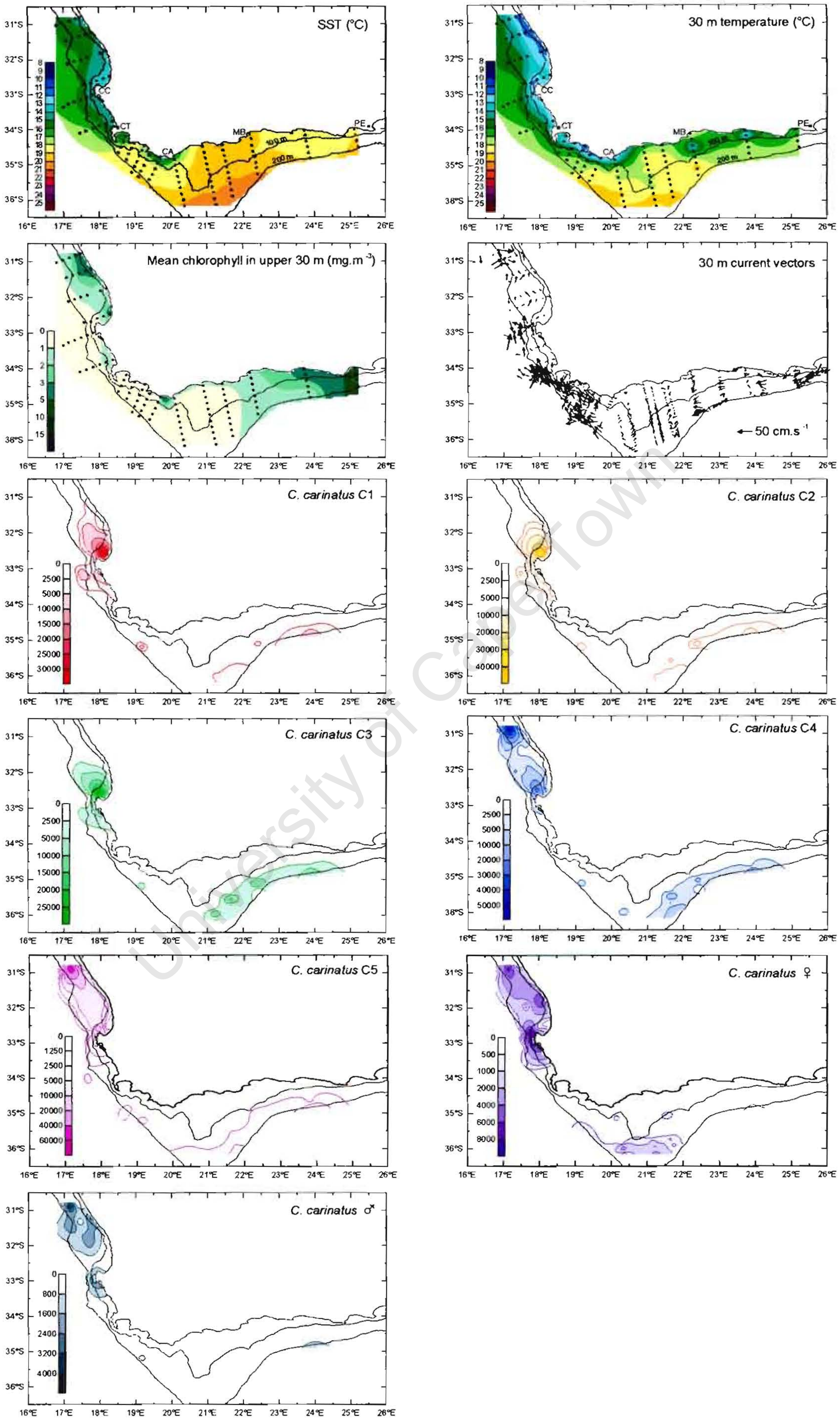
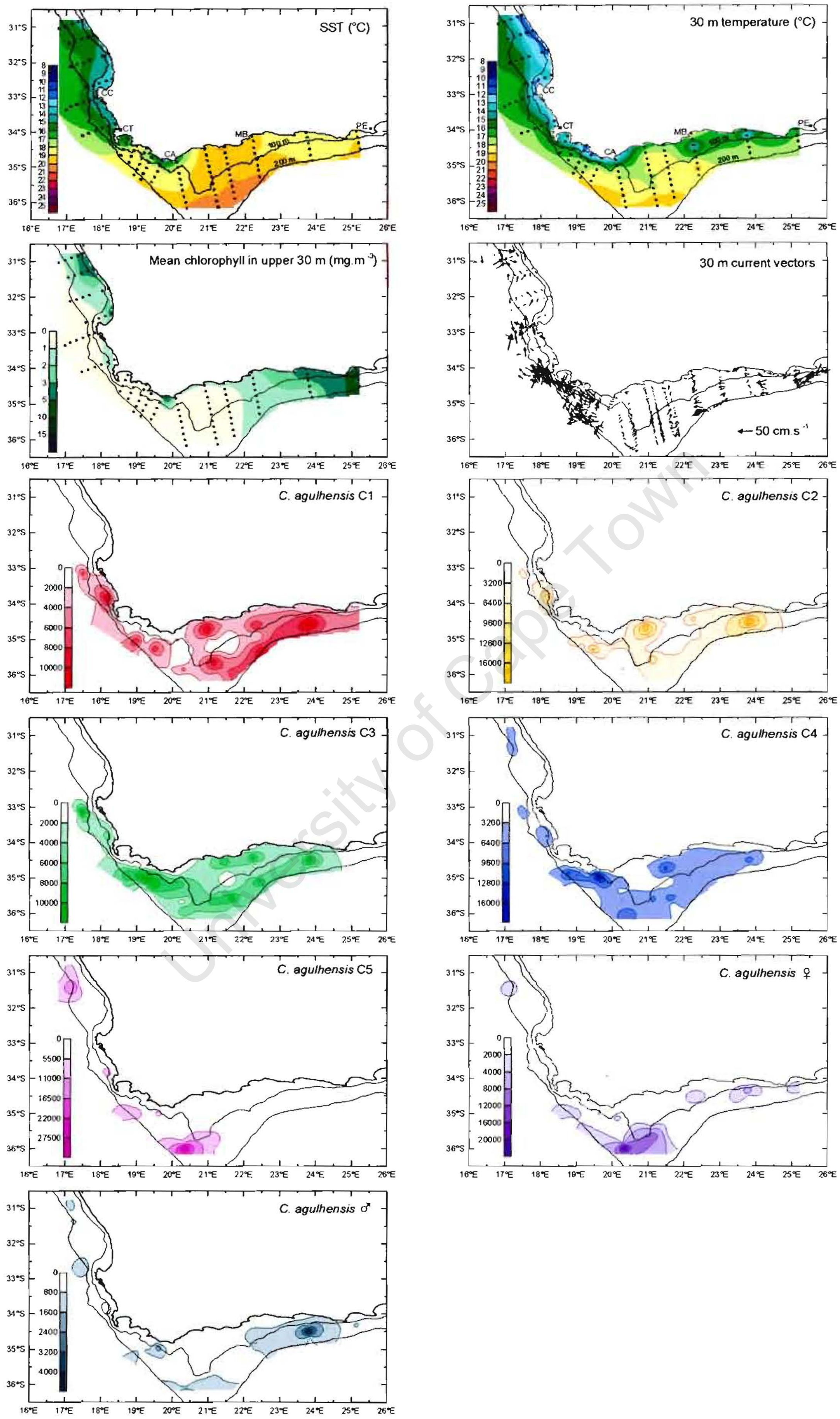
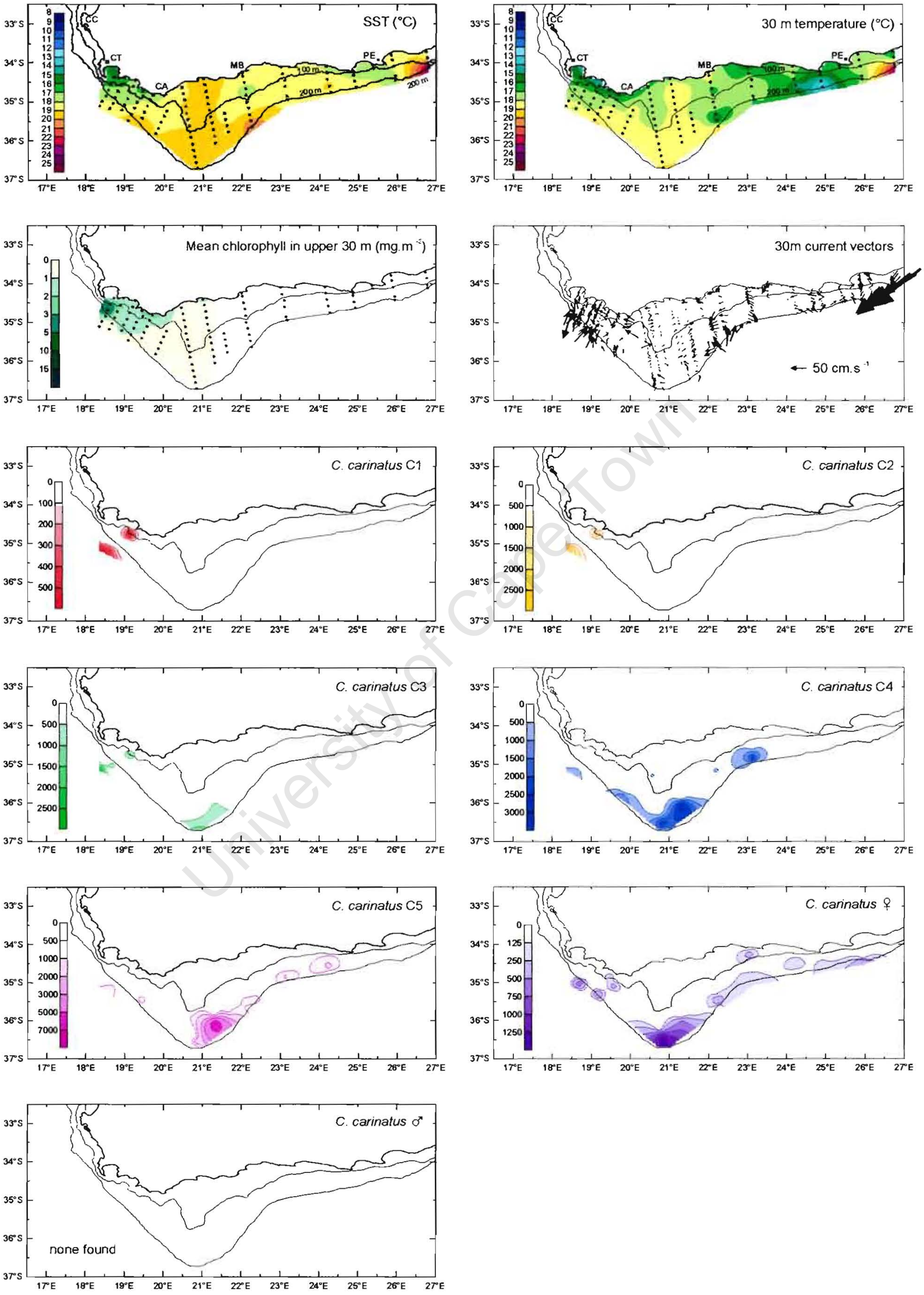


NOVEMBER 1995 – *C. agulhensis*



NOVEMBER 1996 – *C. carinatus*



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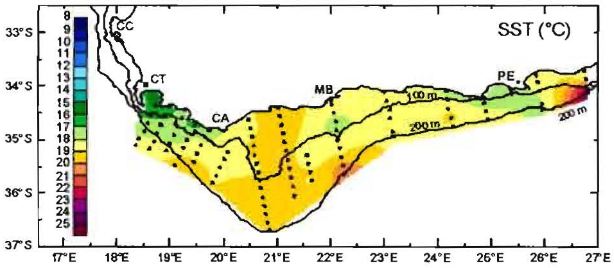
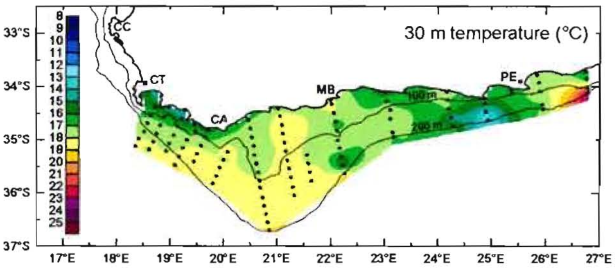
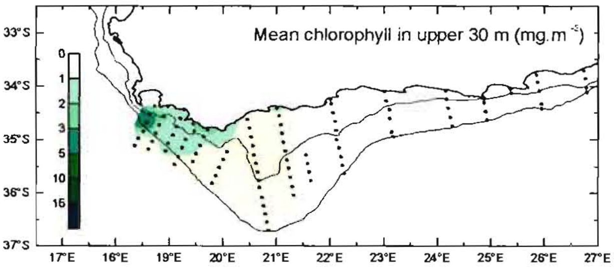
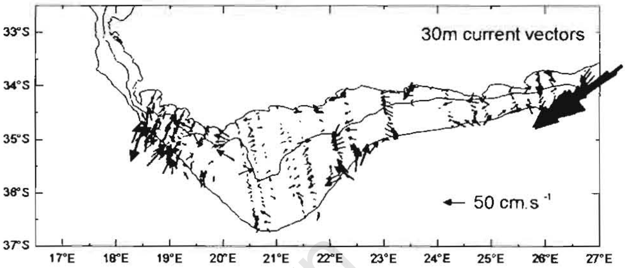
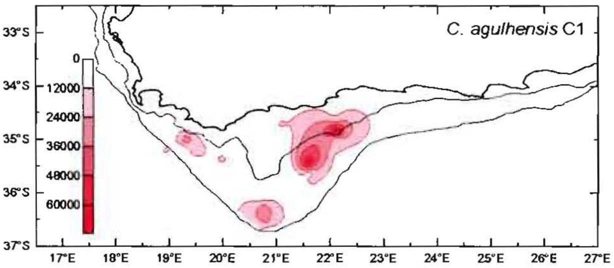
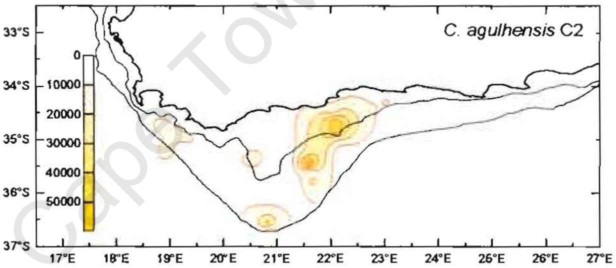


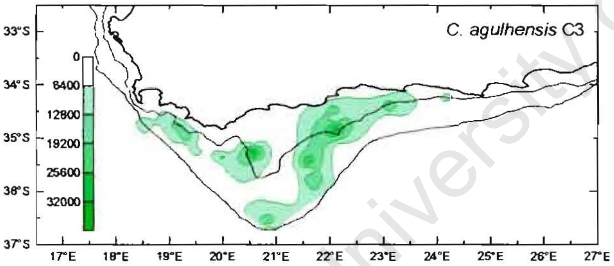


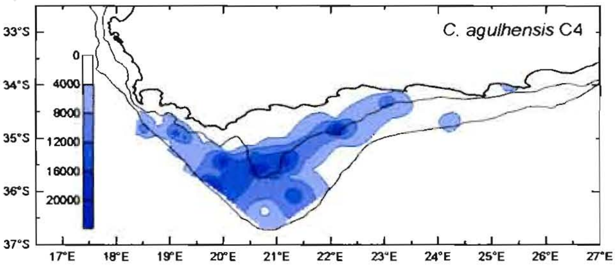


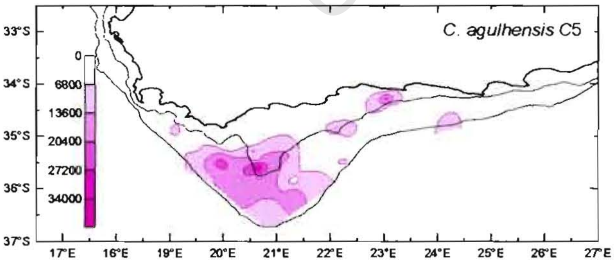


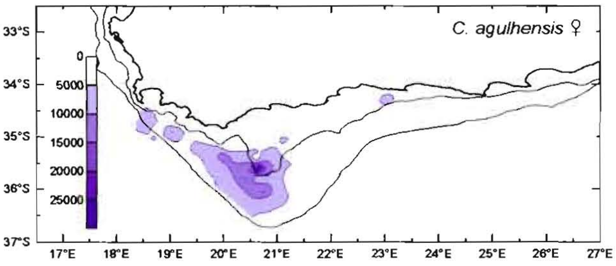


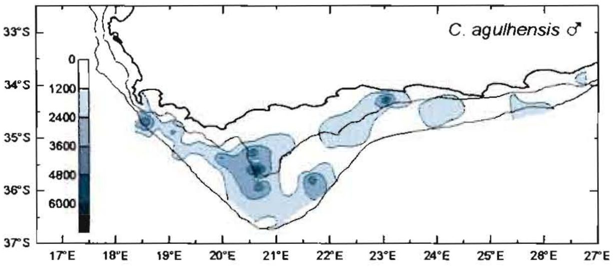




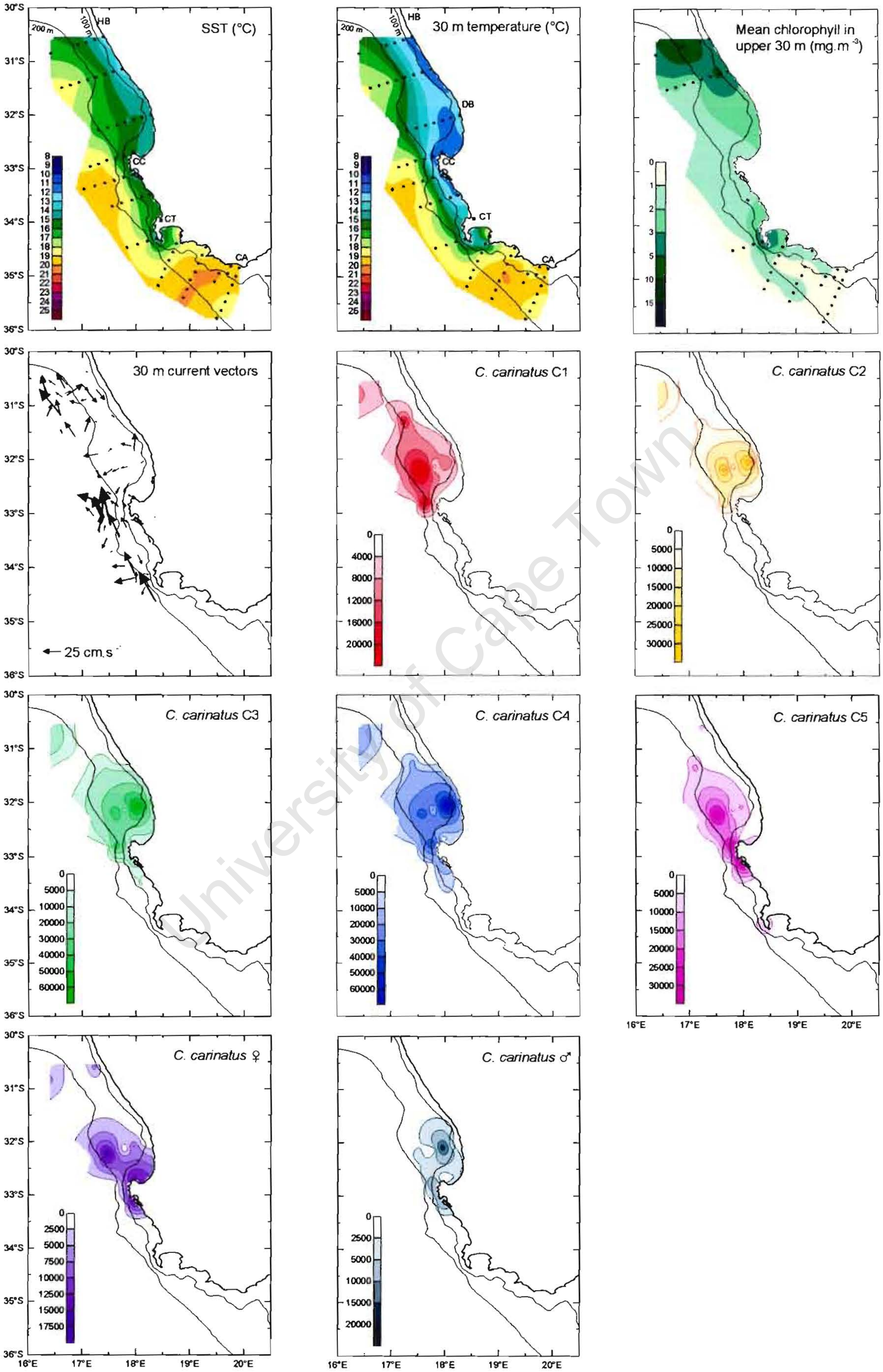




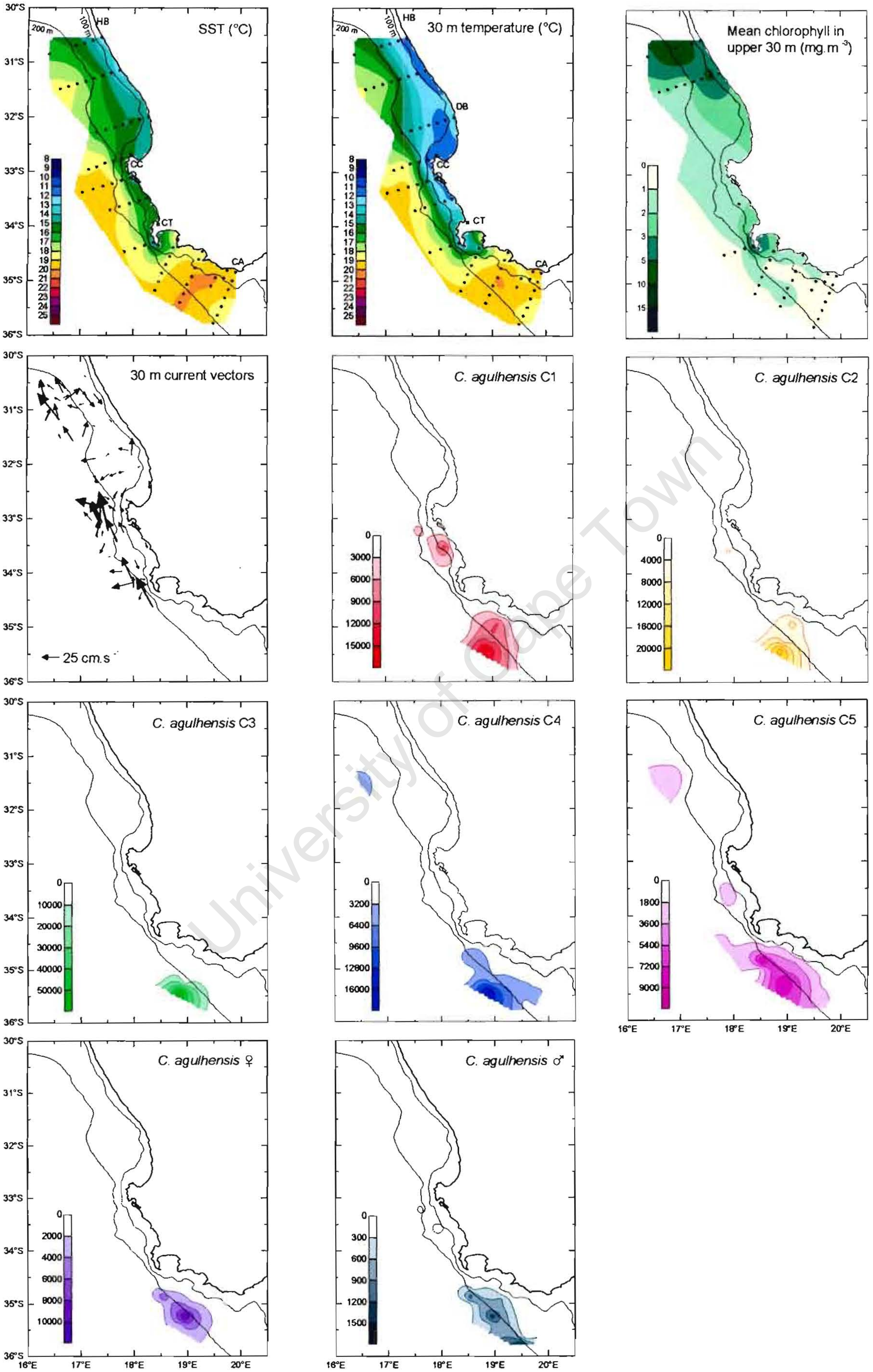




NOVEMBER 1997 – *C. carinatus*



NOVEMBER 1997 – *C. agulhensis*



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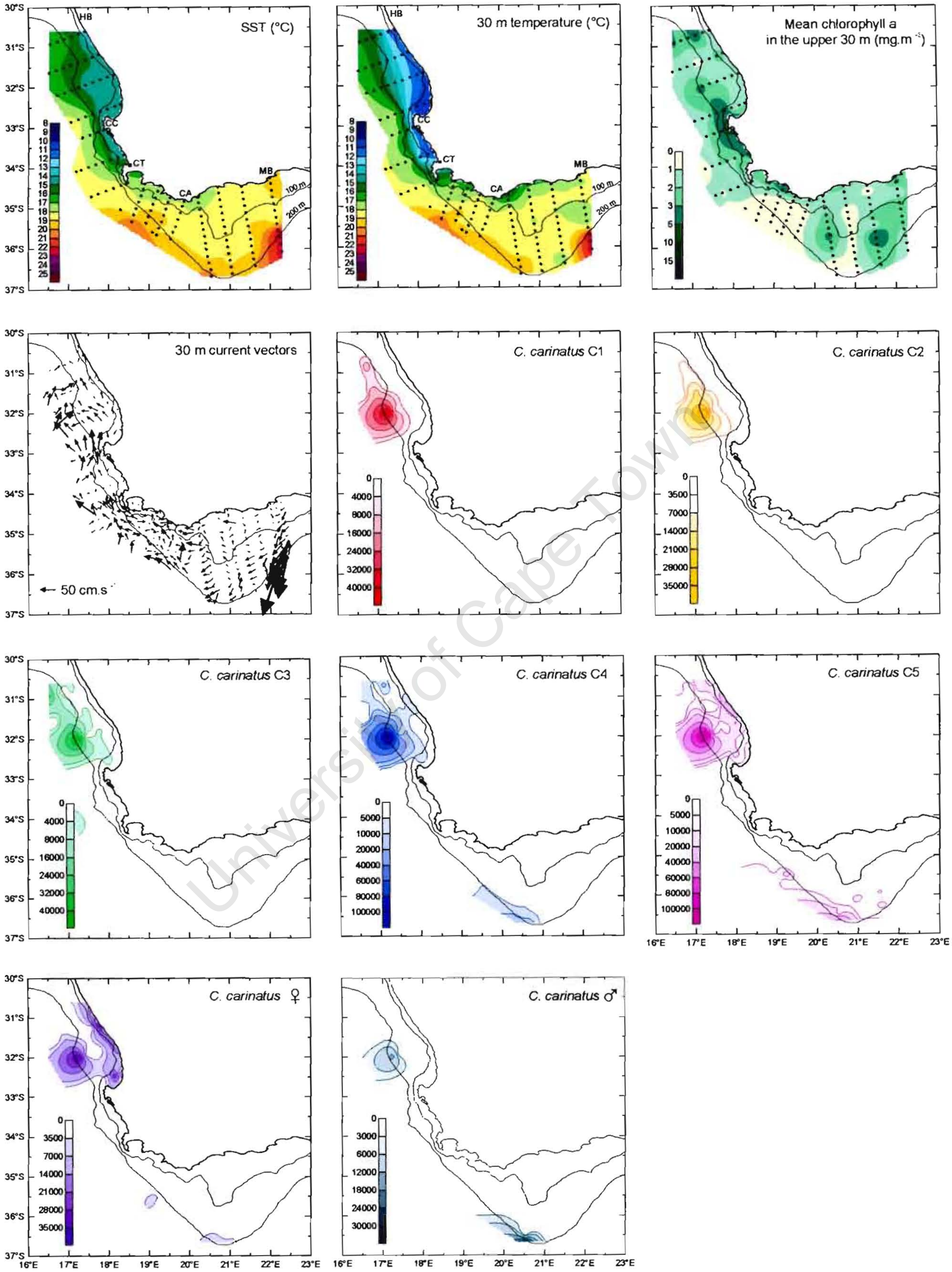

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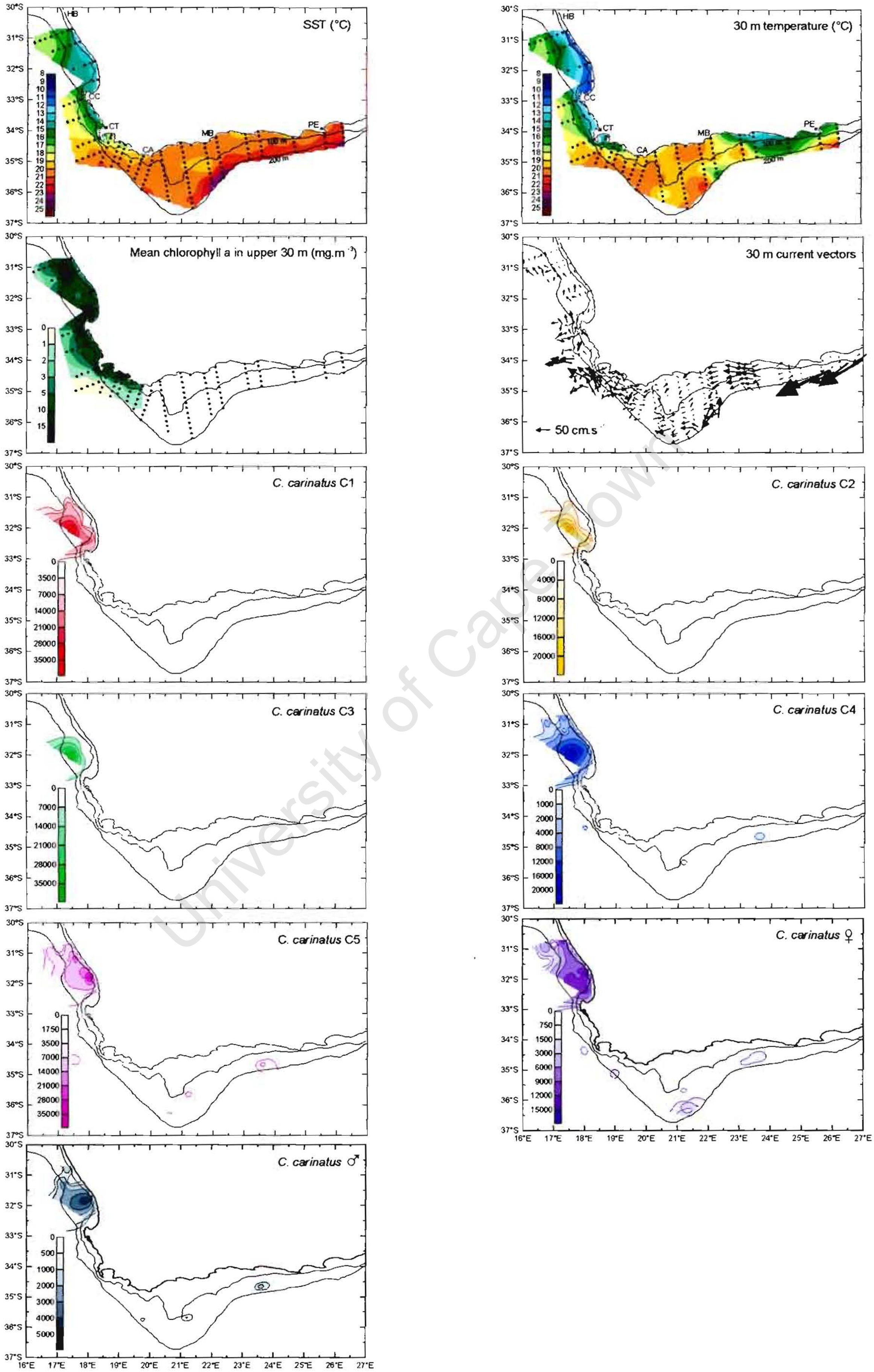

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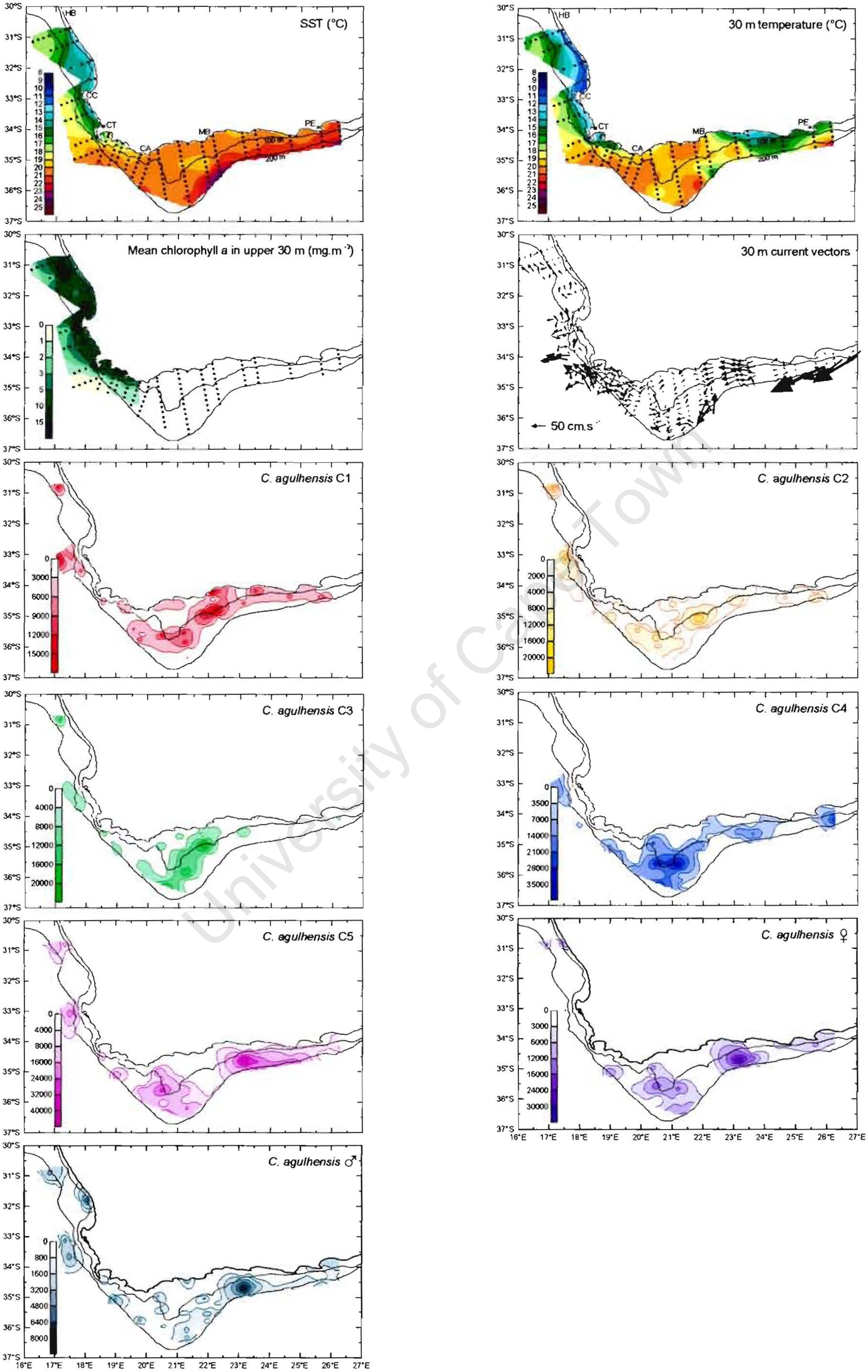

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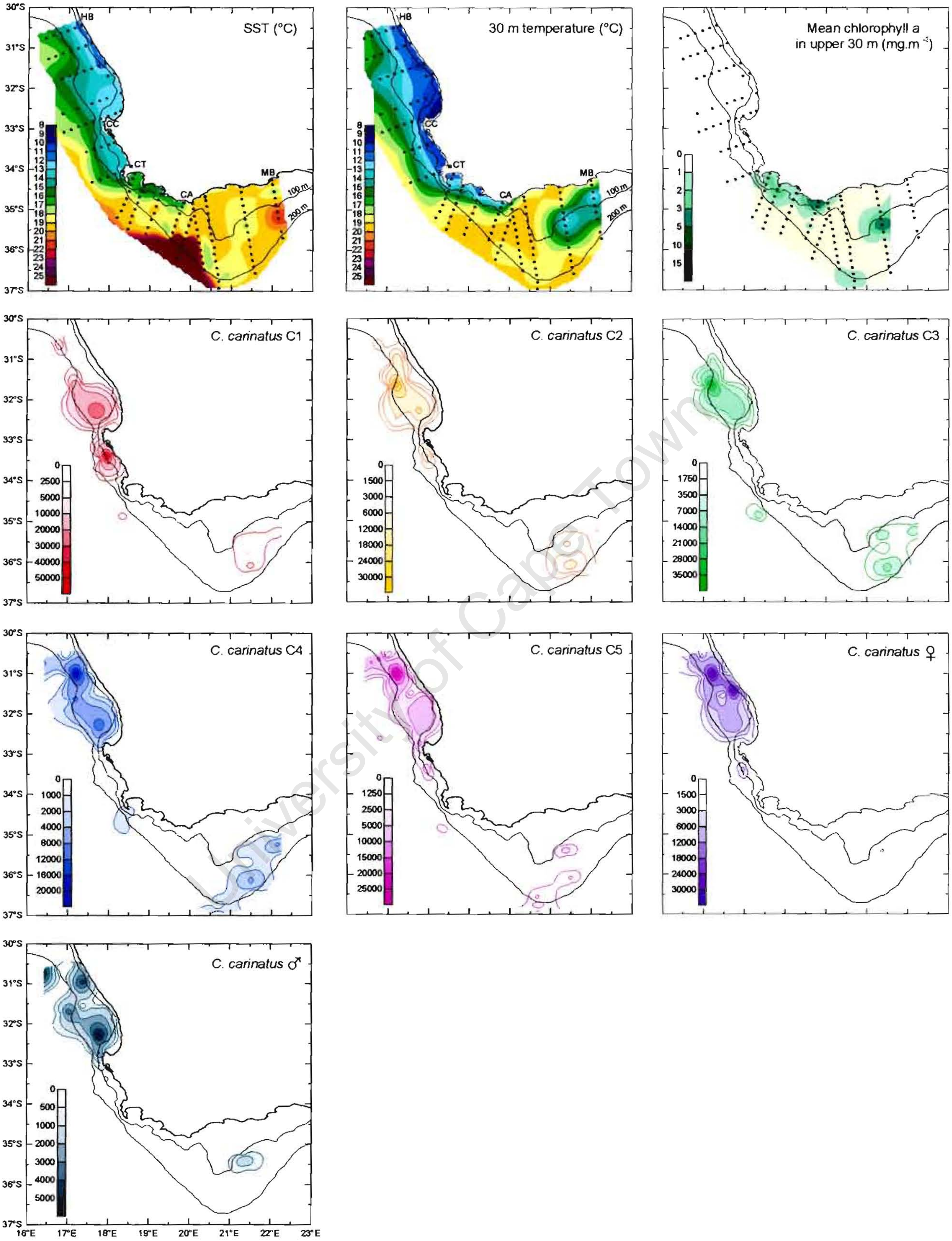

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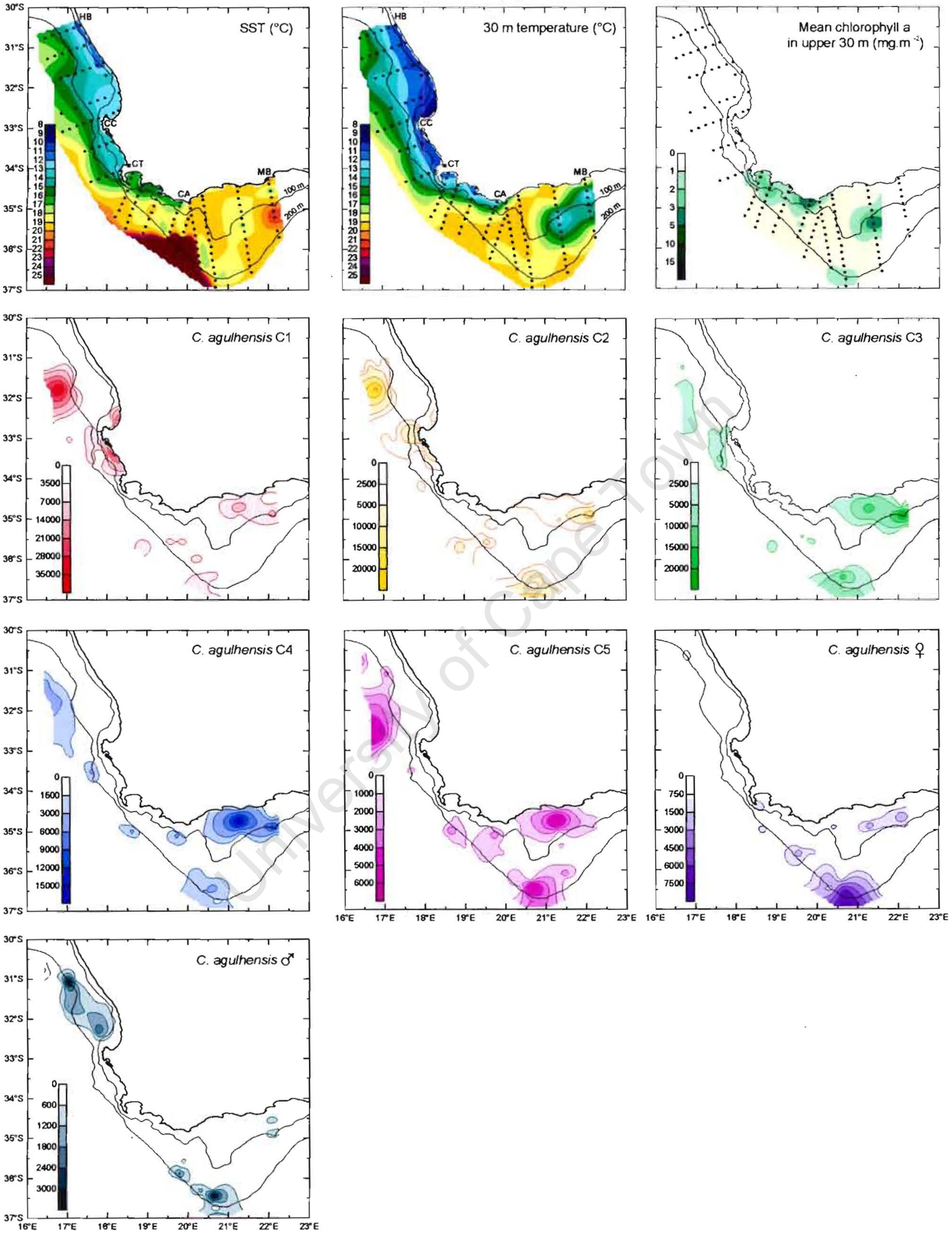
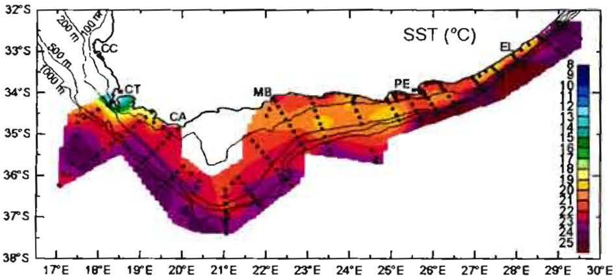
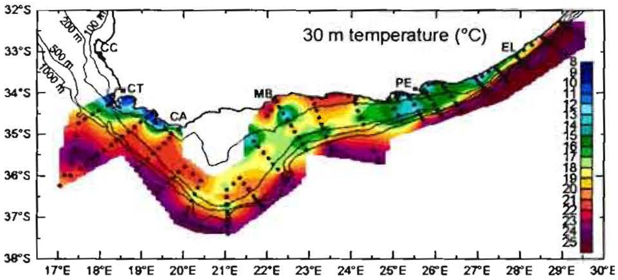
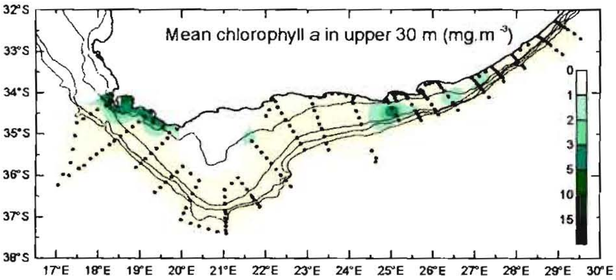
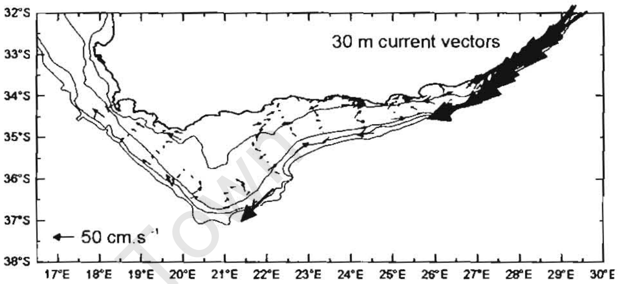


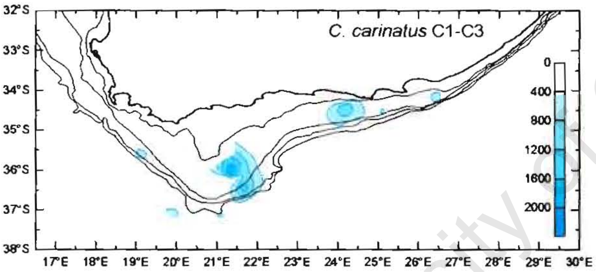
JANUARY 1992 – *C. carinatus*

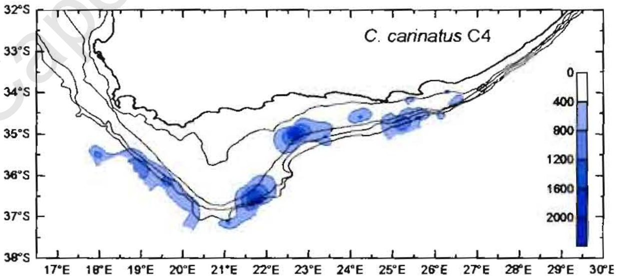


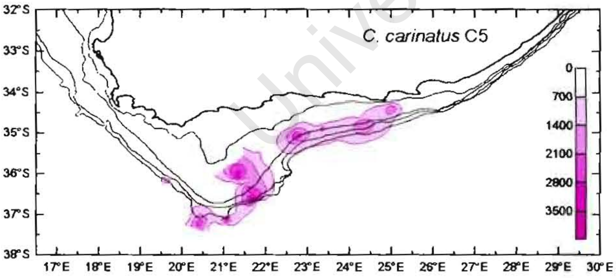


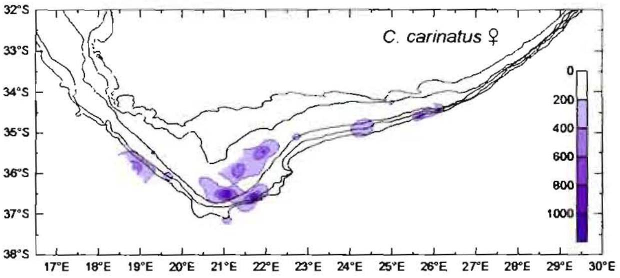


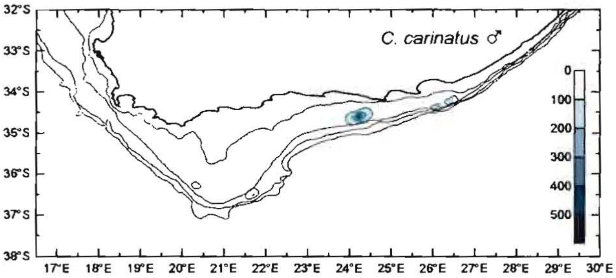




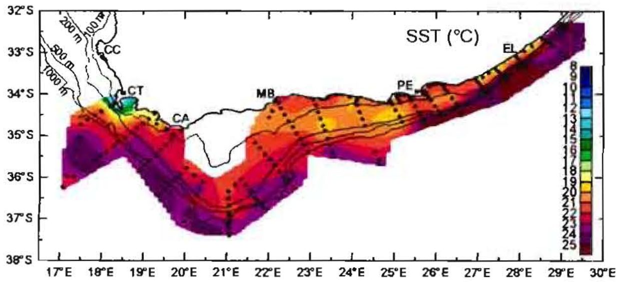


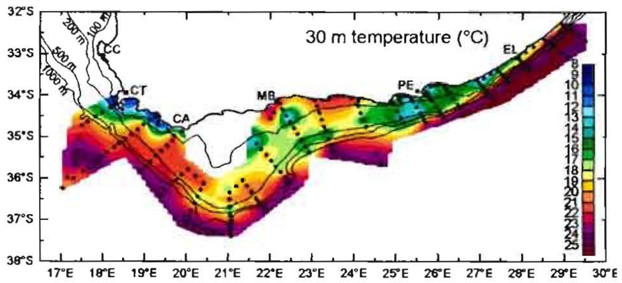


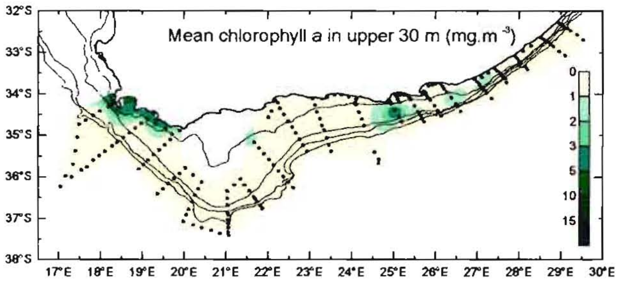


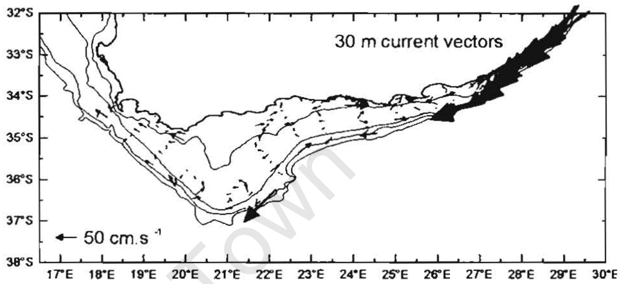


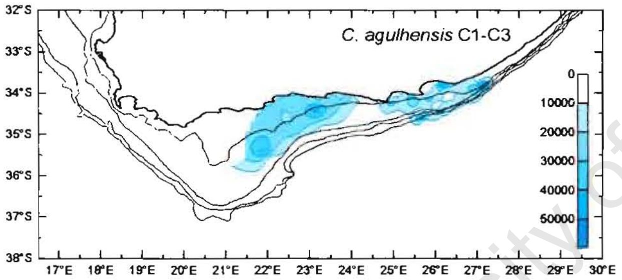
JANUARY 1992 – *C. agulhensis*

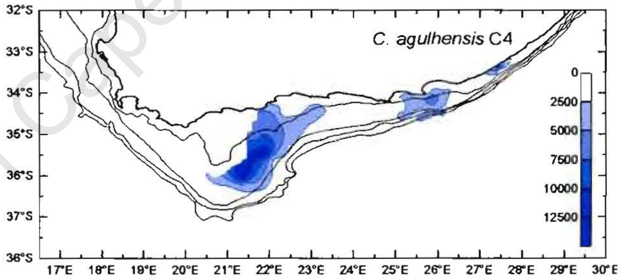


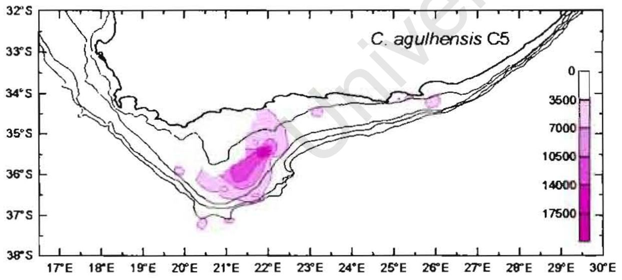


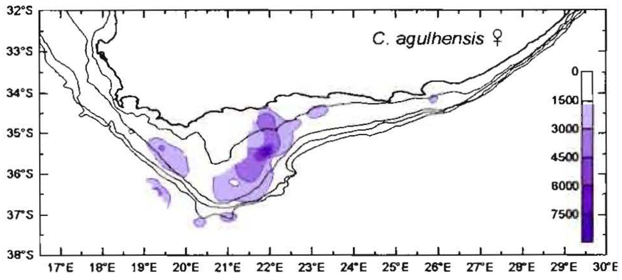


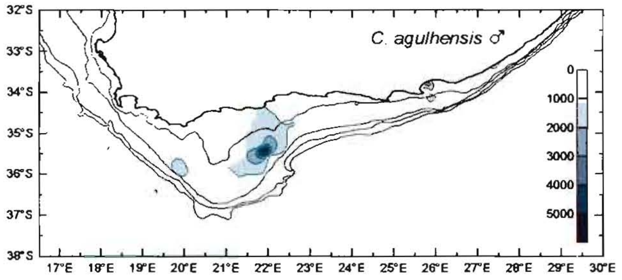




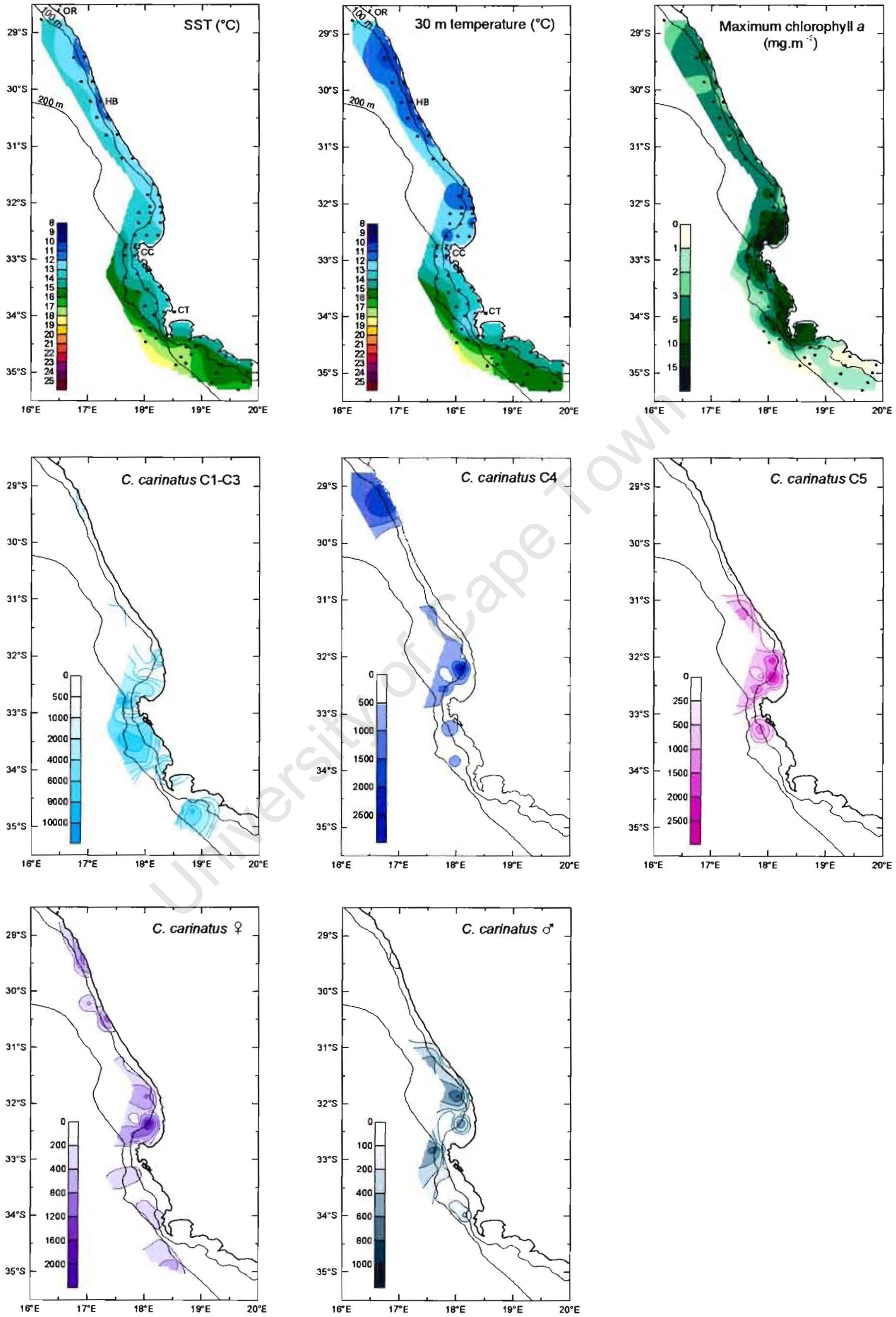




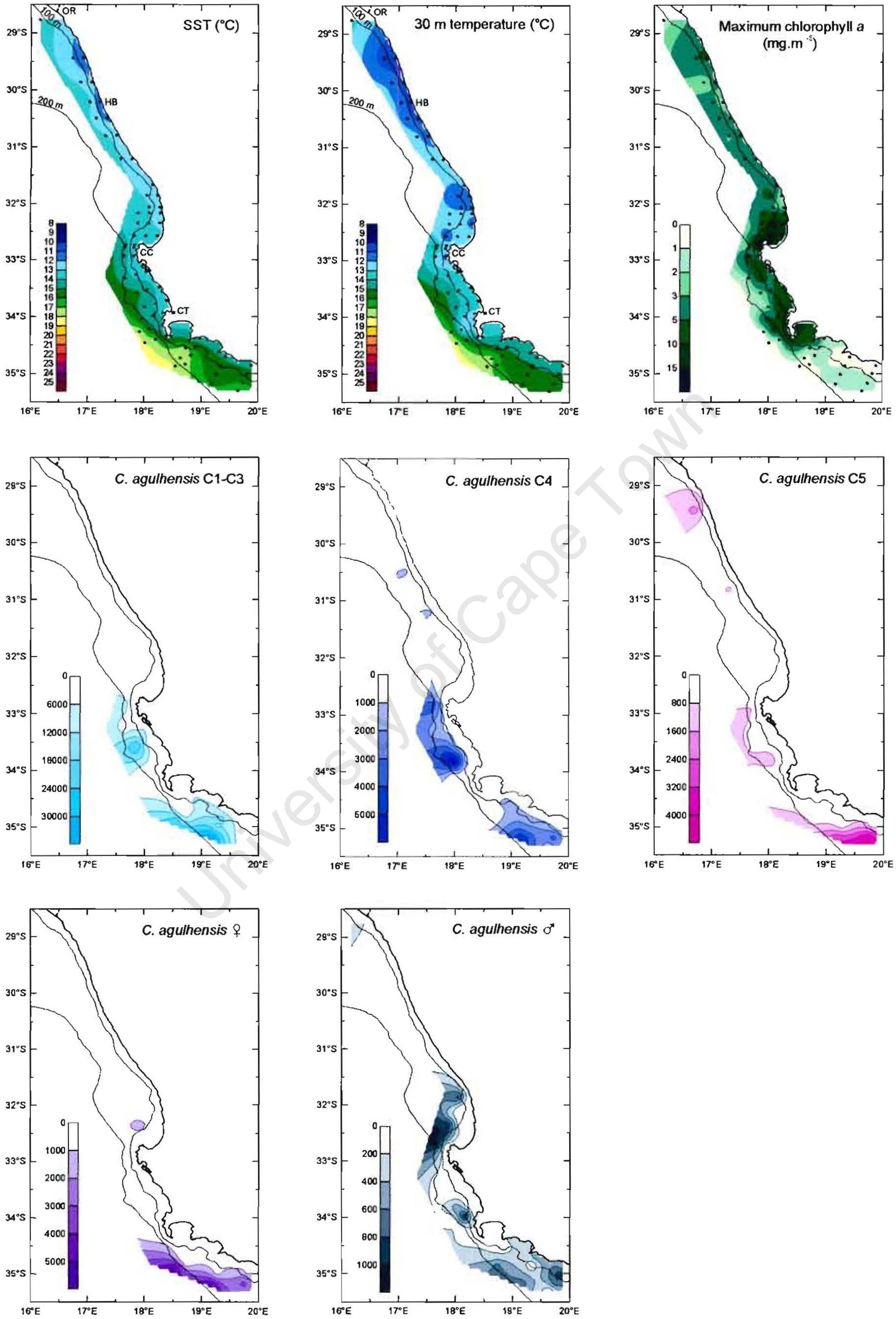




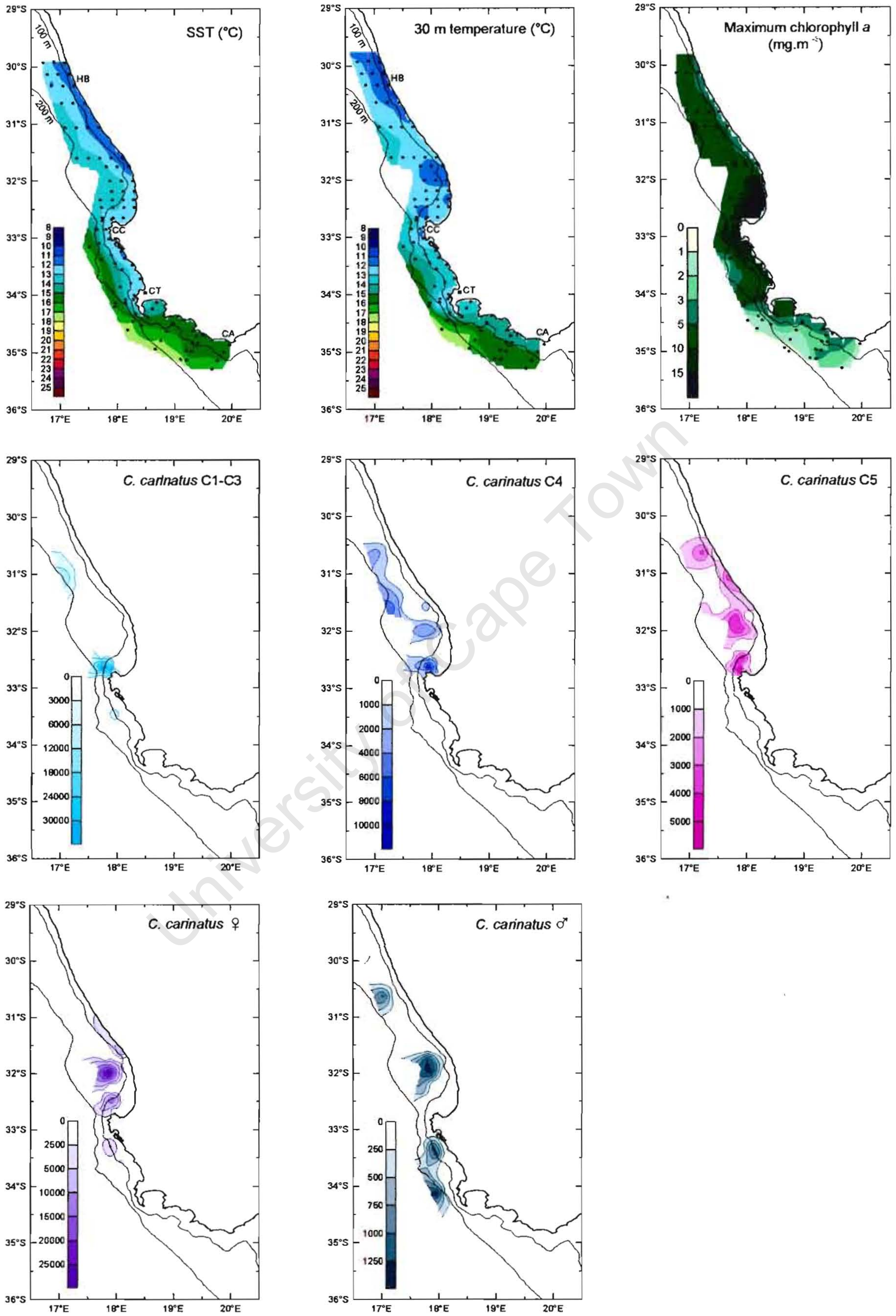
JUNE 1988 – *C. carinatus*



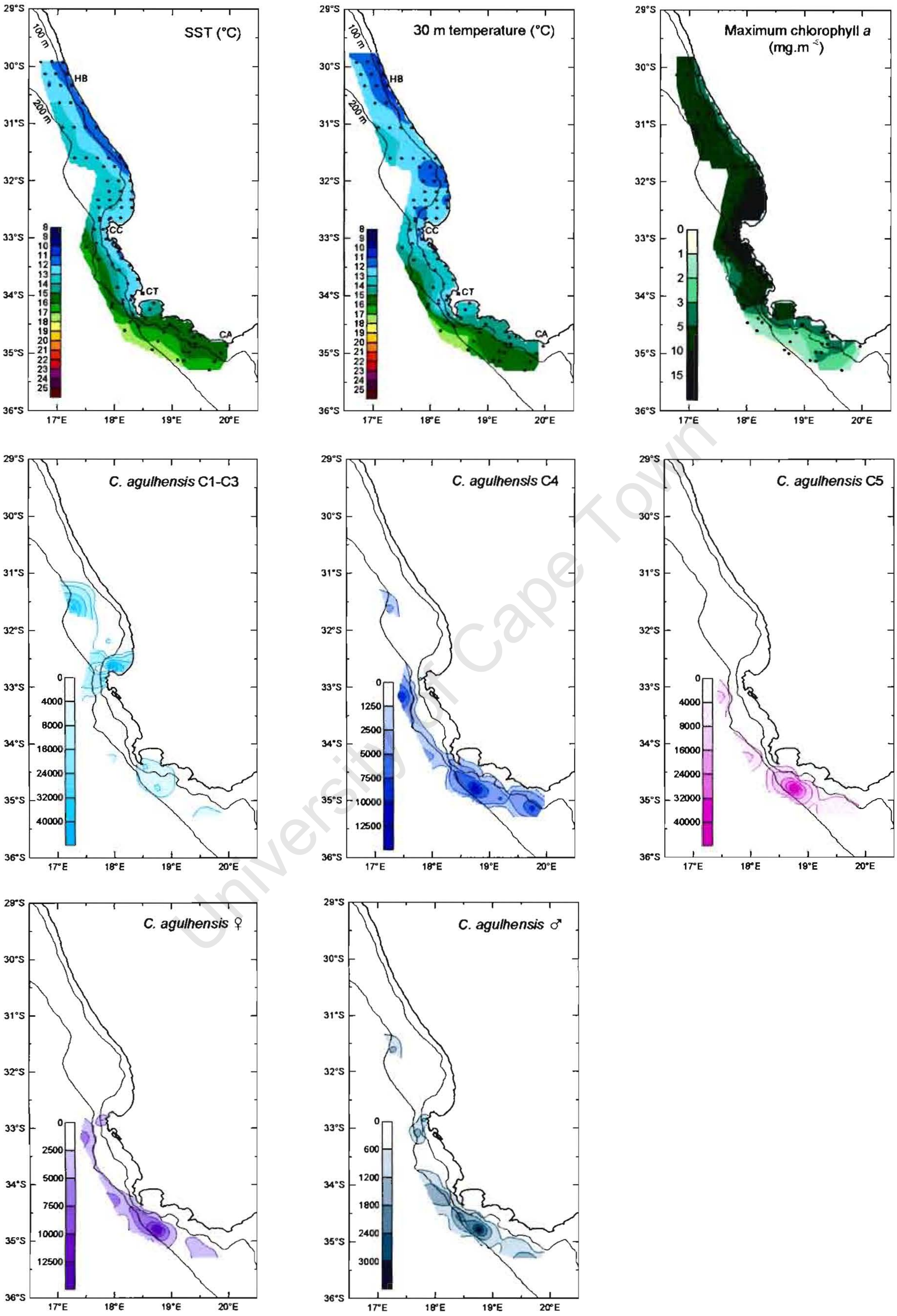
JUNE 1988 – *C. agulhensis*



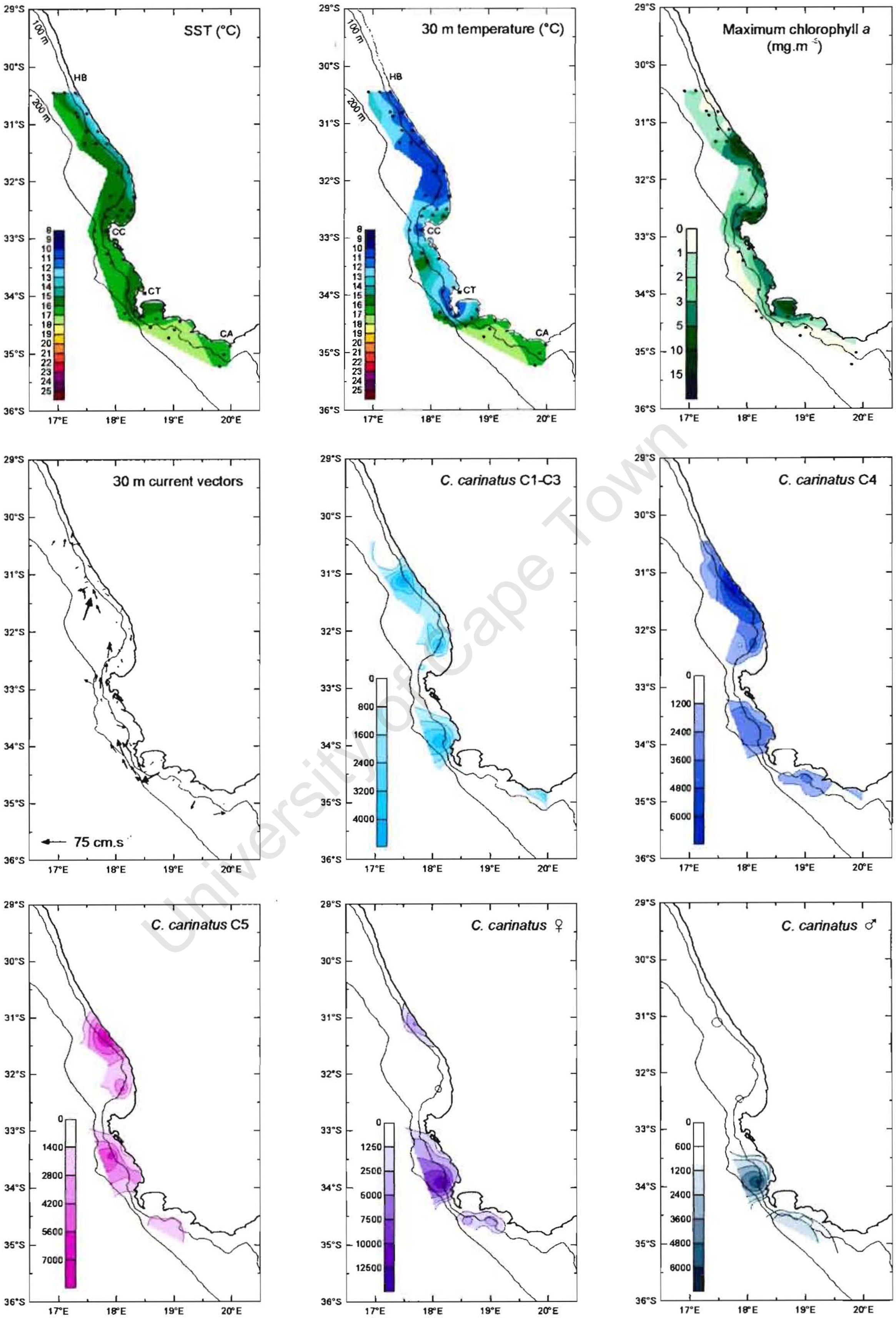
JUNE 1989 – *C. carinatus*



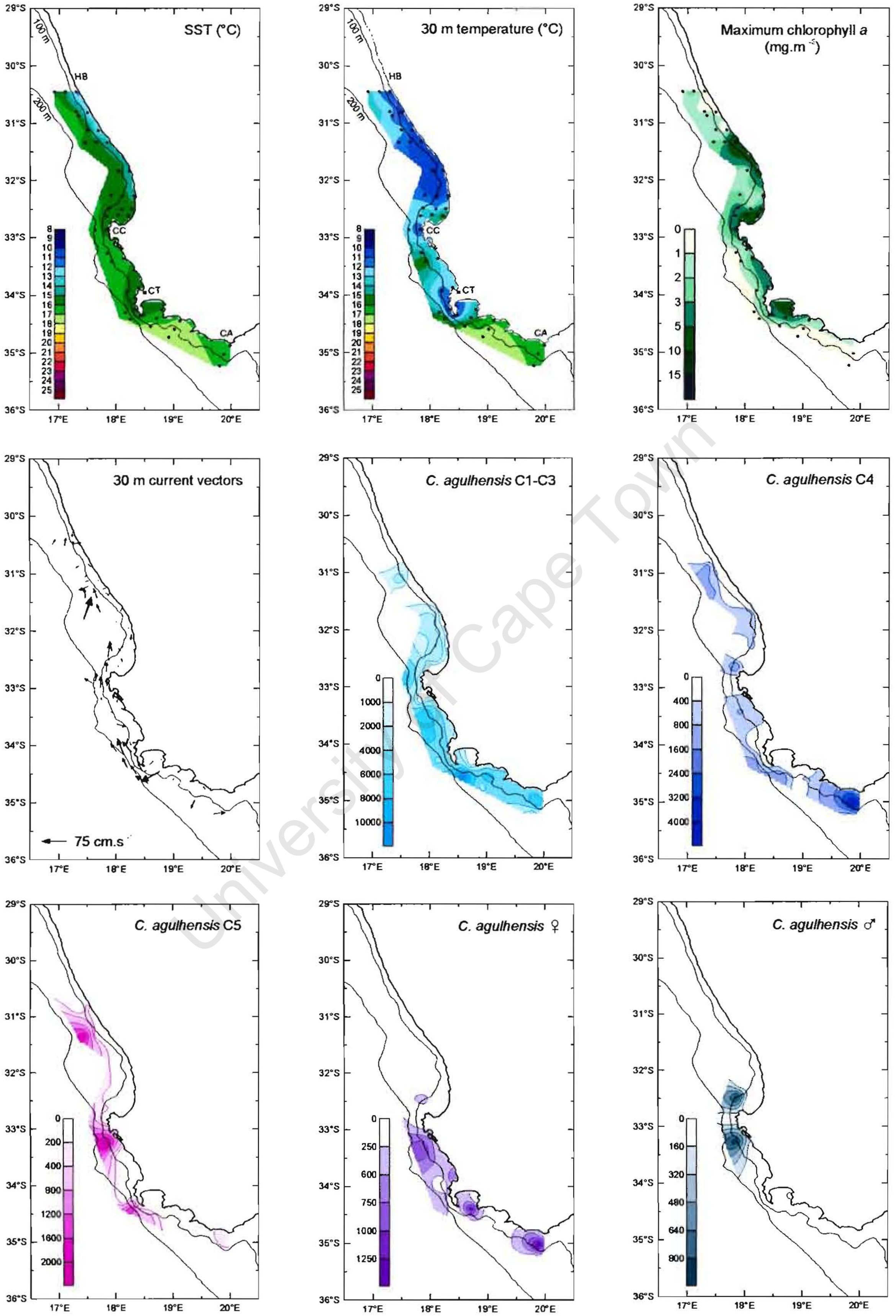
JUNE 1989 – *C. agulhensis*



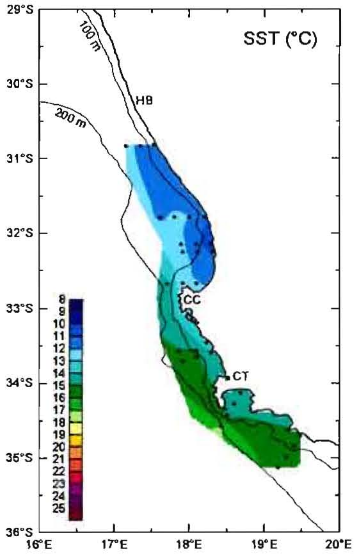
MAY 1990 – *C. carinatus*

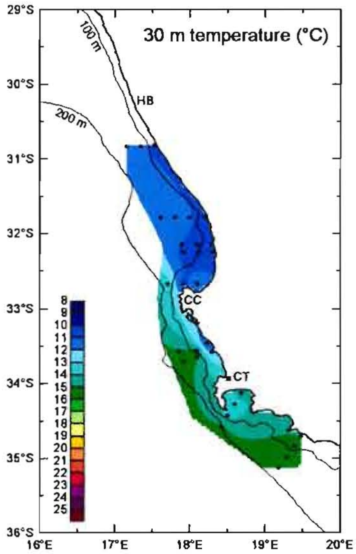


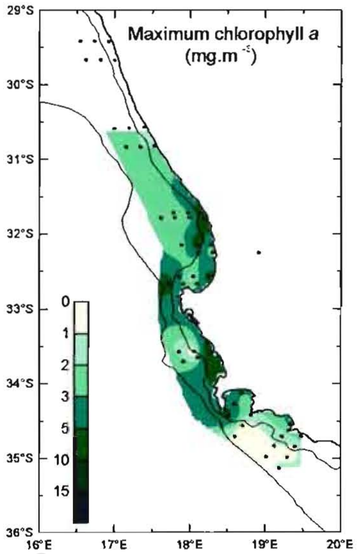
MAY 1990 – *C. agulhensis*

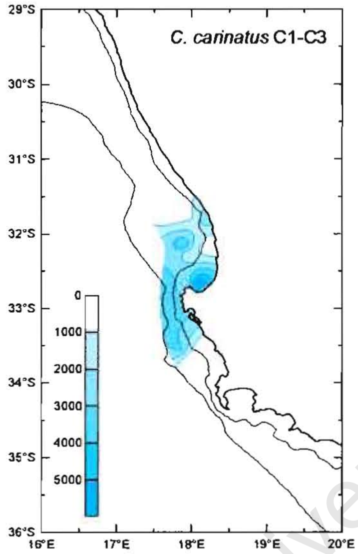


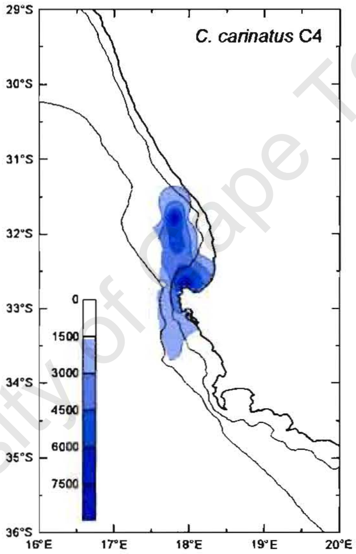
JUNE 1990 – *C. carinatus*

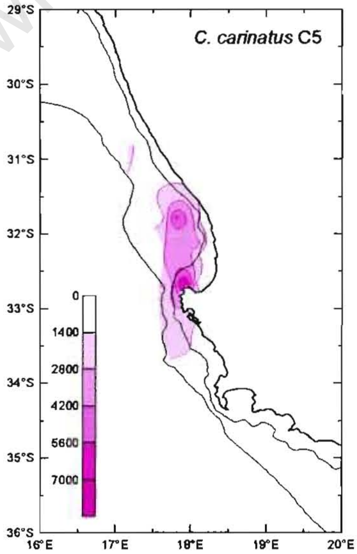


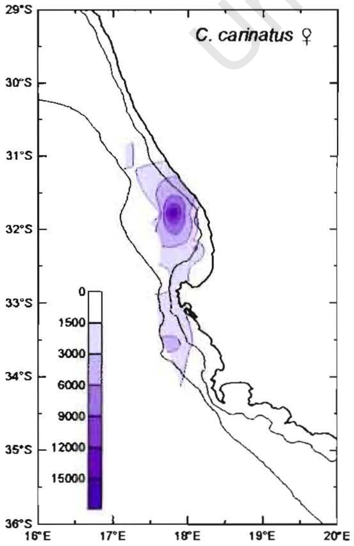


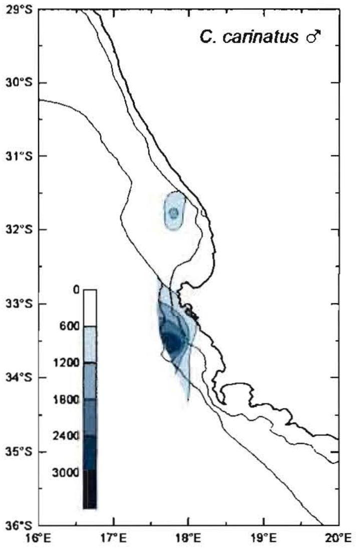




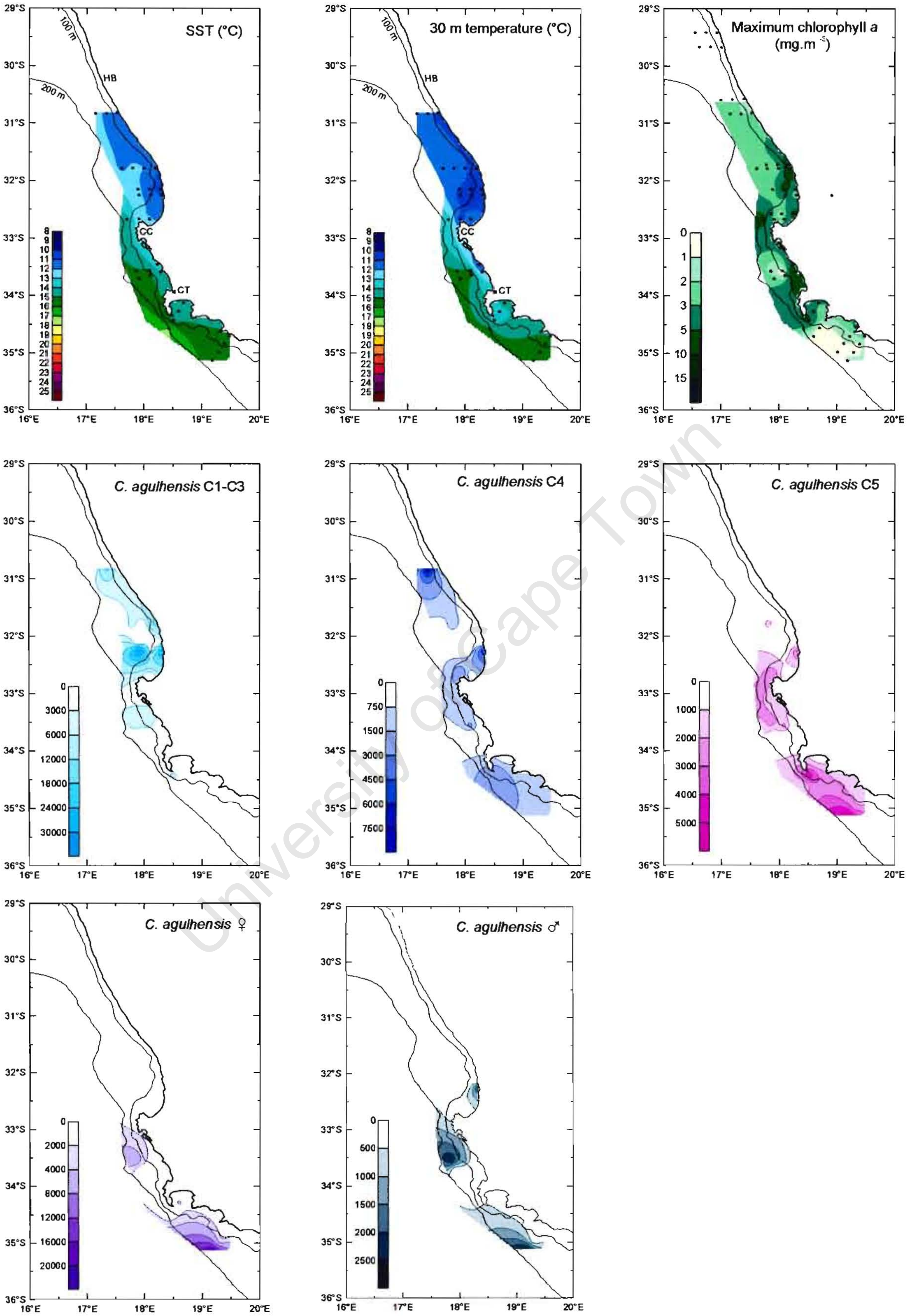




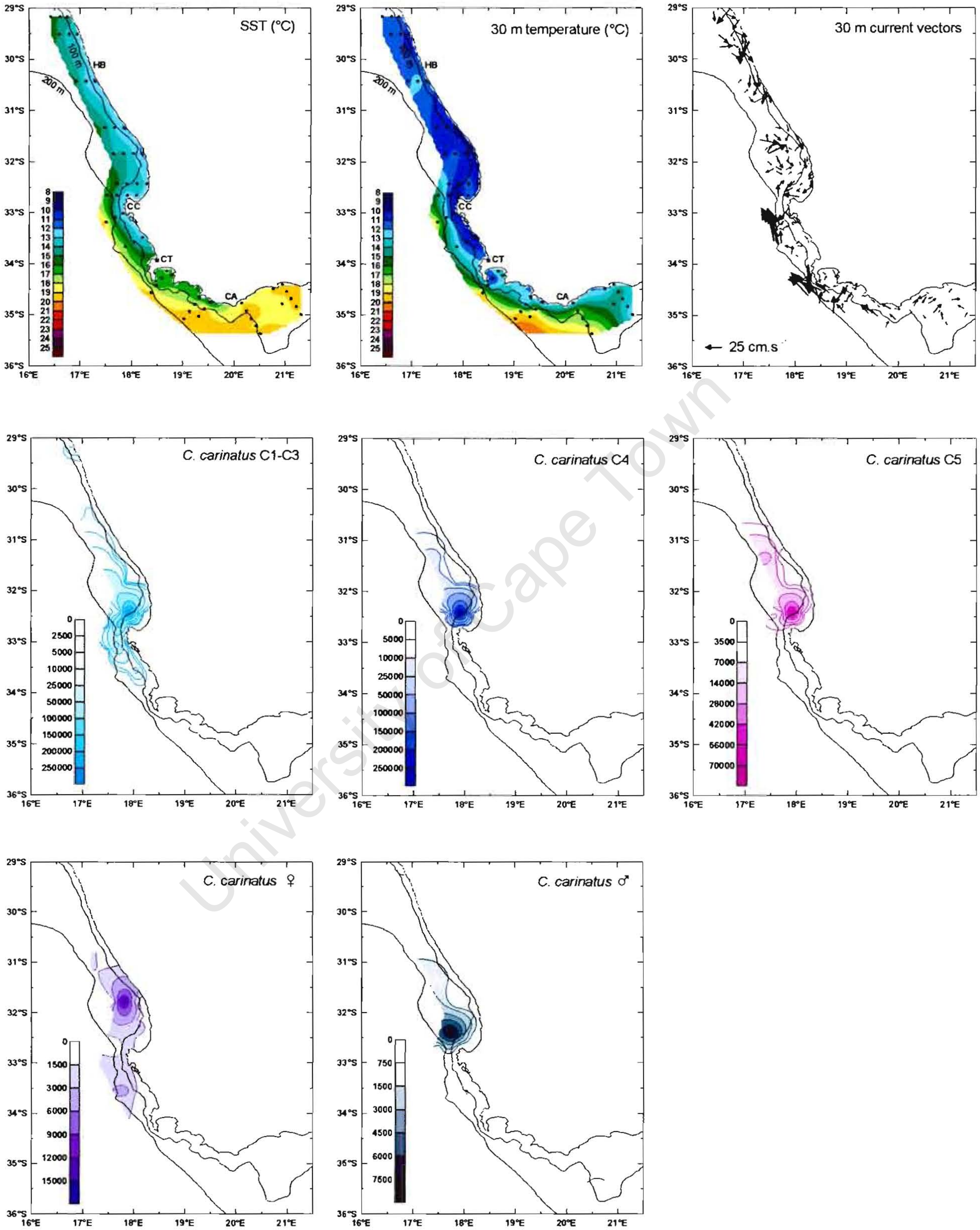




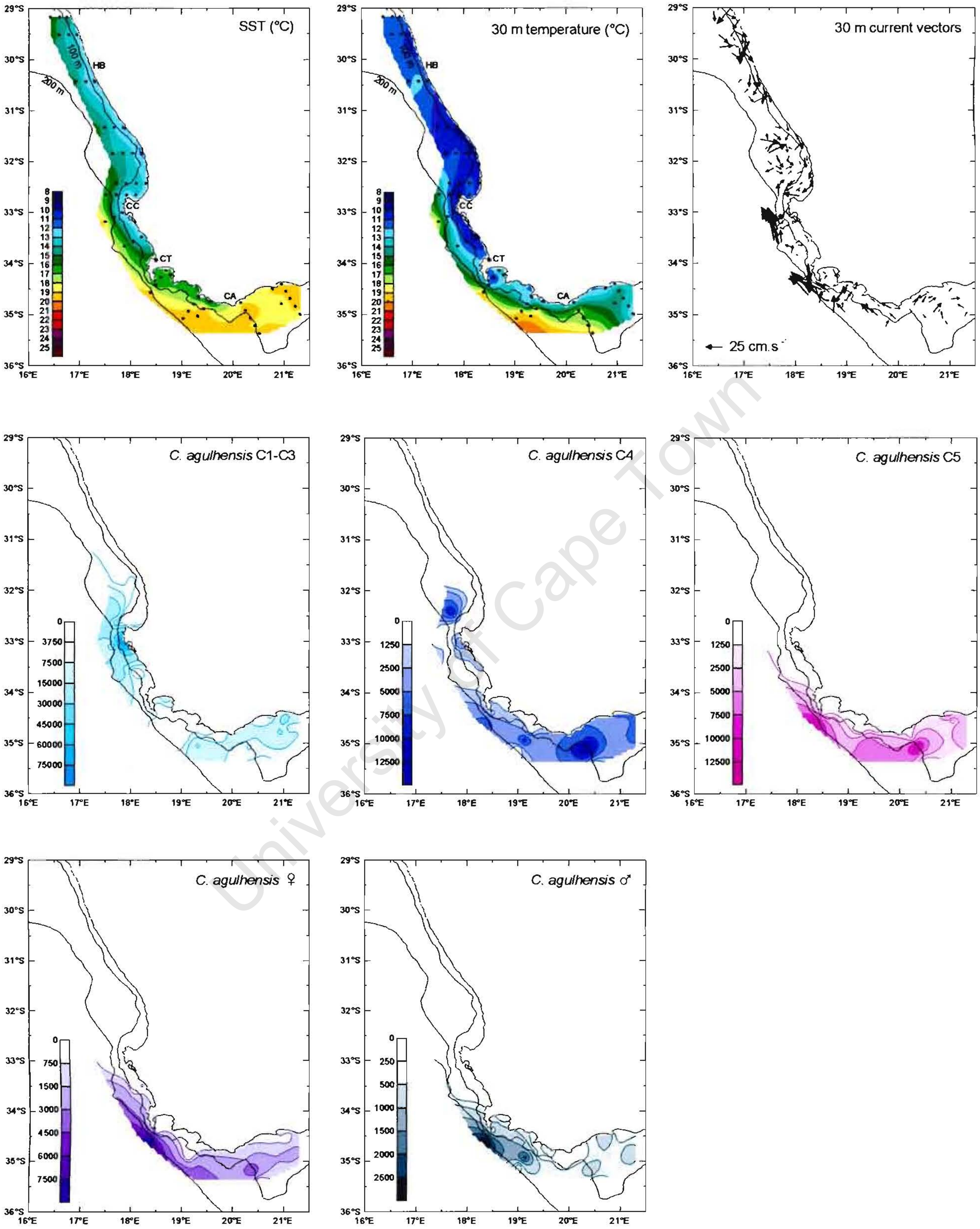
JUNE 1990 – *C. agulhensis*



MAY 1991 – *C. carinatus*



MAY 1991 – *C. agulhensis*



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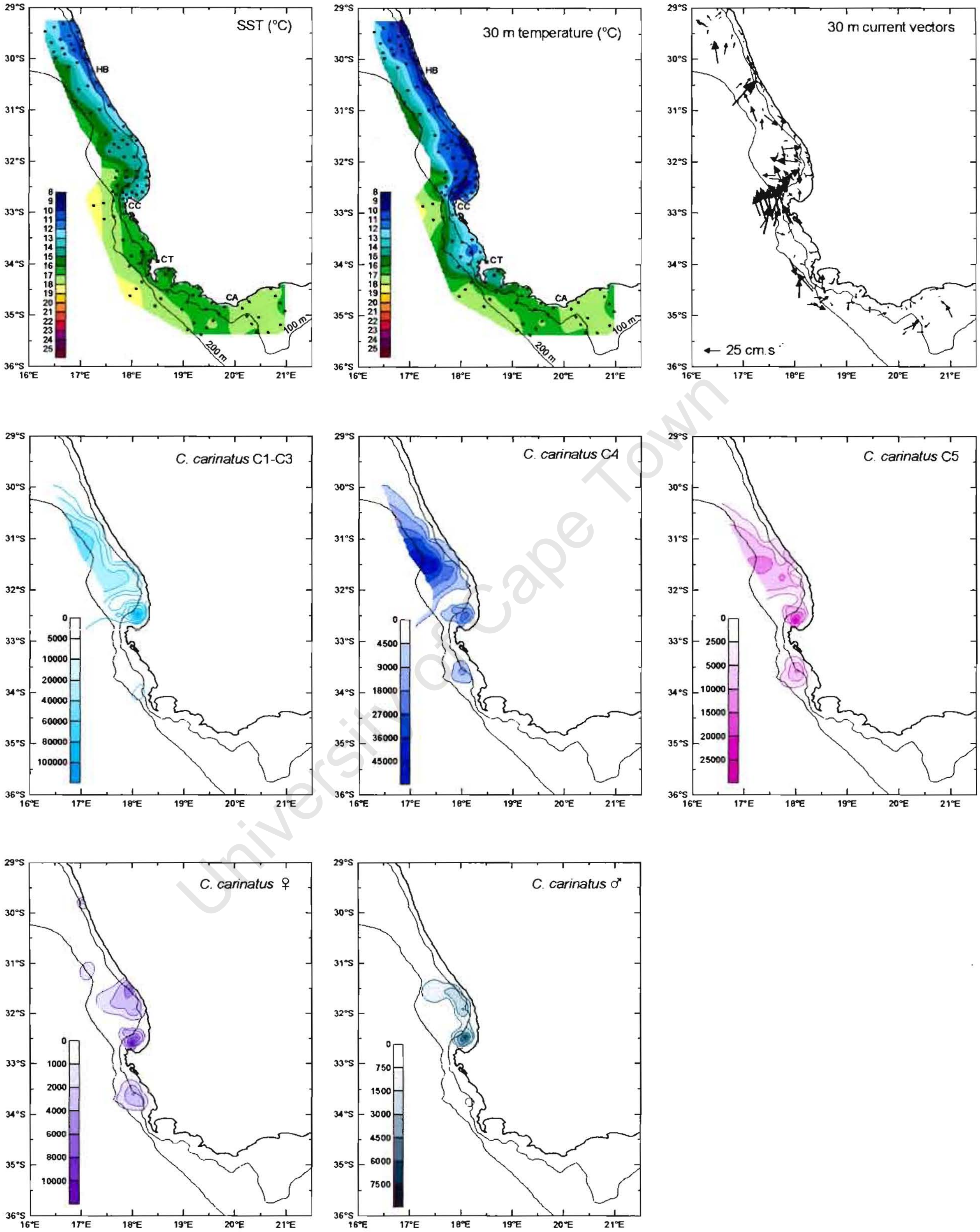

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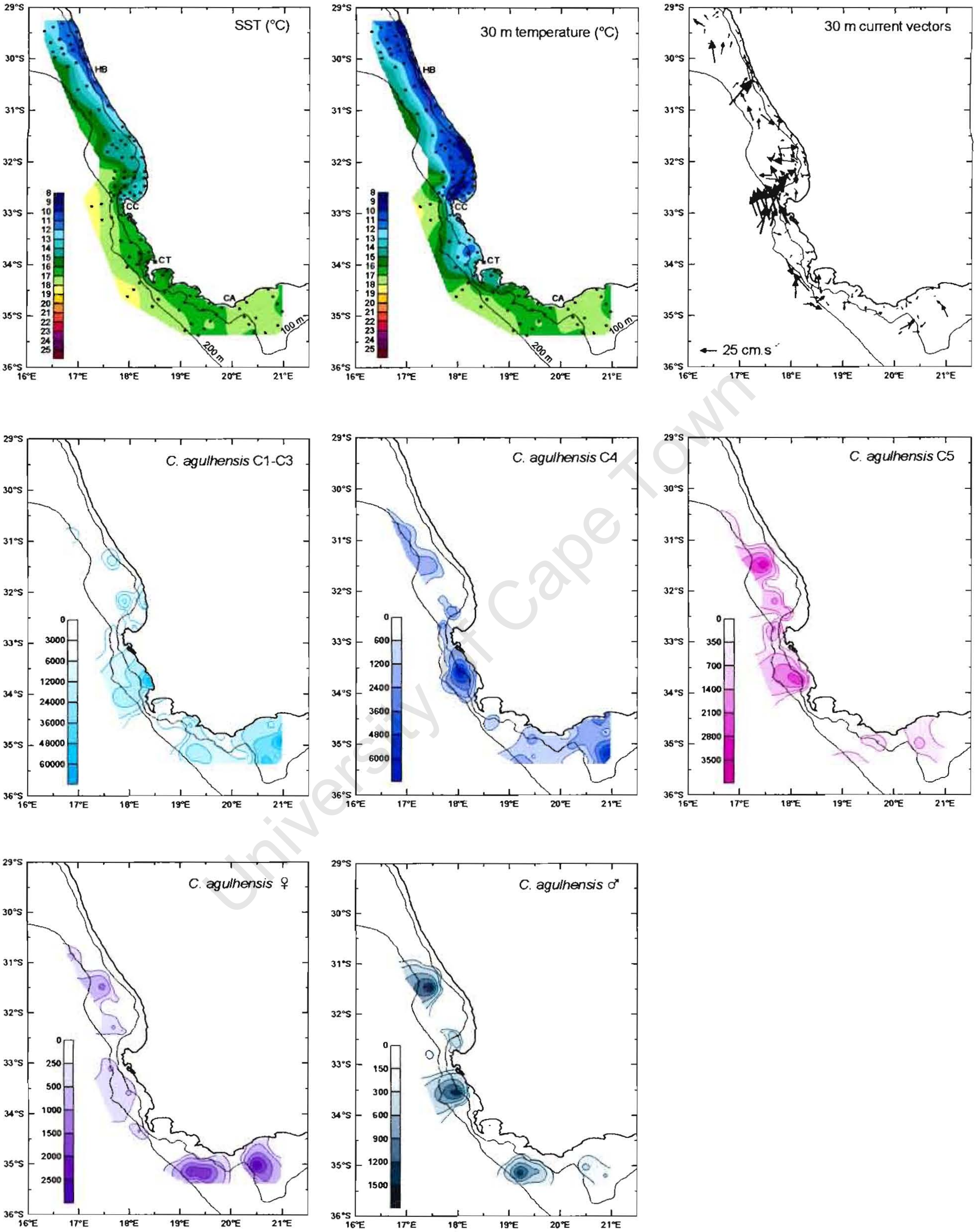

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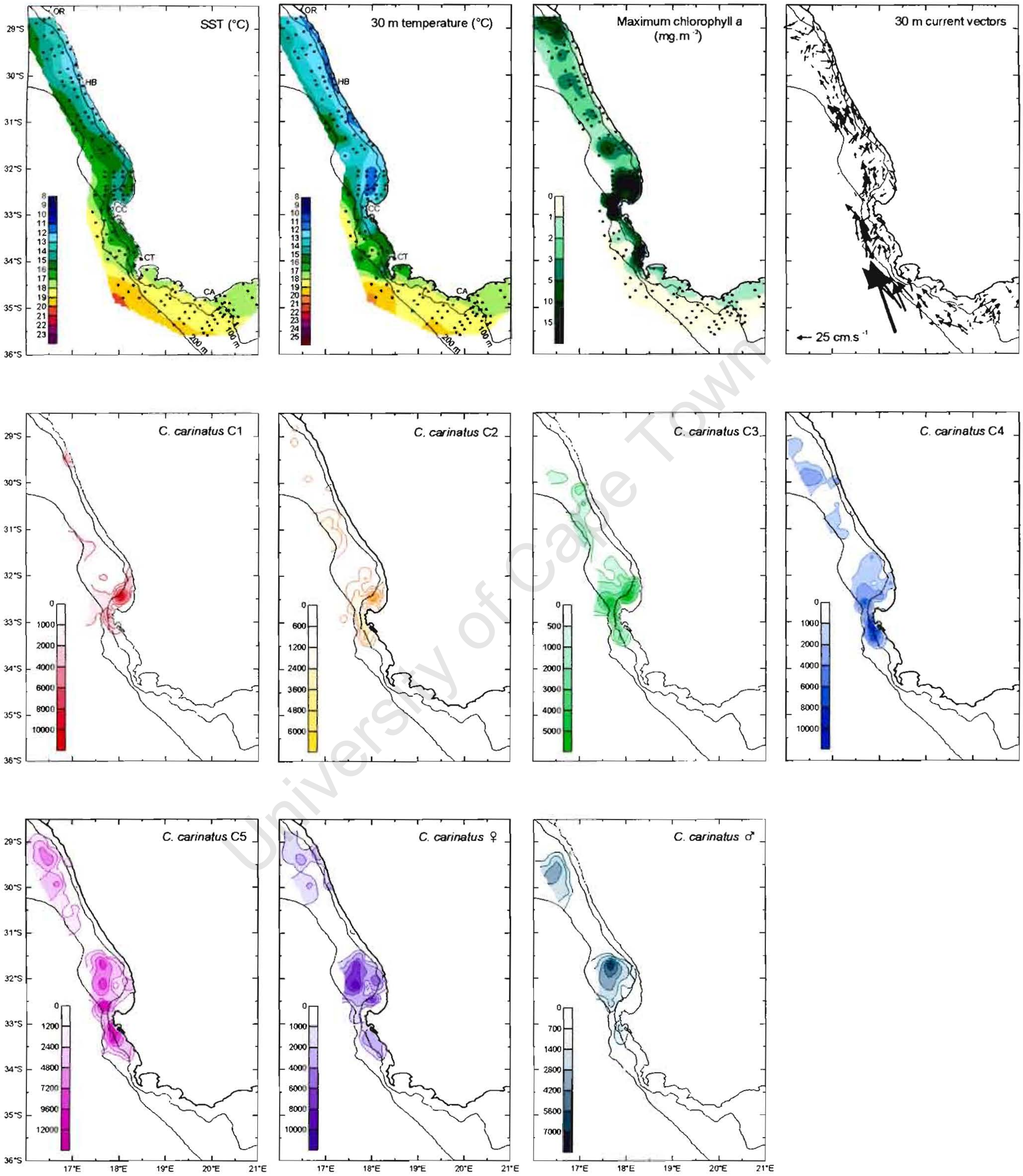

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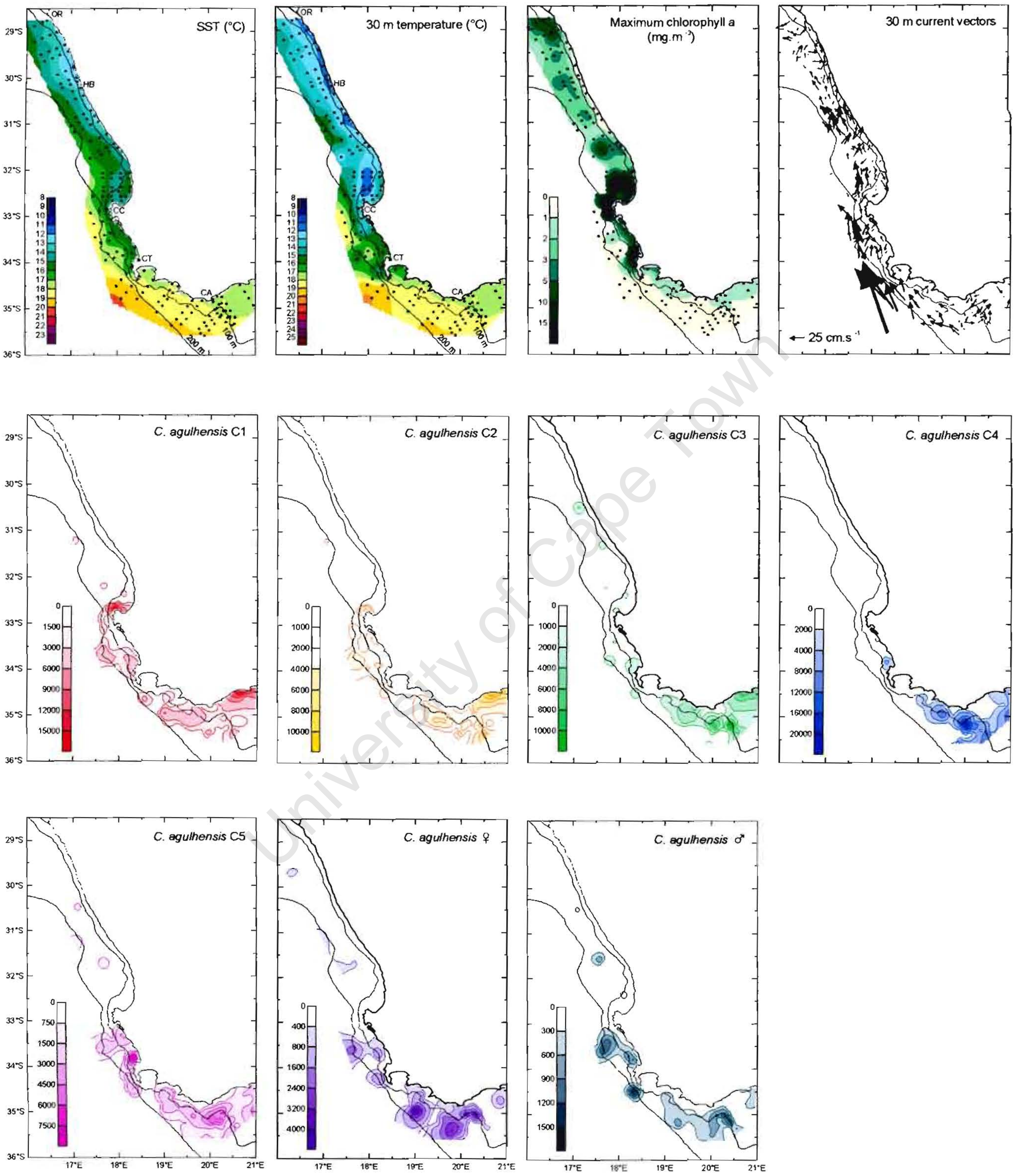

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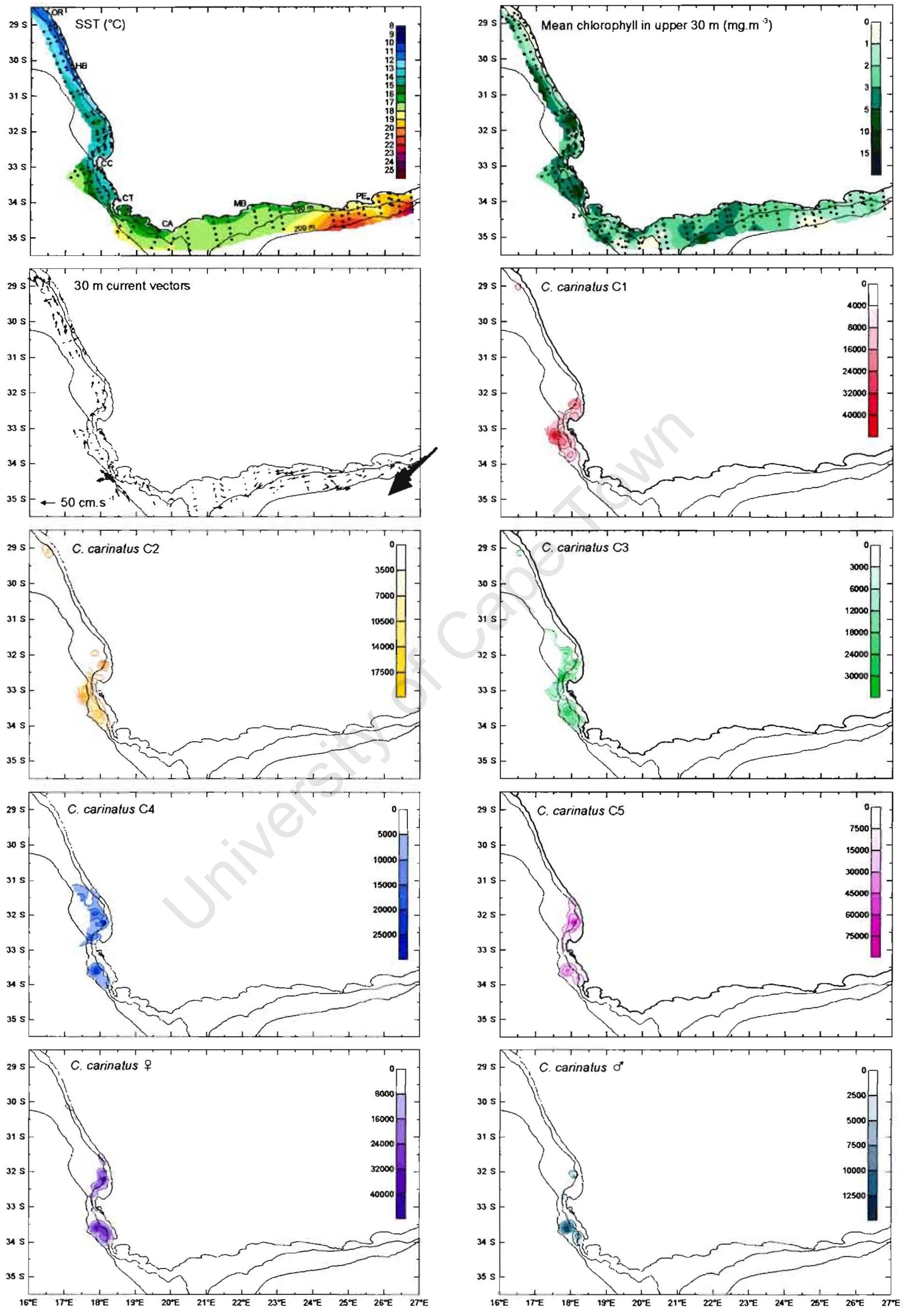

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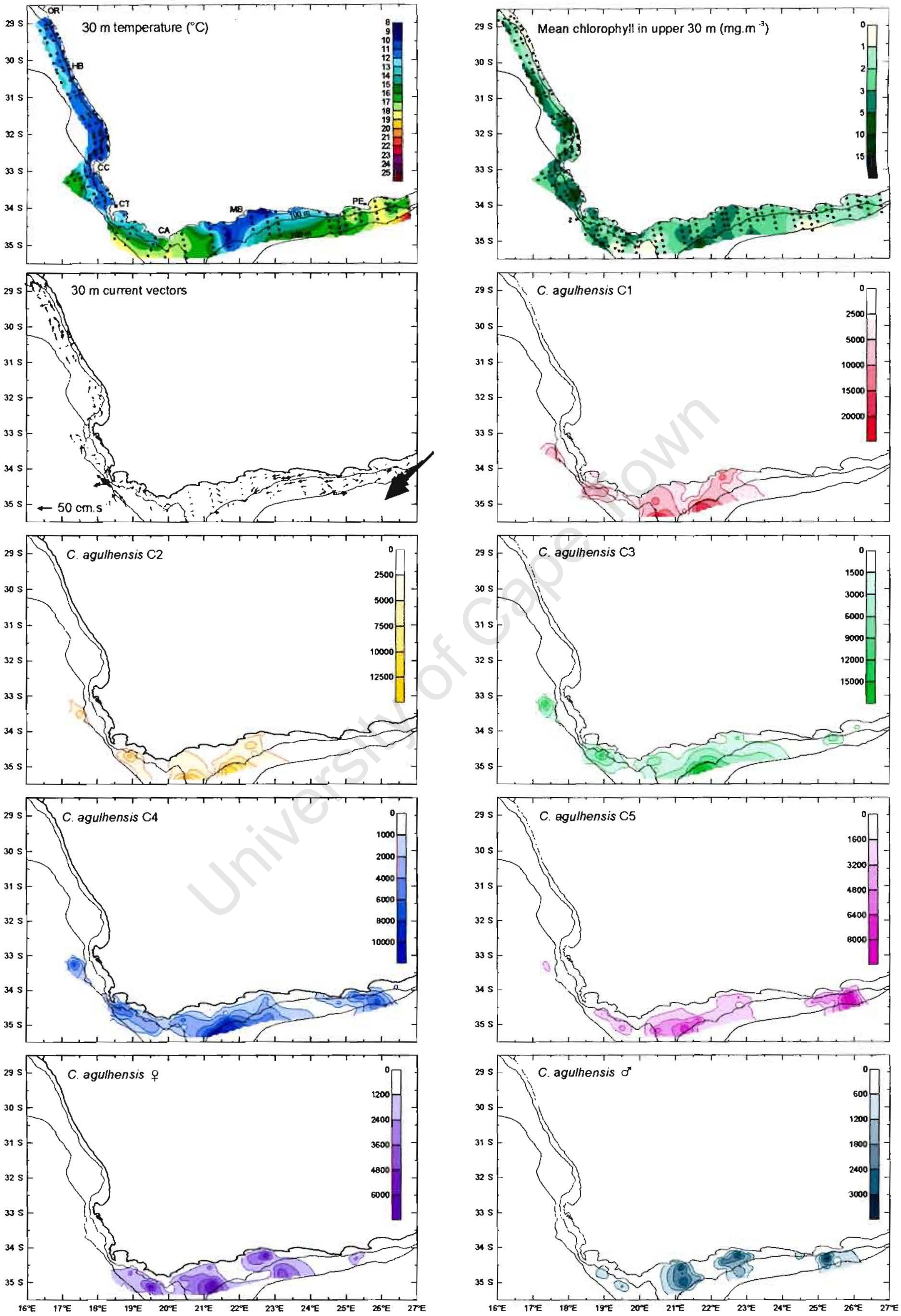
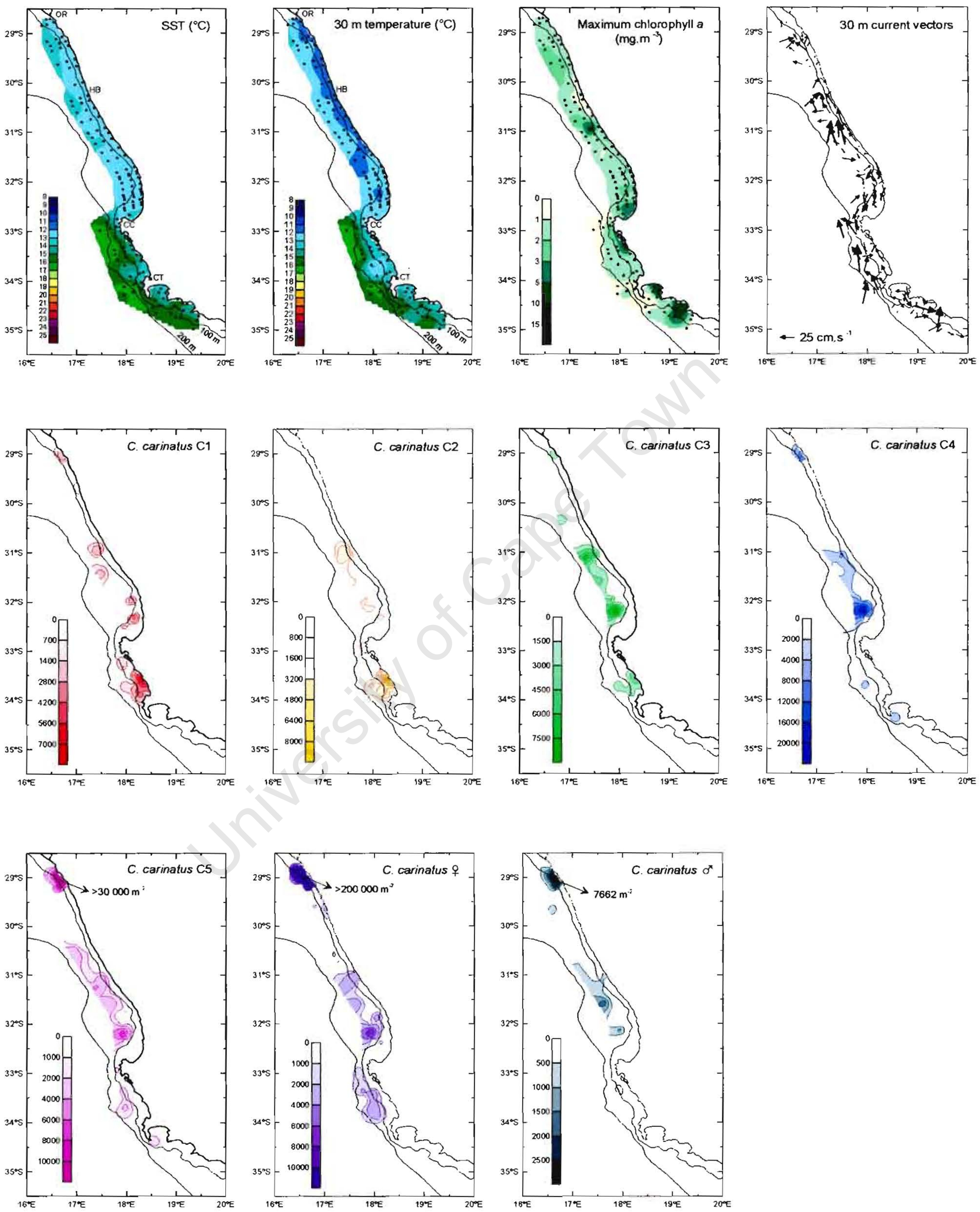


JUNE 1995 – *C. carinatus*



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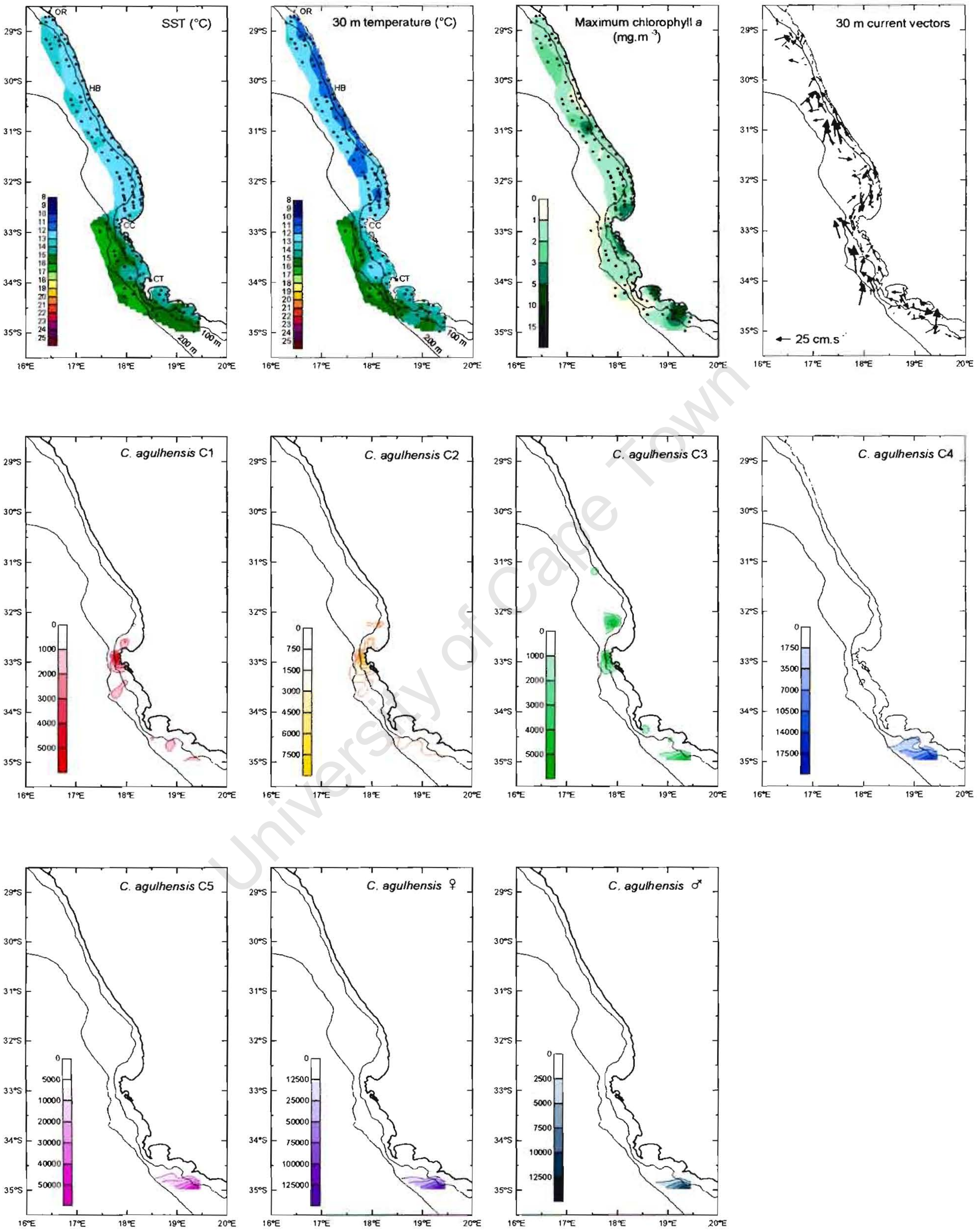

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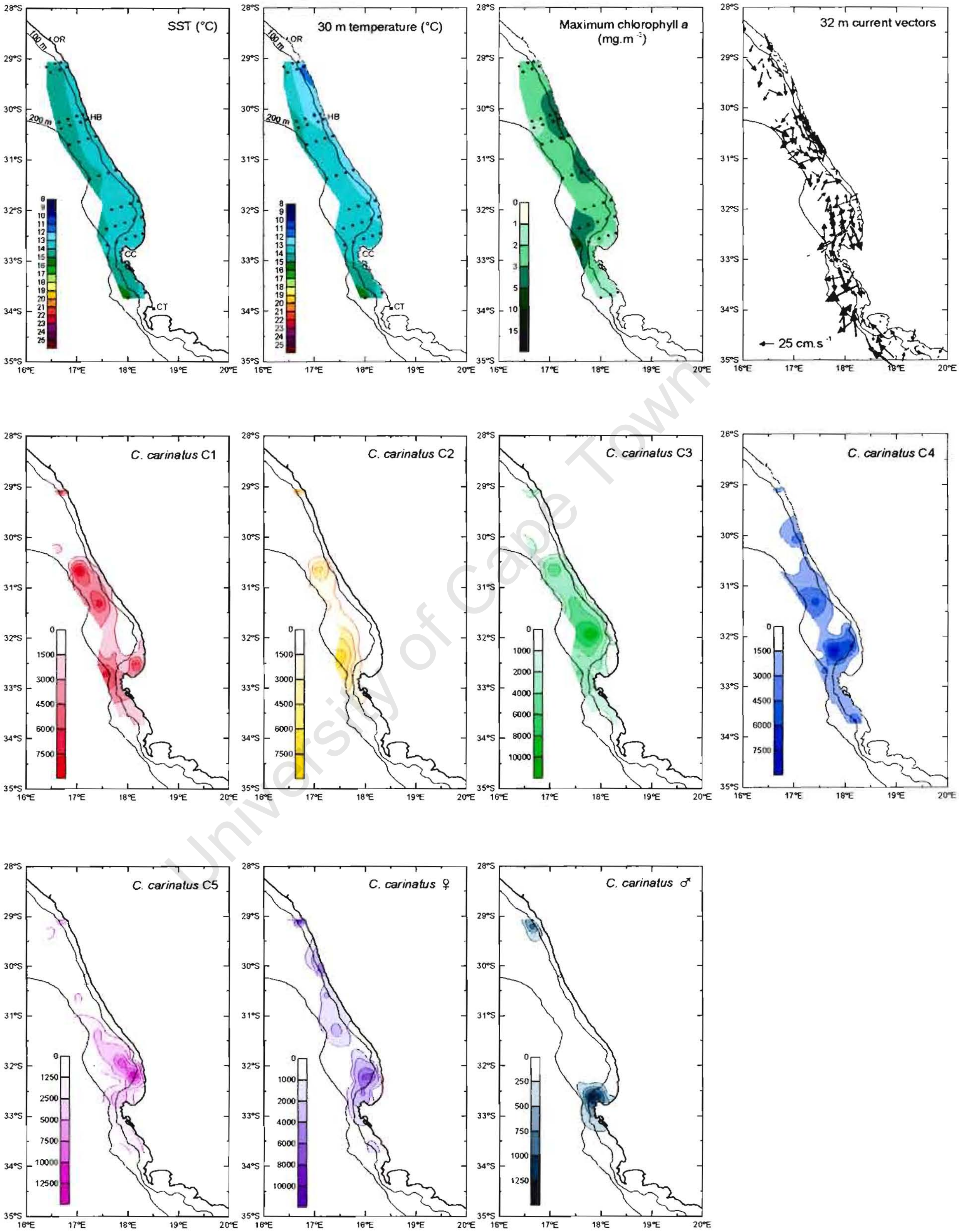

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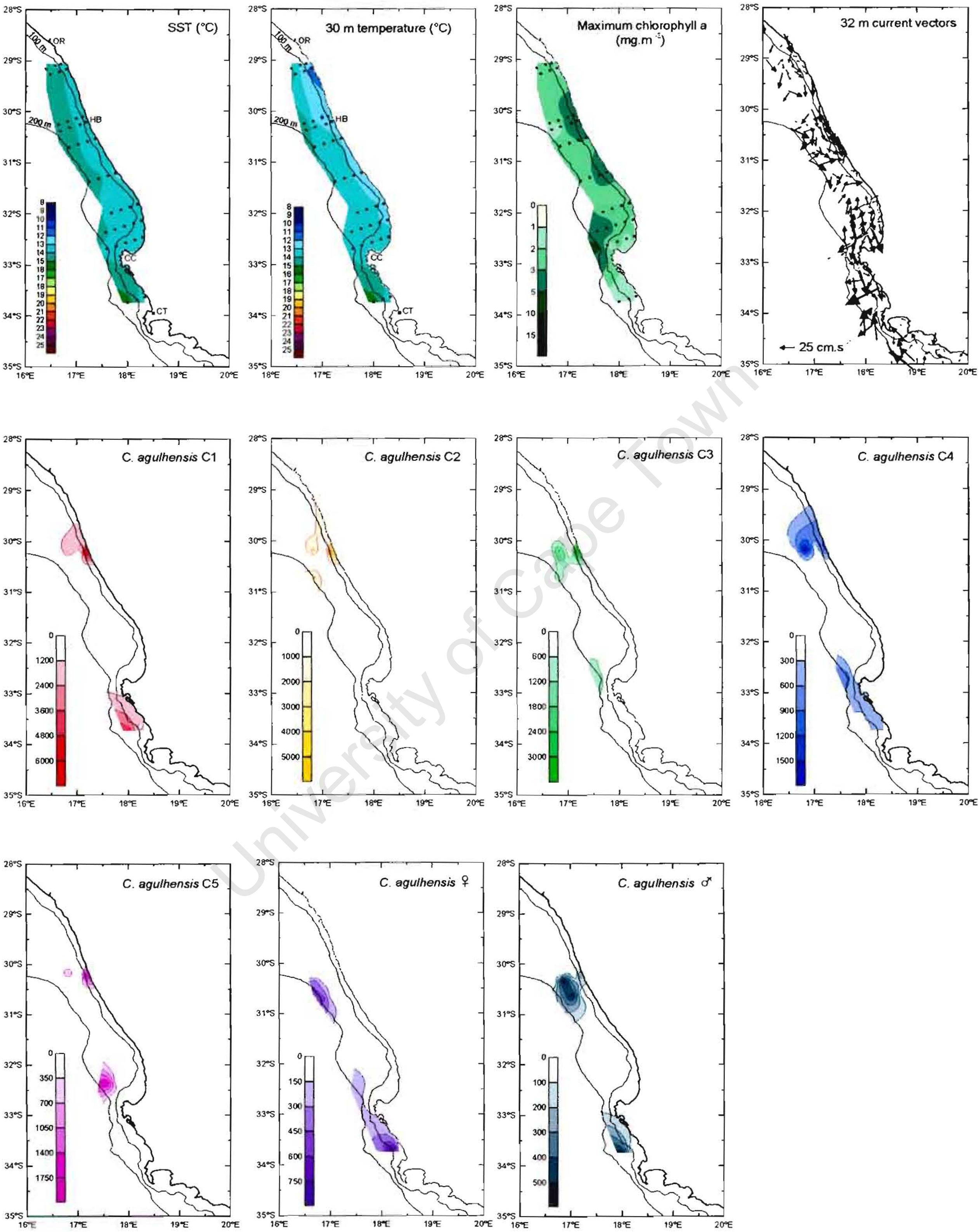

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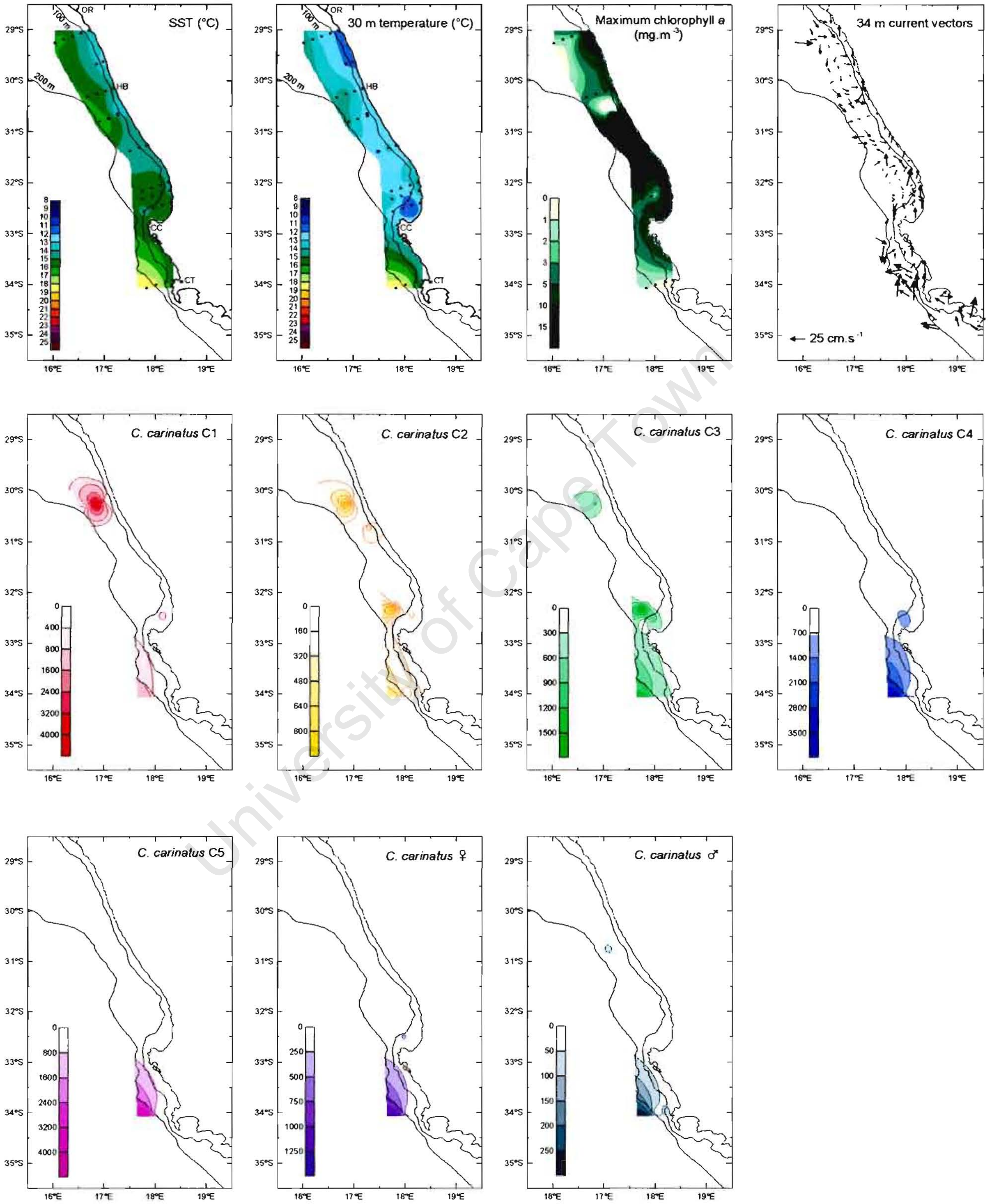

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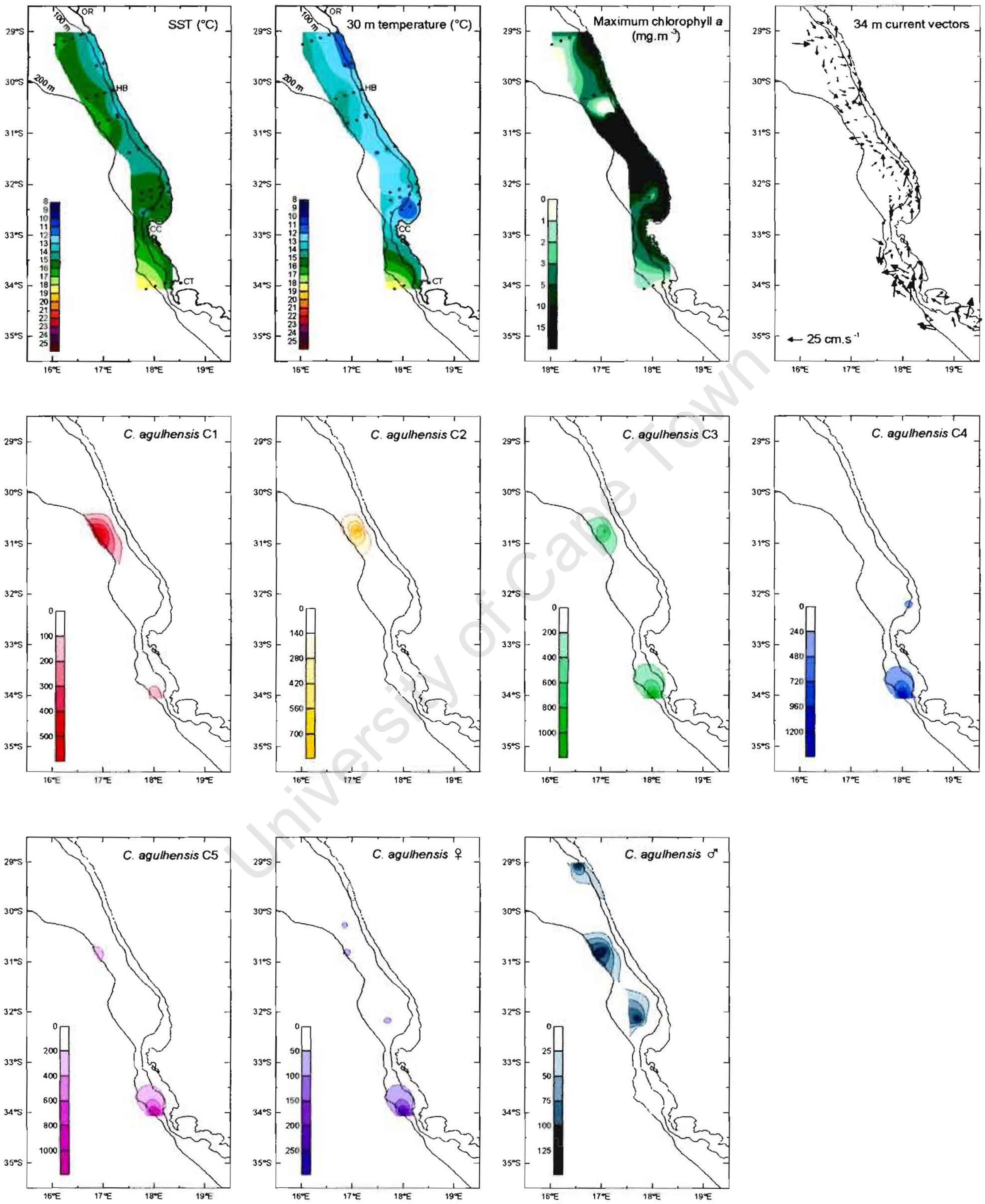

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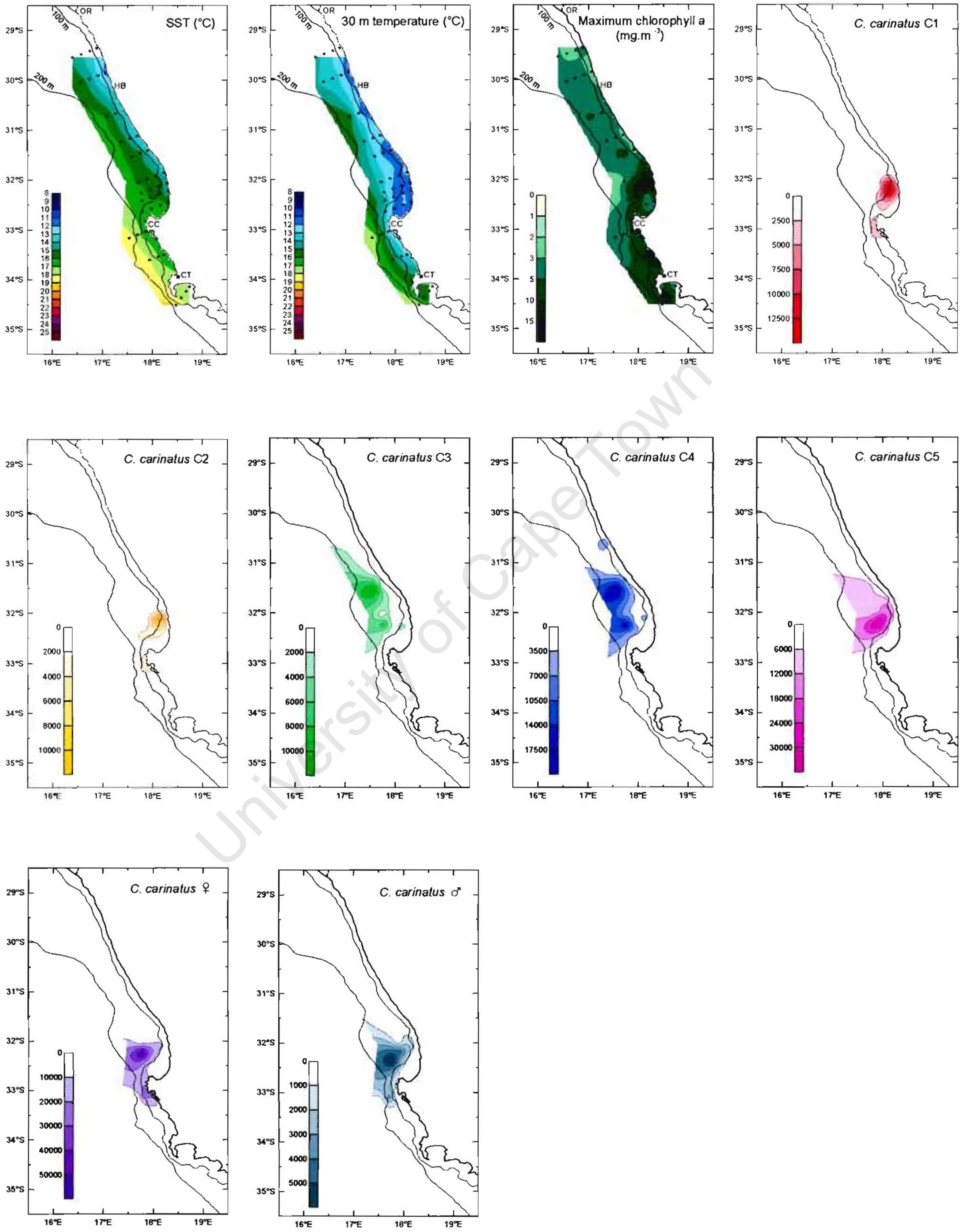

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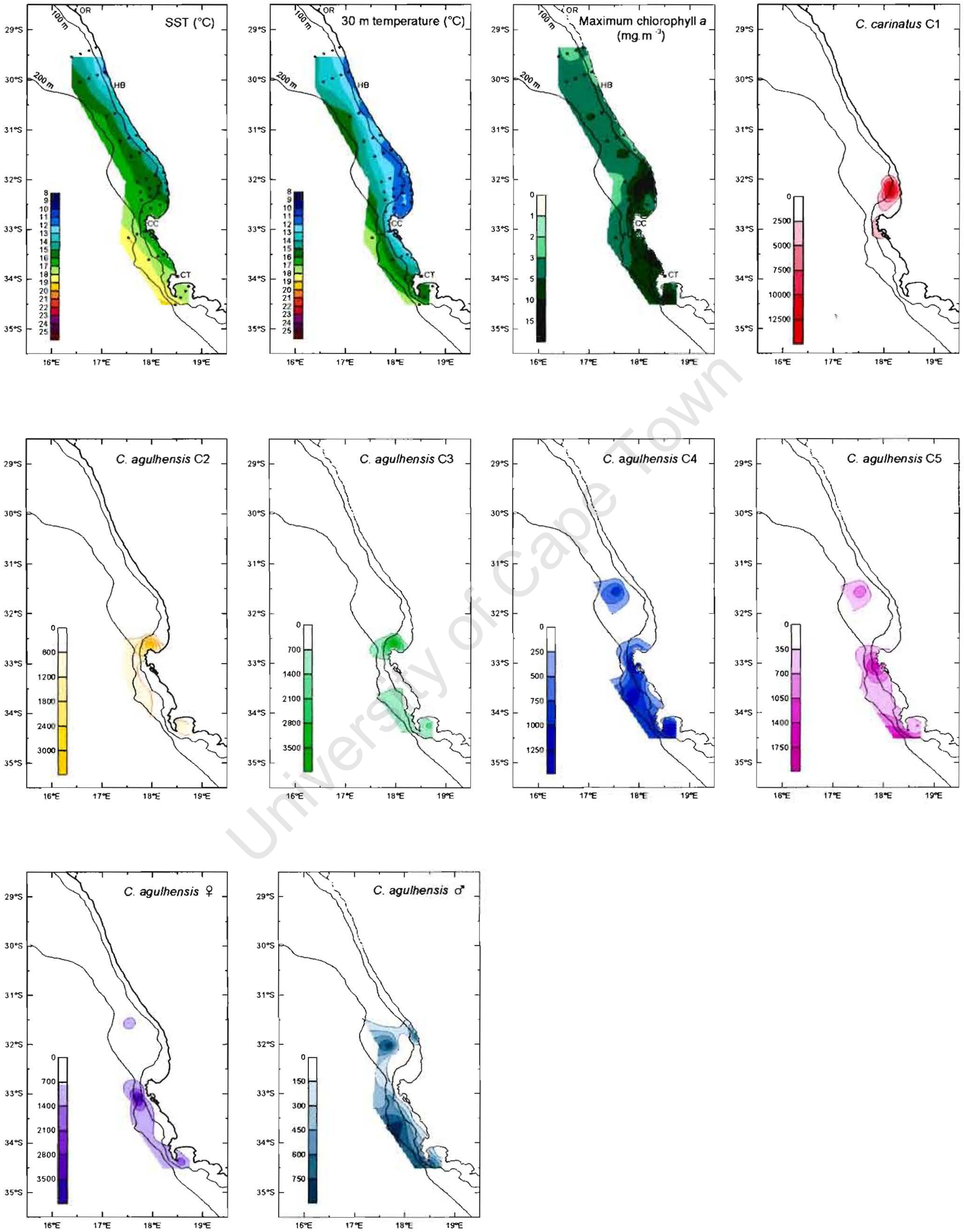

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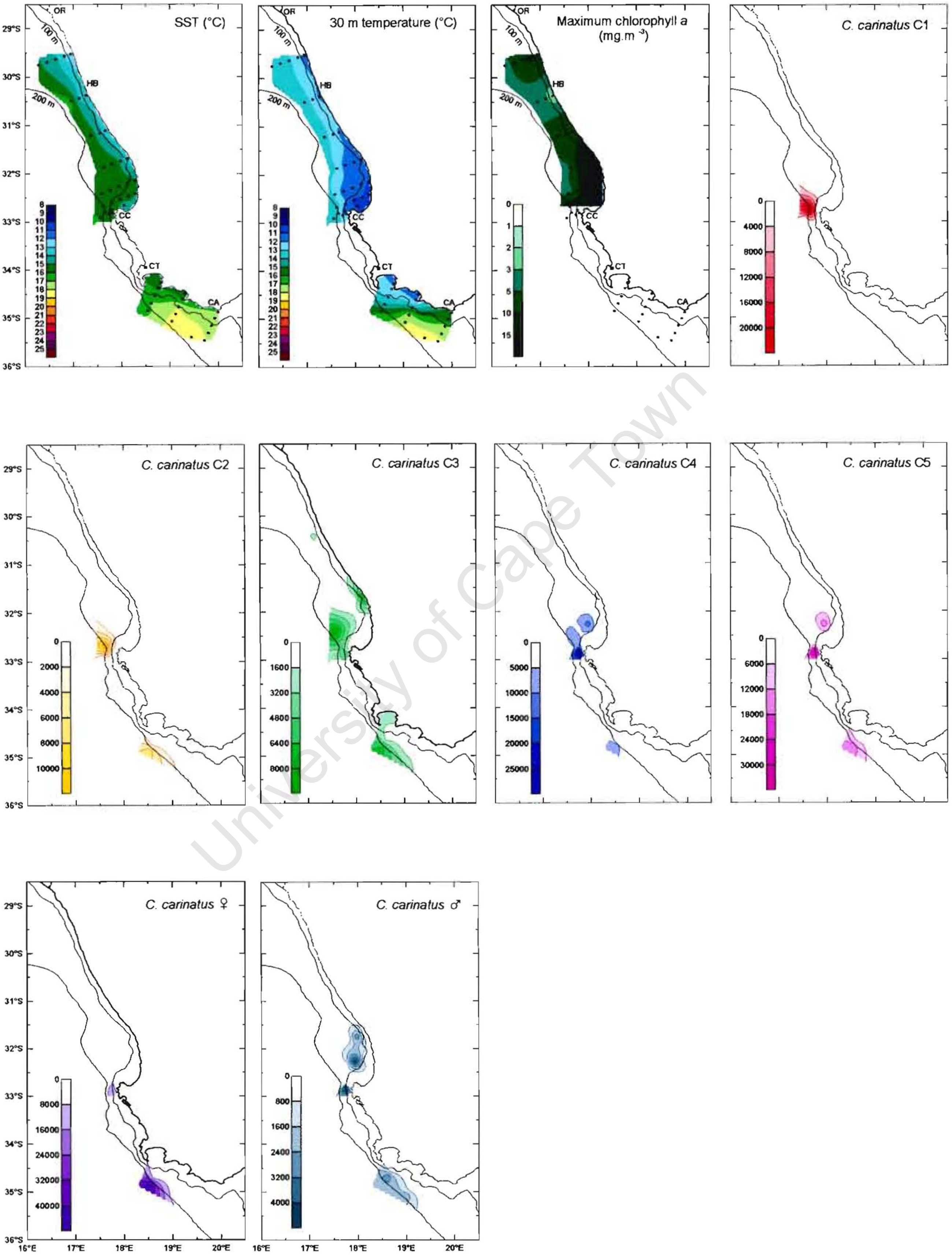
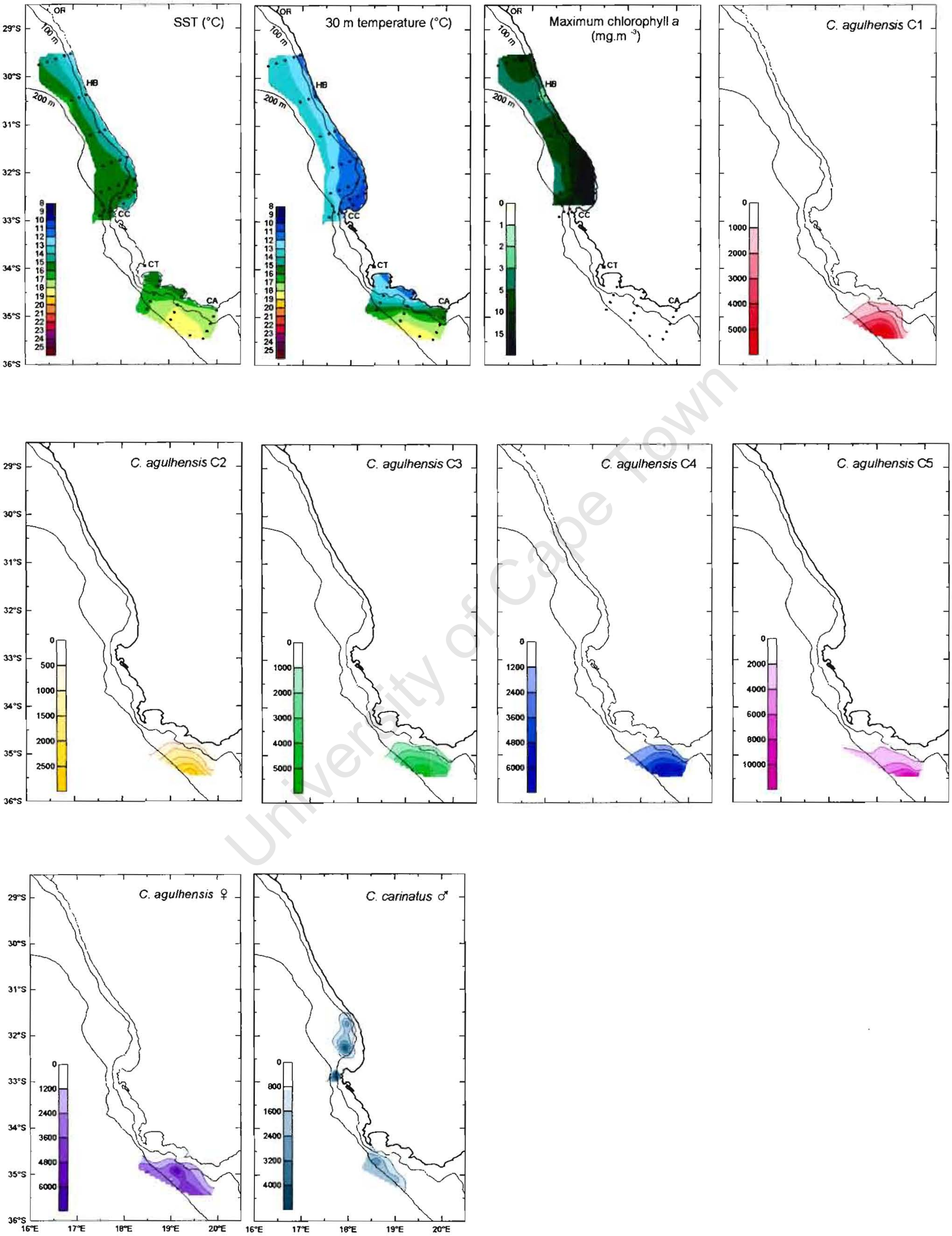
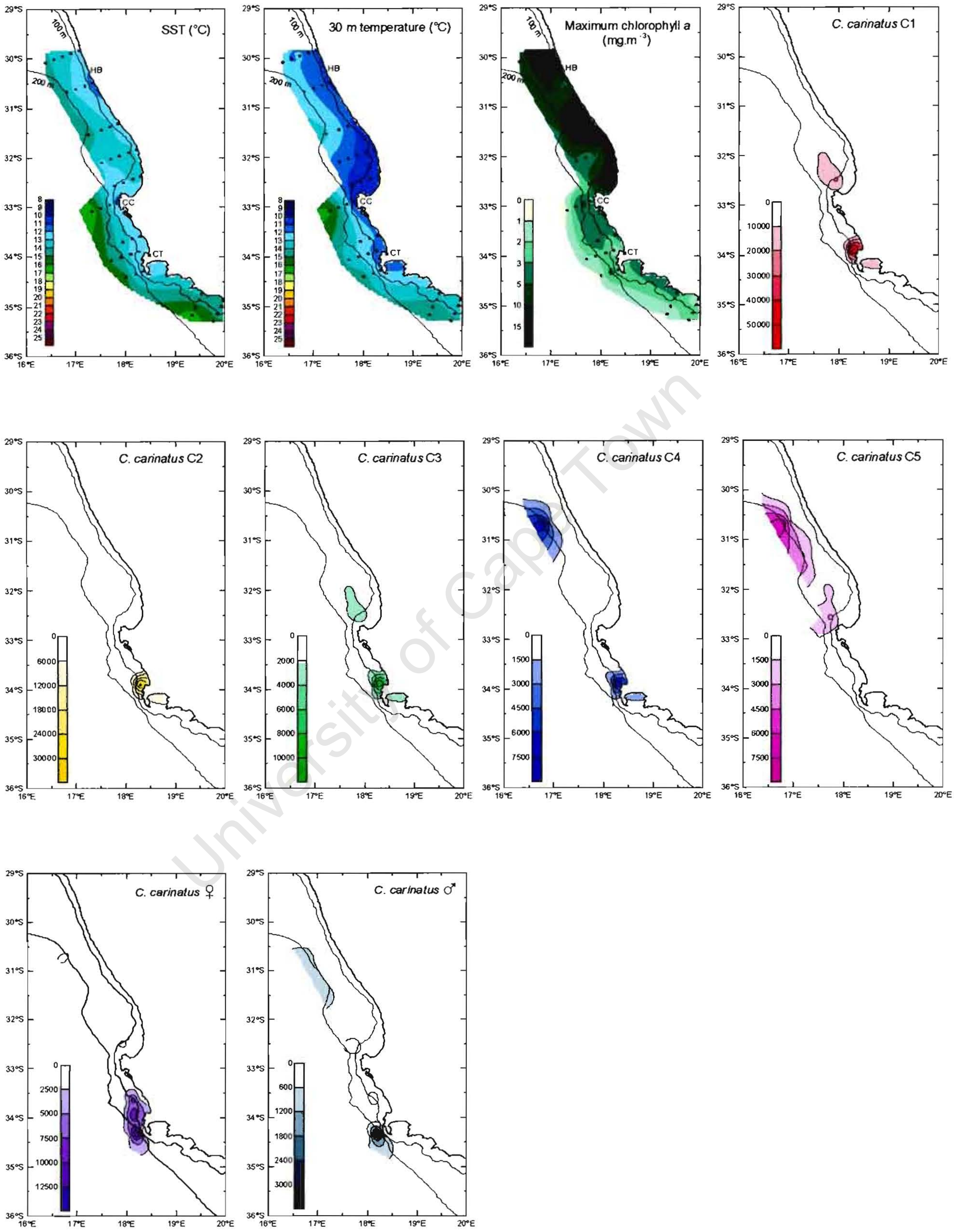


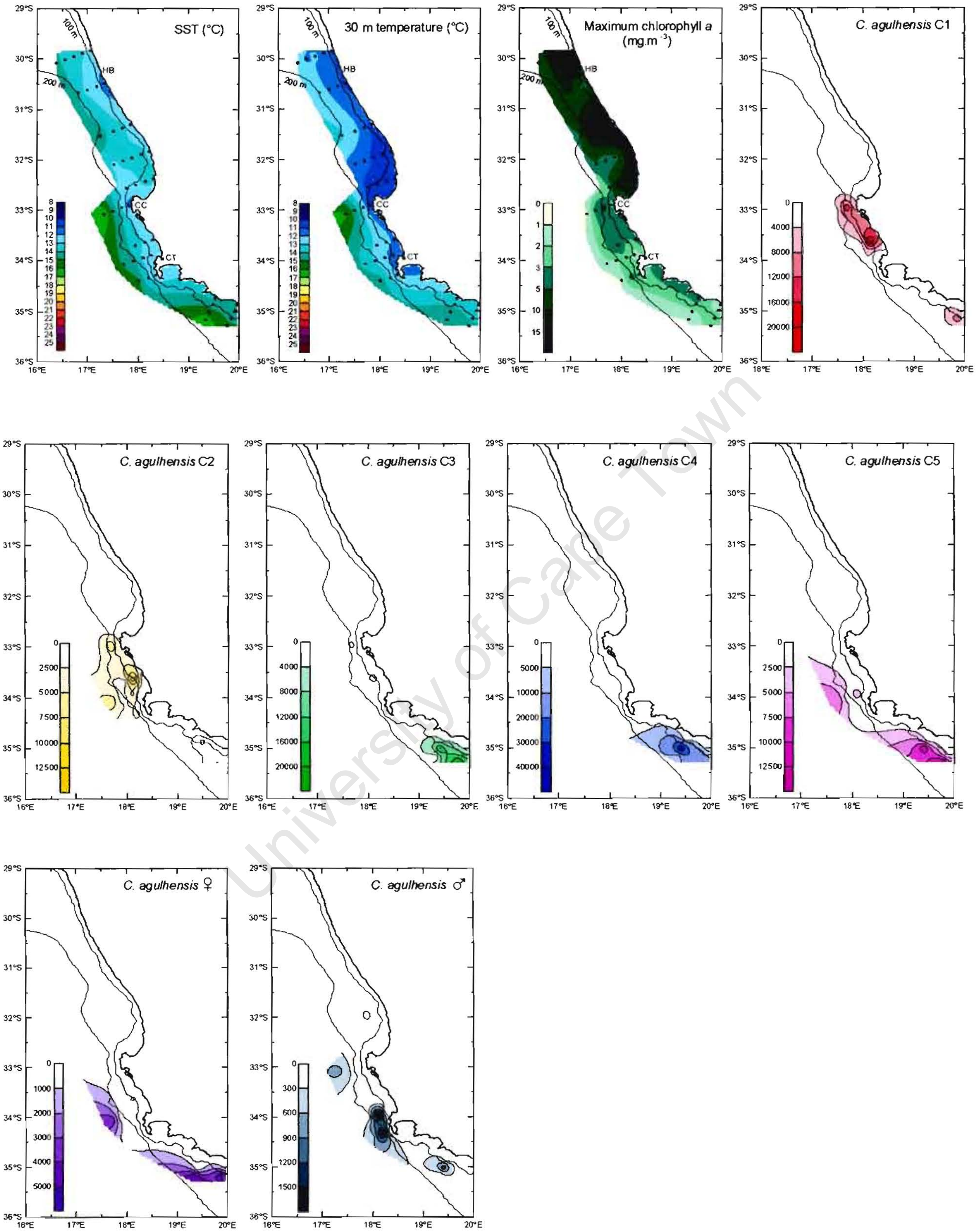
MAY 1999 – *C. agulhensis*



MAY 2000 – *C. carinatus*



MAY 2000 – *C. agulhensis*

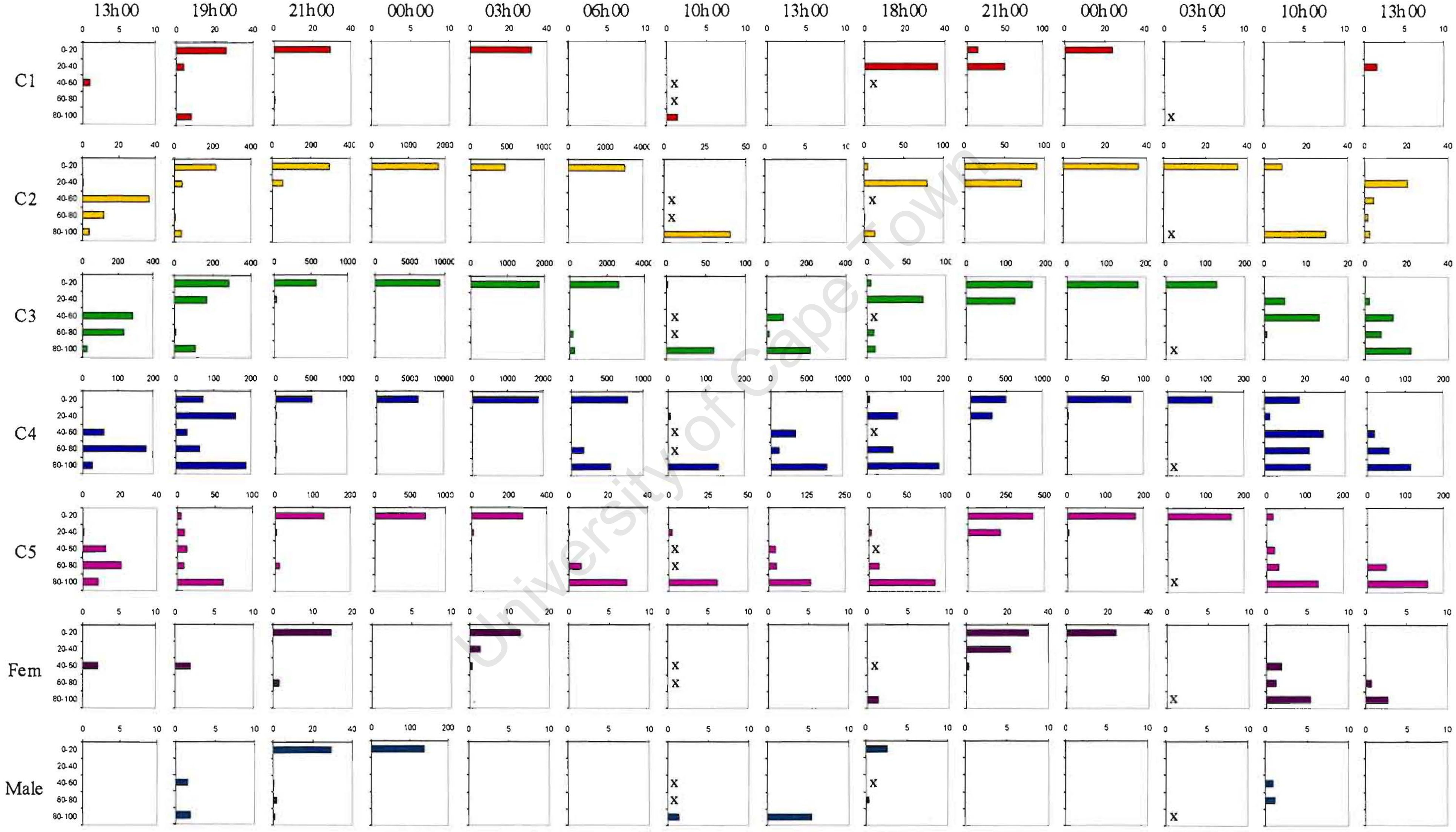


APPENDIX 2

Vertical distribution and abundance (No. m^{-3}) of various life-history stages of *C. agulhensis* and *C. carinatus* collected with an RMT 1×6 net at Stations 1-3 during the Agulhas Ridge cruise (March 1994). Time of sampling is shown above the graphs, and the grid number (sequential sampling reference number) below. Note different scales of x-axes. On some graphs an "x" indicates no samples from that depth were available. In the last column of graphs for Station 2, a bracket indicates samples collected with a Vertical Bongo net.

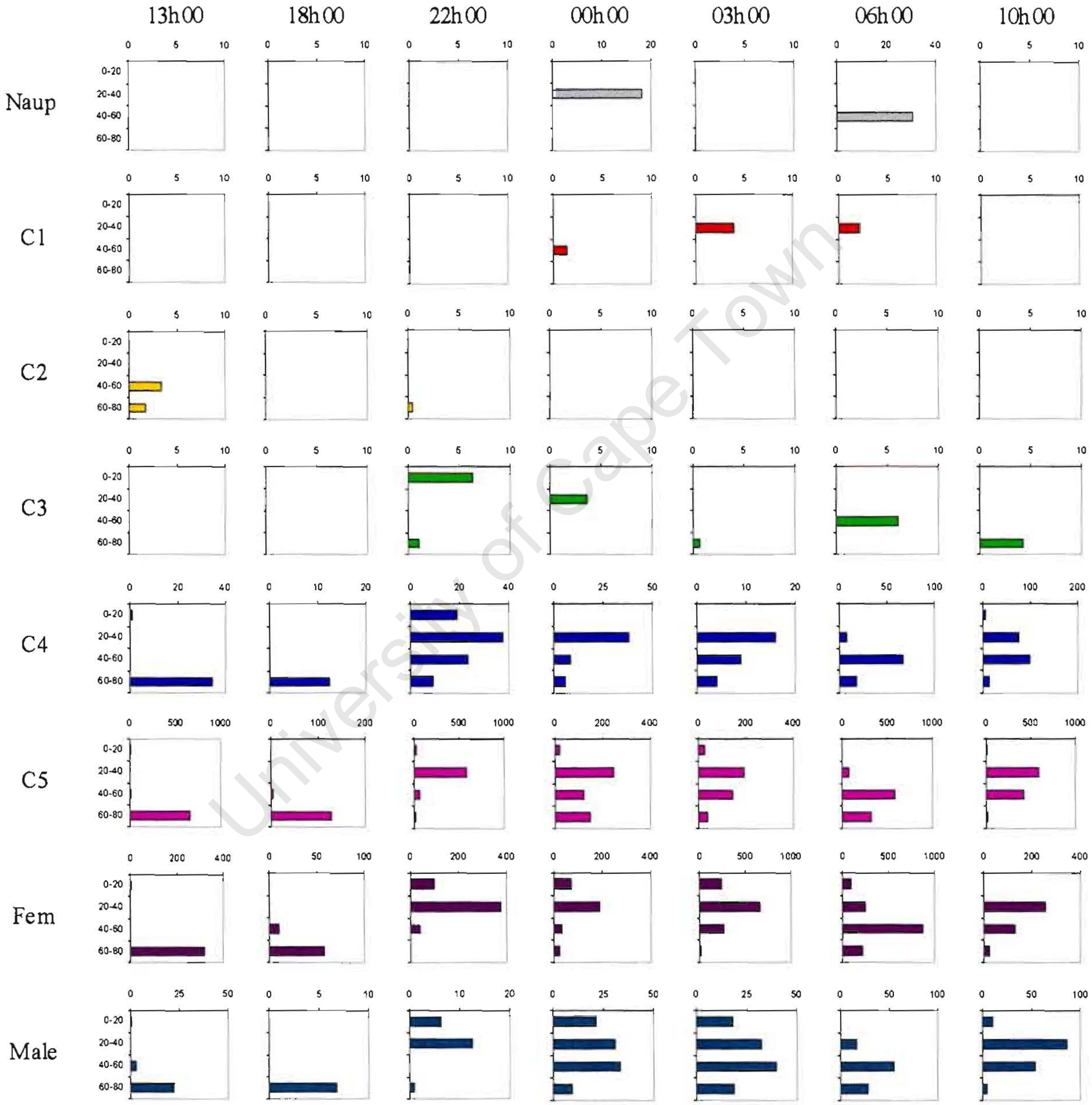
Vertical distribution of *C. agulhensis* at Station 1.

Vertical distribution of *C. carinatus* at Station 1.



Vertical distribution of *C. agulhensis* at Station 2.

Vertical distribution of *C. carinatus* at Station 2.


Vertical distribution of *C. agulhensis* at Station 3.

Vertical distribution of *C. carinatus* at Station 3.