

# NEAR-SURFACE COPEPOD DISTRIBUTION IN THE SOUTH-WESTERN INDIAN AND SOUTH-EASTERN ATLANTIC OCEAN

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(With 5 figures, 80 maps, and 2 tables)

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## ABSTRACT

Continuous underway sampling of near-surface plankton by centrifugal pump over a total distance of nearly 26 000 nautical miles yielded 123 species of free-living copepods in 645 samples. Distribution maps of 80 species are presented, with comments on the physical environment, diel migration, standing stock, and species diversity. Interpretation of a number of distribution patterns is attempted with reference to major current systems.

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## INTRODUCTION

Biological exploration of the oceanic crossroads south of Africa has not kept pace with recent advances in the physical oceanography of the area.

Research on the area's pelagic marine copepods, the most abundant and diverse group of the zooplankton, has been reviewed by De Decker (1962). Subsequent contributions were made by Fukase (1962), Senô *et al.* (1963a, 1963b, 1966), and Tanaka (1964) on transects between Antarctica and South Africa; by Kollmer (1963), Unterüberbacher (1964), Stander & De Decker (1969), Coetzee (1974), and De Decker & Coetzee (1979) in the northern Benguela Current; by Grice & Hülsemann (1967) south of Madagascar; by Carter (1977) in the Agulhas Current area; by De Decker (1968, 1973) and Hutchings (1979) in the southern Benguela Current and western Agulhas Bank; by Wiborg (1964) around Tristan da Cunha; and by Grindley & Lane (1979) around Marion Island.



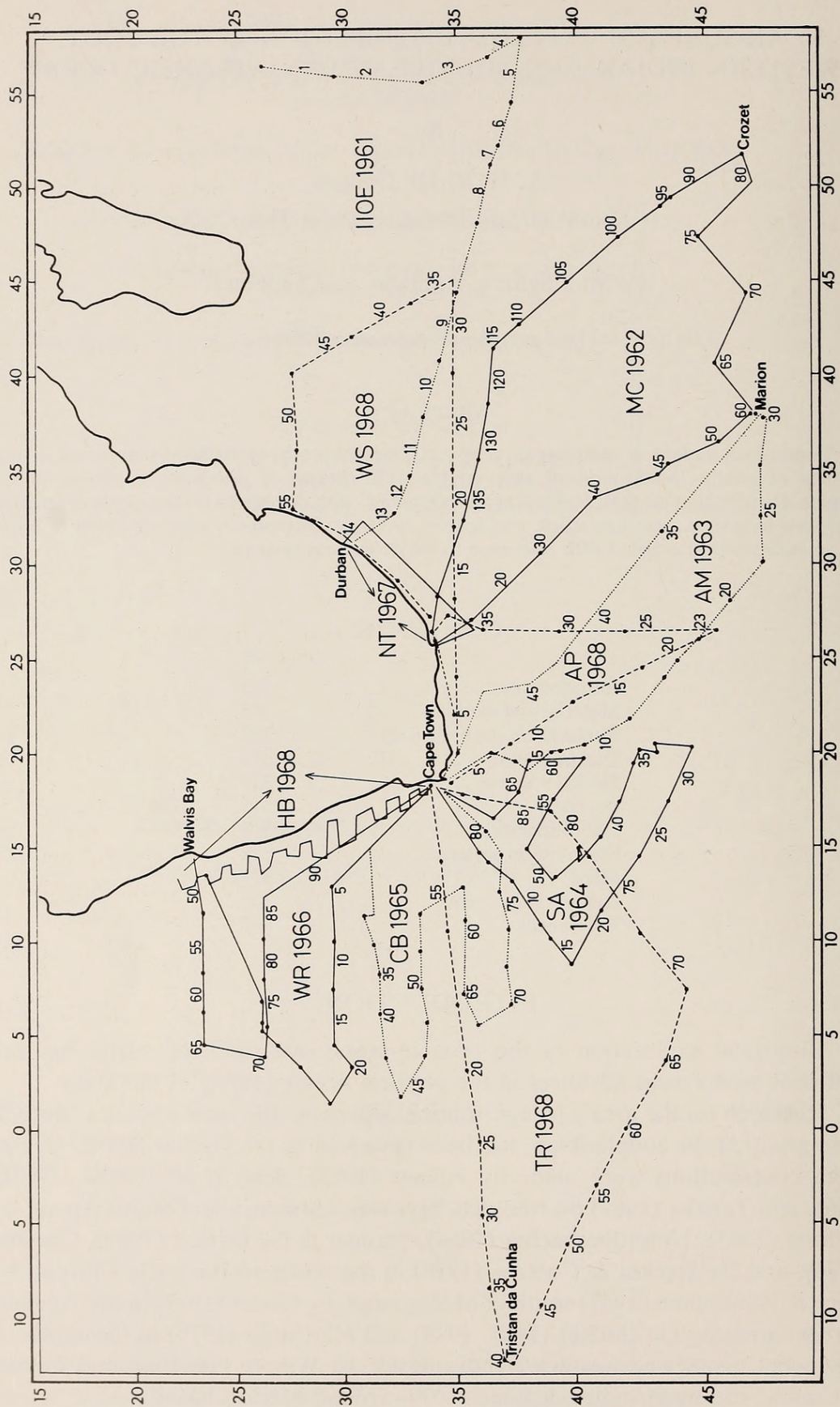


Fig. 1 Cruise tracks, with indications of the serial numbering of the samples.



As a whole, this research lacks methodological uniformity and spatial extension. The distributional data in the present report, although superficial in more ways than one, are an attempt towards a comprehensive and homogeneous biogeographical image of the complex environment surrounding southern Africa.

On the physical side, surface temperature imagery obtained by satellite, combined with trajectories of satellite-tracked buoys, revealed a wealth of detail about the dynamics of the surface waters and provided a unifying background for previous research. The relevant data and literature have been compiled and interpreted by Lutjeharms (1981a-c) and Lutjeharms *et al.* (1981).

Many of the distribution patterns shown in the present report agree well with the conceptual image derived from these physical studies; others point to aspects still in need of clarification.

## MATERIAL AND METHODS

During the deep-sea cruises of R.S. *Africana II* in the years 1961 to 1968, a continuous sampler was used to collect plankton at keel depth while steaming between stations.

From 1961 to 1966 six oceanic sectors were surveyed at a rate of one every year, starting from the latitude of Maputo (26°S) in the Indian Ocean and proceeding clock-wise to the latitude of Walvis Bay (23°S) in the Atlantic (Fig. 1).

In 1967 and 1968 two areas not covered by these six cruises were visited, viz. the inshore waters along the south and south-eastern coasts between Cape Town and Durban comprising the Agulhas Bank, the core region of the Agulhas Current and the inshore upwelling along the south-eastern coast; and a 100 to 150 nautical miles-wide inshore belt along the west coast between Cape Town and Walvis Bay, where the Benguela coastal upwelling is the dominant feature. Also in 1968 three more deep-sea cruises were undertaken: one as far as Tristan da Cunha with a southward deviation across the Subtropical Convergence; one southward between the Agulhas Bank and the West Wind Drift; and the third to the east as far as the Madagascar Ridge (Fig. 1).

The total distance covered by underway sampling was close to 26 000 nautical miles, and the number of samples analysed was 645.

Table 1 gives some particulars about the cruises and the symbols used in this text to designate each cruise.

The continuous sampler consisted of a centrifugal pump conveying seawater through a pipe connecting an intake near the keel directly with a tap in the ship's laboratory. A 30 cm-long cylindrical straining sock of 200  $\mu$  mesh nylon gauze was fixed to the tap and ended in a removable bucket of the type used on the N70 Discovery plankton net (Kemp & Hardy 1929). The pump's capacity was approximately 30 l min.<sup>-1</sup>.

The plankton retained in the bucket was removed at 4-hourly intervals or when the ship reduced speed on arriving at station, whichever was the shortest. The plankton obtained over each individual stretch was preserved in 4 per cent



TABLE 1  
Data on cruises and collections.

Cruise	Dates	Samples examined	Copepod species identified	Settled volume ranges (% frequency) ml h <sup>-1</sup>					Average standing stock (ml 1000 m <sup>-3</sup> )
				< 0,25	to 0,50	to 1	to 2	> 2	
IIOE 1961	4-15 July	16	68						
MC 1962	19 June- 12 July	98	79	90	5	5			70
AM 1963	3-19 April	47	80	90	4	6			70
SA 1964	10-29 March	65	91	30	37	30	3		280
CB 1965	2-24 April	52	78	61	18	18	3		210
WR 1966	6-27 July	99	64	82	16	2			140
NT 1967	11-24 July	25	83	43	15	19	23		303
TR 1968	4-21 March	88	77	93	5	2			70
AP 1968	13-22 June	47	62						
WS 1968	4-22 Sept.	59	85	37	17	20	6		210
HB 1968	5-13 April	49	56	23	21	24	27	5	470

formalin, allowed to settle in a graduated cylinder for about 12 hours, and stored in a vial. Settled volume figures were converted to ml h<sup>-1</sup>. While on station, the water delivered by the pump was allowed to run off in a sink, in order to have the system completely flushed before the continuous sampling resumed. The collecting bucket was replaced when the ship got under way.

Since normal cruising speed was 10 knots, each 4-hour sample contained plankton caught over a distance of 40 nautical miles, a unit length conferring sufficient resolution to the distribution patterns in an oceanic area stretching over more than 3 000 nautical miles longitudinally and nearly 1 500 nautical miles latitudinally. Reduced speed in bad weather enhances the resolution without affecting the catch figures, as these are based on time intervals, not on distances. During the 1961 cruise when the method was first attempted, starting from a station south of Mauritius, the catch was not subdivided in 4-hour sections, but each sample was taken from one station to the next, i.e. over approximately 100 nautical miles.

Copepods caught by the continuous pump suffered no more damage than those caught by a plankton net hauled at low speed. The pump, however, seems to be selective against larger plankton organisms such as salps, medusae, euphausiids, etc. It was repeatedly observed that in areas where all plankton nets, including those towed horizontally at or near the surface, were utterly clogged with salps at successive stations, the pump samples obtained under way between these stations contained hardly any salps. This selectivity is probably due to the low suction power of the pump having to contend with the inertia of organisms sweeping past the intake at a speed of 10 knots: the larger the organism, the less it will be affected by suction perpendicular to its relative motion. This interpretation is supported by the fact that large amounts of salps or euphausiids were sometimes caught in pump samples taken while the ship was stationary.

Selectivity against larger organisms is an obvious advantage when sampling is directed at small forms such as copepods, although it may affect the quantita-



tive aspect of the results as larger copepods could well be affected by it to an unknown extent in relation to smaller ones.

Further advantages of pump sampling are its practicability in all weather conditions, the virtual elimination of the effects of plankton patchiness, the smaller likelihood of mixing different plankton communities in one sample, as can happen in vertical net hauls across a thermocline, the improved chances of capturing less abundant forms and, correlatively, of tracing a species to the limit of its distribution area where it becomes rarefied. Finally, this method does not impose delay on the ship and is not affected by loss of gear.

No attempt was made to obtain a complete repertory of all copepod species present. Non-identifiable juveniles were ignored and so were adults whose identification was uncertain or too time-consuming.

### REMARKS ON THE HYDROLOGY

The hydrological conditions prevailing during individual cruises have been described in detail by Orren (1963, 1966), Duncan (1968), Visser (1969), Shannon & van Rijswijck (1969), Welsh & Visser (1970), and Henry (1972). Bang (1973) and Andrews & Hutchings (1980) gave detailed accounts of the Southern Benguela System; Duncan (1970) and Harris & Van Foreest (1977) presented a general interpretation of existing physical data on the Agulhas Current System. A conceptual image of the dynamics of the central part of the area under discussion, based mainly on satellite imagery, was constructed by Lutjeharms (1981a) (Fig. 2). The general outline of the physical structure of the seas around southern Africa has been repeatedly described and does not need to be given here. Only a few features which may be relevant to the interpretation of the plankton distribution patterns will be discussed; they are based on physical data collected during the cruises, with due regard to the picture emerging from some of the more recent publications mentioned above.

The SA cruise in March 1964 took place at the time when a short-circuiting in the *southern Agulhas Current retroflexion* had generated an extensive anticyclonic eddy or warm ring centered near the Schmitt-Ott Seamount at about 40°S 15°E, with a diameter of approximately 300 km (Fig. 3) and a depth in excess of 1 200 m (Fig. 4A). This eddy, called the 'Schmitt-Ott eddy' in the present context, has been described in detail by Duncan (1968) and Visser (1969). Lying astride the average latitude of the Subtropical Convergence, its effect on the latter was either an extensive southward displacement (beyond the survey area) or, more probably, a complete disintegration. The Agulhas Current proper ran southward along the 20°E meridian, to the east of the eddy.

The TR cruise in March 1968 crossed the area where the eddy had been 4 years earlier and passed over the Schmitt-Ott Seamount, but a warm ring was not found. Instead, a thermal front (the Subtropical Convergence) separated the Subantarctic surface water from a comparatively shallow and wide trough of



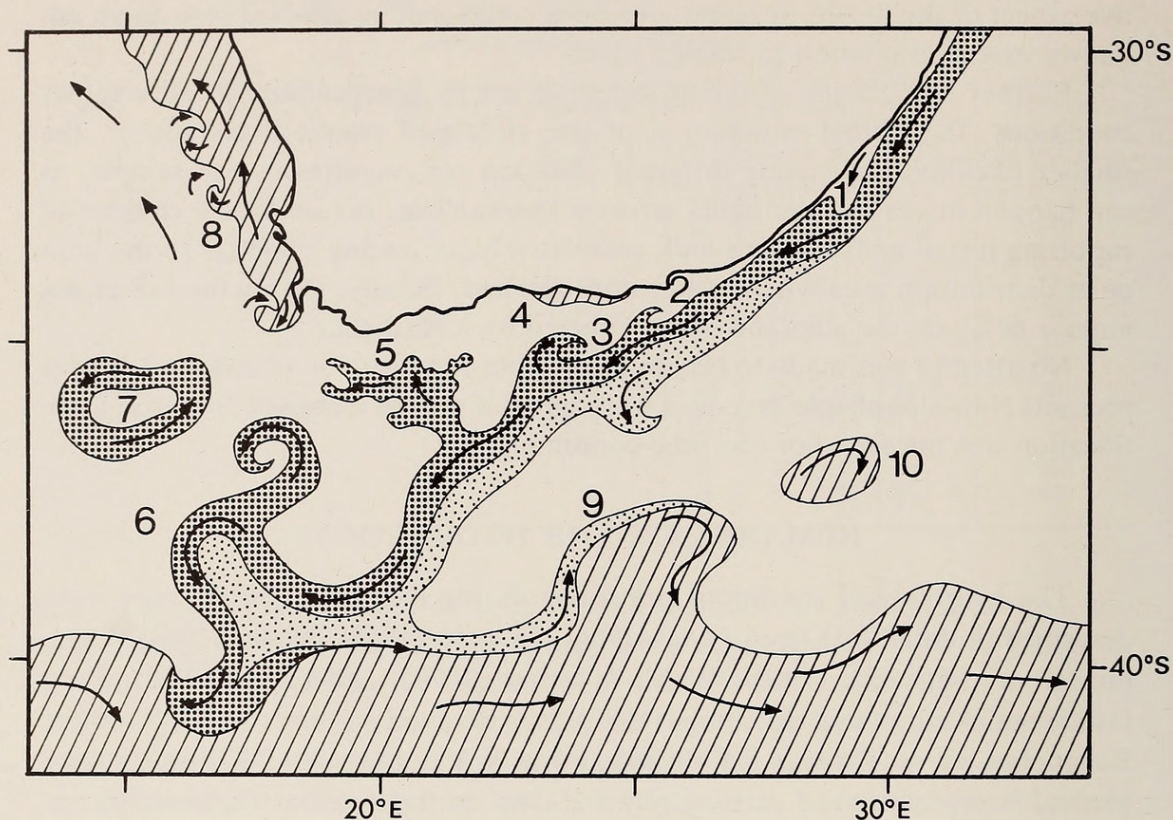


Fig. 2. A conceptual image of the Agulhas Current System. Heavy dots indicate warm water, lighter dots colder water, and hatching cold subtropical surface water and upwelled water. The line demarcating the subtropical water at about 40°S latitude is the Subtropical Convergence. 1. The embryonic stages of a Natal pulse. 2. Small waves or disturbances on the Agulhas Current border. 3. Shear edge effects, warm-water plumes or shear edge eddies. 4. Cold upwelled water. 5. The dispersion of a shear edge feature attached to an Agulhas Current meander. 6. The Agulhas Current retroflexion. 7. An Agulhas Current Ring being advected northward. 8. The Cape upwelling regime with frontal eddies in evidence. 9. A planetary wave on the Agulhas Return Current-Subtropical Convergence. 10. An independent cold-water eddy spawned by an unstable planetary wave. (From Lutjeharms 1981a.)

warm saline water about 270 km north-east of the Schmitt-Ott Seamount, with a subsurface salinity maximum of 35,4‰ just below the 200 m level. As one crossing only was made, it is not possible to conclude from the single vertical section whether this trough represents a decaying warm ring or a terminal branch of the Agulhas Current (Fig. 4B).

Warm rings separated from the Agulhas Current near its retroflexion area are assumed to be moving northward over considerable distances in the south-eastern Atlantic. This view gained strong support, if not conclusive proof, from an experiment involving a satellite-tracked buoy placed in an Agulhas Current fragment detected on enhanced infra-red images received from Meteosat (Lutjeharms & Valentine 1981). A number of distribution patterns in the present report appear to illustrate this mode of advection of Indian Ocean species into the south-eastern Atlantic.



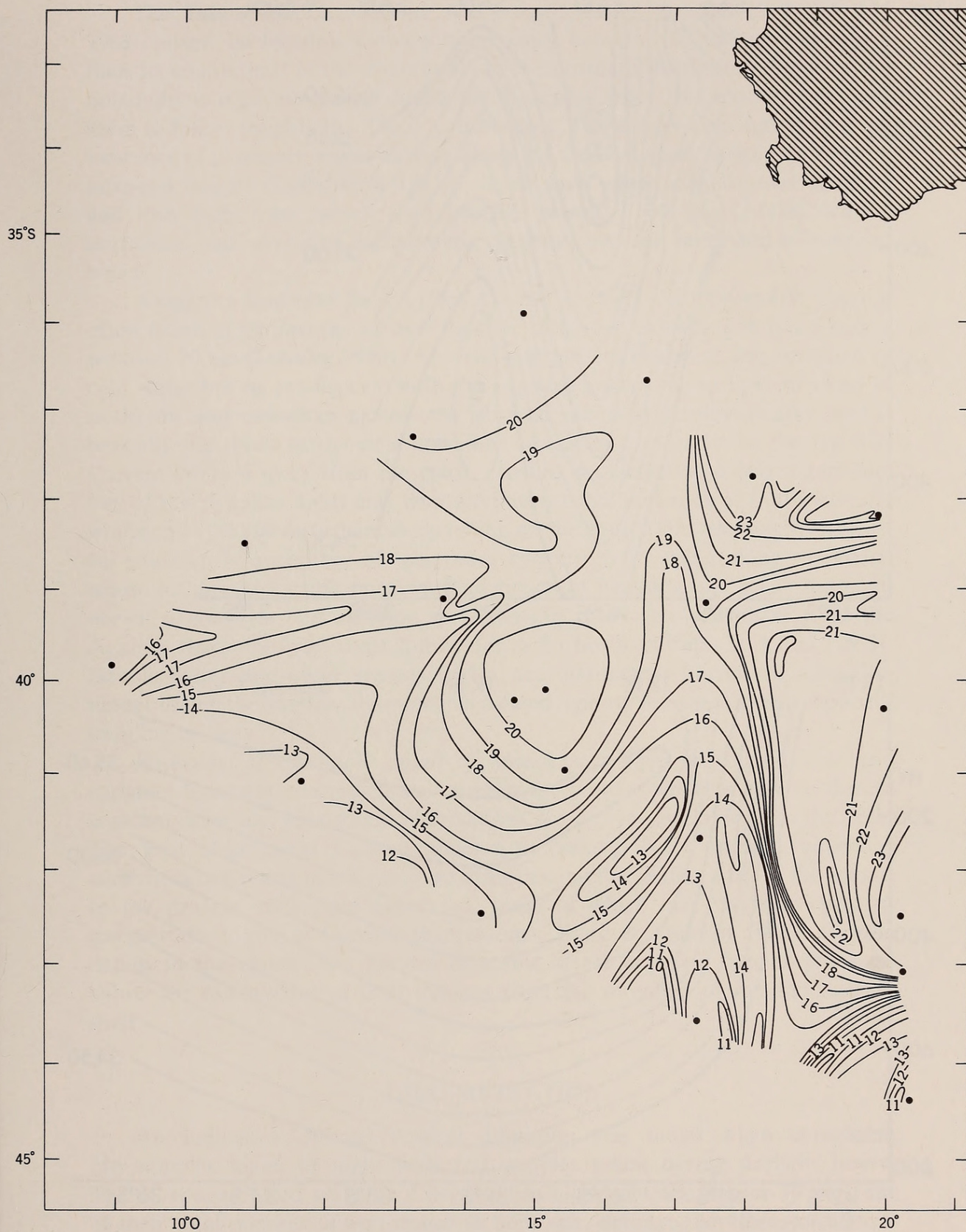


Fig. 3. Cruise SA 1964; sea surface temperature ( $^{\circ}\text{C}$ ) constructed from continuous thermograph recordings (from Visser 1969).



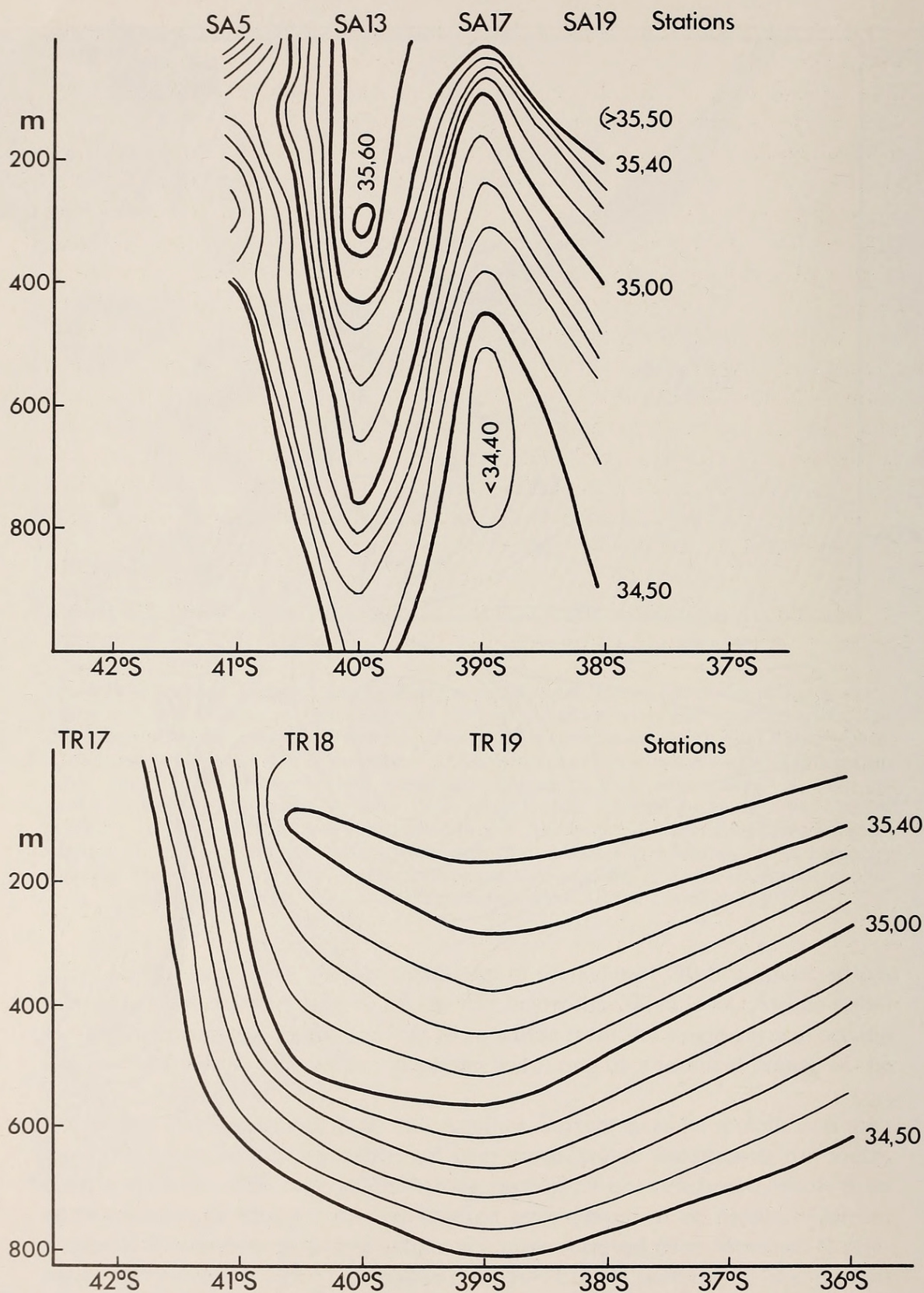


Fig. 4. A. Salinity section across the Schmitt-Ott eddy, cruise SA 1964.  
B. Salinity section along the south-west to north-east leg of cruise TR 1968.



The *Subtropical Convergence* was crossed during the MC 1962 and AM 1963 cruises. Its location shows a discrepancy between the two cruises, which finds its counterpart in the discrepancy in the northern distribution limits of the Subantarctic copepod species during the successive visits. The species concerned seem to follow roughly the 5 to 6 °C isotherms. This observation agrees with the existence of planetary waves moving along the Convergence, as seen on satellite infra-red images (Lutjeharms 1981a). Some such waves may become unstable and lose their tops, which then become separate cold-core eddies drifting northward and advecting Subantarctic plankton into the notal and subtropical zones.

Along the *landward flank of the Agulhas Current*, cold low-saline water is often found at various places over variable distances, extending at times over a width of 20 km (Duncan 1970). According to present evidence, this surfacing of cold water has its predisposition in the near-permanent, steep upward trend of isotherms and isohalines against the slope to relatively shallow depths, and is basically the result of dynamic upwelling whenever a meander of the Agulhas Current swerves away from the coast, creating a divergence. Concomitant factors of this dynamic uplift may be atmospheric conditions such as south-westerly winds and cyclonic disturbances travelling up the coast. The resulting hydrological situation is a number of temporary cyclonic cells strung along the coast, whose inshore arcs cause northward advection of plankton and act in the manner of a conveyer-belt carrying surface-living cold-water organisms from the Agulhas Bank and west coast sometimes as far north as Cape St. Lucia (28°S). Deeper-living cold-water species find a near-permanent northward advection tunnel under the shallow thermocline created against the slope by the upward-trending isolines.

*Hydrological conditions south of Madagascar* have proved intricate and variable: apparent contradictions between the various workers may be due to seasonal reversals; year-round observations are not yet available from the area. The East Madagascar Current appears to behave like a western boundary current, retroflecting north-eastward after passing the southern tip of the island. In the process eddies are generated, some of which may migrate westward towards the Agulhas Current (Lutjeharms, Bang & Duncan 1981). Certain details in the distribution pattern of a few of the copepod species discussed below are reminiscent of such influxes from the direction of the Madagascar shelf.

## DIEL MIGRATION

An indication of diel vertical migration was found when comparing 216 samples taken at night with 160 samples taken during daylight hours. The 28 species listed in Table 2 occurred in night samples in over 70 per cent of their total number of occurrence in both sets, and are therefore considered migrators.



TABLE 2

Diel vertical migration, as deduced from 216 night samples and 160 daylight samples.

	No. of occurrences	
	Total	% at night
<i>Calanopia minor</i>	3	100
<i>Clytemnestra scutellata</i>	10	100
<i>Pleuromamma robusta</i>	4	100
<i>Heterorhabdus papilliger</i>	33	97
<i>Scolecithricella glacialis</i>	14	93
<i>Candacia simplex</i>	12	92
<i>Clytemnestra rostrata</i>	11	91
<i>Undeuchaeta plumosa</i>	28	89
<i>Centropages furcatus</i>	9	88
<i>Pleuromamma abdominalis</i>	56	88
<i>Euchaeta acuta</i>	17	87
<i>Pleuromamma piseki</i>	116	86
<i>Pleuromamma borealis</i>	65	86
<i>Rhincalanus nasutus</i>	40	85
<i>Undinula darwinii</i>	13	85
<i>Candacia bipinnata</i>	14	85
<i>Eucalanus elongatus</i>	8	83
<i>Pleuromamma gracilis</i>	63	83
<i>Candacia ethiopica</i>	27	81
<i>Euchaeta marina</i>	35	80
<i>Pleuromamma xiphias</i>	19	79
<i>Lucicutia flavicornis</i>	111	77
<i>Calanoides carinatus</i>	22	76
<i>Neocalanus gracilis</i>	75	76
<i>Metridia lucens</i>	83	75
<i>Calanus tenuicornis</i>	89	74
<i>Eucalanus subcrassus</i>	15	73
<i>Scolecithrix danae</i>	31	71

Some species falling in the lower percentage range of night-time occurrence, even below 70 per cent, show increased abundance at night. Such species are *Calanus simillimus*, *Ctenocalanus vanus*, *Macrosetella gracilis*, *Microsetella norvegica*, *Calanoides carinatus*, *Clausocalanus ingens*, *Lucicutia flavicornis*, and *Metridia lucens*.

### SETTLED VOLUMES

As the settled volumes were generally small—only 7 per cent of the samples exceeded  $1 \text{ ml h}^{-1}$ —a notable margin of error is attached to the recorded values. Nevertheless, a regional trend emerges when comparing the average settled volumes for the individual cruises (Table 1) or when mapping the areas where volumes of  $0.5 \text{ ml h}^{-1}$  or more were obtained occasionally.

These larger volumes are grouped near the continent and around the islands, as could be expected, and also in the Schmitt-Ott area and the neighbouring southern branch of the Agulhas Current. Since the percentage of night



samples taken during the cruise in the latter area was much higher than during the other cruises, a possible bias was avoided by comparing only the night samples of the different cruises. This test confirmed the higher abundance of small zooplankton in the Schmitt-Ott area as compared with the surrounding areas.

### DIVERSITY

The pattern of diversity—i.e. the number of species per sample—reflects the large-scale hydrological structure of the survey area (Fig. 5).

The diversity was lowest in the Subantarctic water and along the Benguela coastal upwelling. The transition to higher diversity in the South Indian and South Atlantic central gyres seems to occur somewhat further north in the Atlantic than in the Indian Ocean, in agreement with the average hydrological conditions for these areas as recorded in the '*Monatskarten*' published by the Deutsches Hydrographisches Institut (1960, 1971). Meisenheimer (1905) found a similar difference in the distribution limits of pteropods in both oceans and attributed it to warming by the Return Agulhas Current in the southern Indian Ocean.

Two patches of high diversity, based on three and four samples respectively, were found in the Atlantic and contained between 29 and 47 species per sample. One patch lay west of the Cape of Good Hope (TR 2, 3 and 4) and the other reached as far north as 31°S (CB 8, 9, 10 and 15). These patches contained assemblages in which the percentage contribution of Indian Ocean species decreased from the southern to the northern samples in the sequence 38, 32 and 36; 34, 28, 28 and 10 per cent respectively. Indian Ocean species are denoted as such in the present context on the basis of their distribution pattern obtained from the material under discussion. The diminishing presence of Indian Ocean faunal elements in a northward direction along the west coast lends support to the idea that the high diversity patches are manifestations of warm rings originating from the Agulhas Current and moving northward in the Atlantic. Four samples taken in the southward branch of the Current (SA 33, 56, 63 and 64) and containing a total of between 35 and 39 species had a percentage of Indian Ocean forms ranging between 28 and 40 per cent. Two samples with 36 species each, taken outside the Agulhas branch but close to its thermal front (SA 32 and 37) contained 20 and 22 per cent of Indian Ocean species, respectively.

One sample of 32 species taken in the Atlantic at 26°S 10°E at night (WR 81) did not contain Agulhas-related species.

### LIST OF SPECIES

Occurrences of scarce and scattered species are indicated here by means of the cruise symbol followed by the sample number (see Fig. 1); occurrences of other species are shown on the maps that are placed in alphabetical order of species names on pages 327–366.



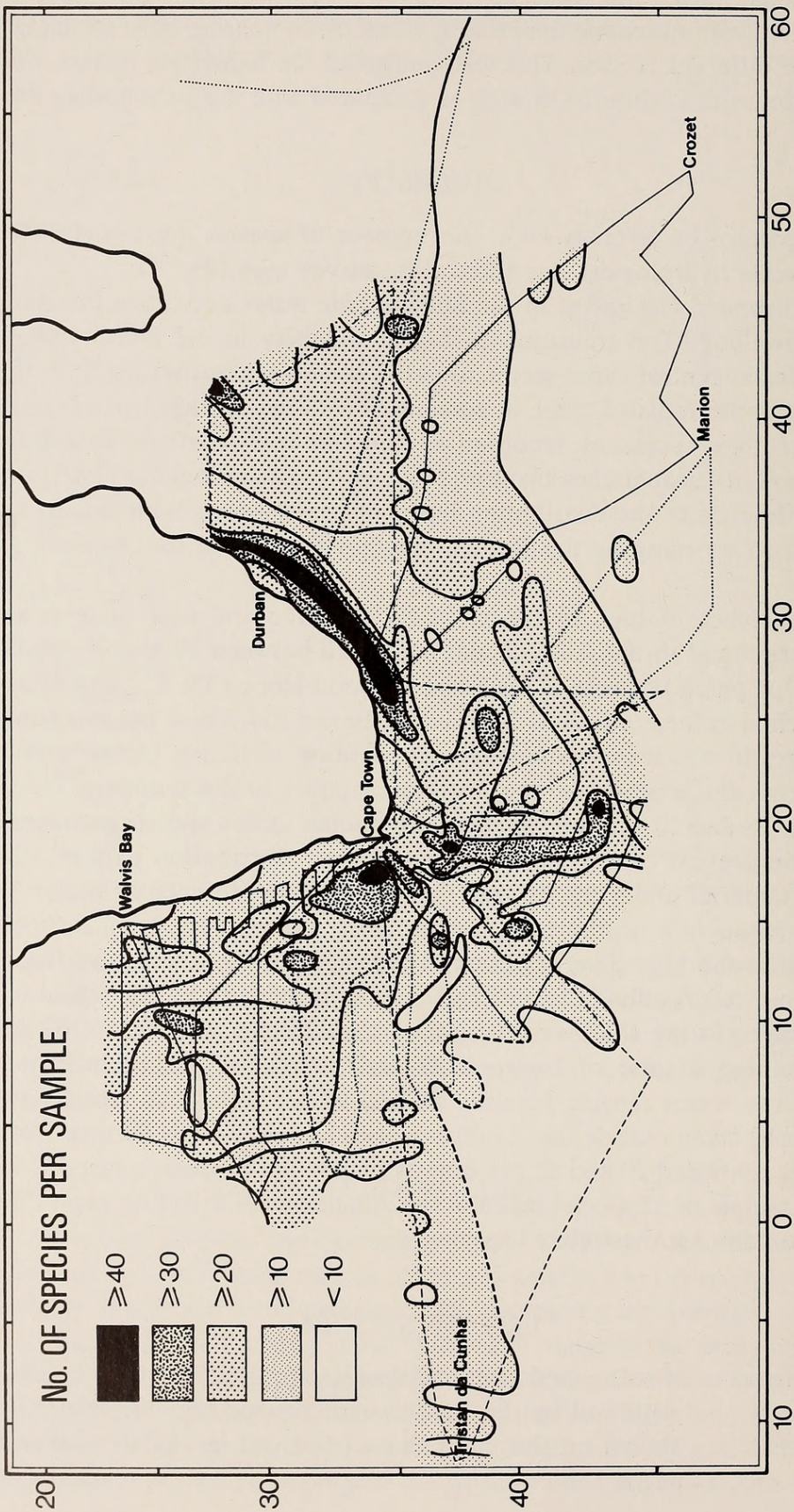


Fig. 5. Diversity distribution.



*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.

#### Order CALANOIDA

##### Family Calanidae

- Calanus finmarchicus* (Gunnerus, 1765) *s.l.* (*sensu lato*)
- C. propinquus* Brady, 1883 (AP 21)
- C. simillimus* Giesbrecht, 1902
- C. tenuicornis* Dana, 1849
- Nannocalanus minor* (Claus, 1863)
- Calanoides carinatus* (Krøyer, 1849)
- C. macrocarinatus* Brodski, 1972
- Canthocalanus pauper* (Giesbrecht, 1888)
- Neocalanus gracilis* (Dana, 1848)
- N. robustior* (Giesbrecht, 1888) (NC 136, 138)
- Undinula darwinii* (Lubbock, 1860)
- U. vulgaris* (Dana, 1849)

##### Family Eucalanidae

- Eucalanus attenuatus* (Dana, 1849) *s.l.*
- E. crassus* Giesbrecht, 1888
- E. hyalinus* (Claus, 1866)
- E. longiceps* Matthews, 1925 (TR 68)
- E. monachus* Giesbrecht, 1888 (SA 33)
- E. mucronatus* Giesbrecht, 1888
- E. pileatus* Giesbrecht, 1888
- E. subcrassus* Giesbrecht, 1888
- E. subtenuis* Giesbrecht, 1888 (MC 147; SA 3, 33; BC 8; TR 2)
- Rhincalanus cornutus* Dana, 1853
- R. gigas* Brady, 1883 (MC 78, 82)
- R. nasutus* Giesbrecht, 1888

##### Family Paracalanidae

- Paracalanus aculeatus* Giesbrecht, 1888
- P. crassirostris* F. Dahl, 1893
- Acrocalanus gibber* Giesbrecht, 1888
- A. gracilis* Giesbrecht, 1888
- A. monachus* Giesbrecht, 1888

##### Family Calocalanidae

- Calocalanus contractus* Farran, 1926
- C. pavo* (Dana, 1849)
- C. plumulosus* (Claus, 1863)
- C. styliremis* Giesbrecht, 1888
- C. tenuis* Farran, 1926
- Mecynocera clausi* I. C. Thompson, 1888

##### Family Pseudocalanidae

- Clausocalanus furcatus* (Brady, 1883)
- C. ingens* Frost & Fleminger, 1968
- C. laticeps* Farran, 1926
- Ctenocalanus vanus* Giesbrecht, 1888
- Drepanopus pectinatus* Brady, 1883



**Family Aetideidae**

- Aetideus armatus* (Boeck, 1872) (AP 3)  
*Euaetideus acutus* (Farran, 1929) (MC 35; WS 46)  
*E. bradyi* (A. Scott, 1909) (IIOE 14)  
*E. giesbrechti* (Cleve, 1904) (CB 61)  
*Gaetanus minor* Farran, 1905 (AM 4; HB 1)  
*Euchirella rostrata* (Claus, 1866)  
*Undeuchaeta plumosa* (Lubbock, 1856)

**Family Euchaetidae**

- Euchaeta acuta* Giesbrecht, 1892  
*E. biloba* (Farran, 1929) (MC 69)  
*E. marina* (Prestandrea, 1833)  
*E. media* Giesbrecht, 1888 (IIOE 14)  
*E. wolfendeni* A. Scott, 1909

**Family Scolecithricidae**

- Scaphocalanus echinatus* (Farran, 1906) (AP 15; WR 51, 52)  
*Scolecithricella glacialis* (Giesbrecht, 1902)  
*Scolecithrix bradyi* Giesbrecht, 1888 (SA 3, 29, 37, 44; WR 44; WS 31)  
*Scolecithrix danae* (Lubbock, 1856)

**Family Phaennidae**

- Phaenna spinifera* Claus, 1863 (AP 10)

**Family Centropagidae**

- Centropages brachiatus* (Dana, 1849)  
*C. bradyi* Wheeler, 1899  
*C. calaninus* (Dana, 1849) (SA 33; IIOE 14)  
*C. chierchiae* Giesbrecht, 1889  
*C. elongatus* Giesbrecht, 1896  
*C. furcatus* (Dana, 1849)  
*C. gracilis* (Dana, 1849) (SA 3, 63; WS 46; IIOE 14)  
*C. longicornis* Mori, 1937 (WS 54)  
*C. orsinii* Giesbrecht, 1889 (WS 55)  
*C. violaceus* (Claus, 1863)

**Family Pseudodiaptomidae**

- Pseudodiaptomus nudus* Tanaka, 1960 (AM 2; AP 1, 2, 3, 7)

**Family Temoridae**

- Temora discaudata* Giesbrecht, 1889  
*T. stylifera* (Dana, 1849) (MC 147; SA 1, 2)  
*T. turbinata* (Dana, 1849)

**Family Metridiidae**

- Metridia lucens* Boeck, 1864  
*Pleuromamma abdominalis* (Lubbock, 1956)  
*P. borealis* (F. Dahl, 1893)  
*P. gracilis* (Claus, 1863)  
*P. piseki* Farran, 1929  
*P. quadrangulata* (F. Dahl, 1894) (AM 4; SA 61)  
*P. robusta* (F. Dahl, 1894) (MC 69, 74, 75, 79)  
*P. xiphias* (Giesbrecht, 1889)



Family **Lucicutiidae**

- Lucicutia flavicornis* (Claus, 1863)  
*L. gaussae* Grice, 1963 (SA 45, 59, 63; TR 12; WR 79)  
*L. clausi* (Giesbrecht, 1889) (AM 4)

Family **Heterorhabdidae**

- Heterorhabdus papilliger* (Claus, 1863)  
*H. spinifrons* (Claus, 1863) (SA 46)

Family **Augaptilidae**

- Haloptilus longicornis* (Claus, 1863) (AM 4)  
*H. oxycephalus* (Giesbrecht, 1889) (SA 46)  
*H. spiniceps* (Giesbrecht, 1892) (WR 81)

Family **Candaciidae**

- Candacia bipinnata* (Giesbrecht, 1888)  
*C. bispinosa* (Claus, 1863) (AM 3; SA 62; WR 41)  
*C. catula* (Giesbrecht, 1889)  
*C. curta* Cleve, 1904 (HB 13, 16, 34; MC 147)  
*C. ethiopica* (Dana, 1849)  
*C. pachydactyla* (Dana, 1849) (MC 147; CB 16; WS 7)  
*C. simplex* (Giesbrecht, 1889)  
*C. truncata* (Dana, 1849) (TR 2; IIOE 14)  
*C. varicans* (Giesbrecht, 1892) (AM 36, 40, 46; TR 2, 5)

Family **Pontellidae**

- Calanopia elliptica* (Dana, 1849) (MC 147)  
*C. minor* A. Scott, 1902  
*Labidocera acuta* (Dana, 1849)  
*L. acutifrons* (Dana, 1849)  
*L. minutum* Giesbrecht, 1889  
*Pontella securifer* Brady, 1883 (TR 85)  
*Pontellina plumata* (Dana, 1849) *s.l.*

Family **Acartiidae**

- Paracartia africana* Steuer, 1915 (WR 47 to 52: Walvis Bay shelf)  
*Acartia amboinensis* Carl, 1907 (WS 55)  
*A. danae* Giesbrecht, 1889  
*A. negligens* Dana, 1849

## Order CYCLOPOIDA

Family **Oncaeidae**

- Lubbockia aculeata* Giesbrecht, 1891 (WS 50, 57)  
*L. squillimana* Claus, 1863 (MC 20; AM 45; IIOE 1, 2)  
*Pachos* sp. (IIOE 14)

Family **Sapphirinidae**

- Corissa parva* Farran, 1936 (IIOE 1)

## Order HARPACTICOIDA

Family **Ectinosomatidae**

- Microsetella norvegica* (Boeck, 1864)  
*M. rosea* (Dana, 1848)



Family **Tachydiidae**

*Euterpina acutifrons* (Dana, 1852)

Family **Clytemnestridae**

*Clytemnestra rostrata* (Brady, 1883)

*C. scutellata* Dana, 1847

Family **Miraciidae**

*Miracia efferata* Dana, 1846 (SA 1, 44, 63, 70)

*Oculosetella gracilis* (Dana, 1852)

*Macrosetella gracilis* (Dana, 1848)

## DISTRIBUTION PATTERNS

The distribution patterns shown in this report are influenced by a number of time-dependent factors, the most obvious being shifting currents, eddies and fronts, and pulses of upwelling, among other physical and chemical conditions, as well as rhythmic events in the life of the species such as diurnal or seasonal migration. To give but one example: had the south-western sector been surveyed in October–November instead of in March, *Calanus tonsus* and *Calanoides macrocarinatus* would have been found at the surface over an extensive inshore area around the Cape of Good Hope (De Decker 1973).

One might expect that the lack of synopticity of the collections could have a disrupting effect on the distribution patterns. In most cases, however, no such effect has been noticed and meaningful patterns have been obtained, at least for species occurring with sufficient frequency. The reason for this may be that the environmental factors (currents, fronts, etc.) governing the dispersal of a species have a reasonable degree of topographical constancy at the scale of the area surveyed.

One exception can be seen in the species found south of the Subtropical Convergence. Here the planetary waves running along the Convergence may be responsible for the discontinuity in the patterns in successive years (MC 1962, AM 1963) and between SA 1964 and TR 1968, south of the Schmitt-Ott Seamount (see e.g. *Clausocalanus laticeps*).

No attempt has been made to force a biogeographical interpretation on species showing a rarefied and thinly scattered occurrence in the present material. Such species are either rare or have their habitat in deeper levels; their occasional capture at the surface can be considered merely incidental and offers no valid basis for a distribution picture.

The two most frequent types of distribution are:

- (i) a widespread distribution mainly north of the Subtropical Convergence in warm and temperate waters, with avoidance of the cold coastal upwelling, and
- (ii) patterns related to the Agulhas Current and its ramifications.



### *Widespread warm-temperate patterns*

The southward extension of this group varies to a notable extent depending on the species. *Mecynocera clausi* advances farthest south, following the surface isolines of 34,30 ‰ salinity and 10 °C temperature; *Acartia danae*, *A. negligens* and *Nannocalanus minor* do not extend below 35,00 ‰ and 13 to 16 °C, whereas *Calocalanus pavo* and *C. plumulosus* are generally confined still further north. The southern limits of the above-mentioned species converge and practically coincide at two places where a strong thermohaline front was crossed: near station MC 3 (40°44'S 33°36'E) where the Subtropical Convergence manifested itself by a temperature gradient of 11 °C (18,5 to 7,5 °C) in less than 70 nautical miles along the north-western-south-eastern route with relatively little wind and current activity (Orren 1966, figs 2 and 5), and near station SA 9 (43°04'S 20°09'E) where the impact of the southward branch of the Agulhas Current on the Subantarctic Water of the West Wind Drift caused a drop in temperature of 10 °C in as many miles (Duncan 1968). At the latter position only *Mecynocera clausi* penetrates farther south than the other warm-temperate species.

The two widespread *Pleuromamma* species, *P. borealis* and *P. gracilis*, advance further south than any of the above-mentioned species, but being active diurnal migrators, their occurrences are scattered due to their absence from the daylight catches, and their southern limit is not well defined. South of the Subtropical Convergence they were caught less frequently. *Pleuromamma abdominalis*, *P. piseki* and *P. xiphias*—especially the latter—were not found as far south.

In most of the warm-temperate species the southern limit lies further north in the Atlantic than in the Indian sector. On the Atlantic Ocean a north-eastward trend of certain species is noticeable on the western flank of the Schmitt-Ott eddy, indicating penetration of Subantarctic Water in direction of the Cape. Within the Schmitt-Ott eddy, however, the warm-temperate species undergo their furthest southward advection.

### *Agulhas Current patterns*

More than twenty species display a pattern more or less closely related to the course of the Agulhas Current and its ramifications. There is a gradation in tolerance of lateral mixing, some species keeping strictly to the warm core of the Current, while others show a more diffuse pattern.

*Centropages furcatus* shows a near-ideal picture of the course of the Current, a main branch reaching as far as 43°S, with a weak northern branch and some spillage into the Atlantic to the west. This species had long been considered as world-wide circumtropical, until Fleminger & Hülsemann (1973) showed that the mid-Atlantic population is a separate species, *C. velificatus* (de Oliveira, 1947). The specimens in the present material may be taken as Indo-Pacific indicators of the Agulhas Current.



Progressively wider dispersion away from the Current core is apparent in species such as *Acrocalanus gracilis*, *A. monachus*, *Temora discaudata*, *Eucalanus mucronatus*, *E. pileatus*, *E. crassus*, *Canthocalanus pauper*, and *Scolecithrix danae*, revealing structural details of the current, viz. a returning branch around 38°S, an eastward retroflexion of the main current in 42–43°S along the Subantarctic Surface Water, penetration of Agulhas Current water into the Atlantic with northward transport on the western side of the Benguela front, and colonization of the warm centre of the Schmitt-Ott eddy.

A most pervading indicator of Agulhas Current admixture is *Macrosetella gracilis*. It penetrates as far north as 30°S into the Atlantic, but has not yet been found in South West African waters, except for one specimen during the 1963 oceanographic anomaly reported by Stander & De Decker (1969). Its world distribution is circumtropical; in the south-western Atlantic it is an indicator of the Brazil Current (Björnberg 1959).

#### *Agulhas Bank patterns*

The Agulhas Bank appears to be the centre of dispersal for *Calanus finmarchicus* s.l., *Candacia bipinnata*, and *Centropages chierchiae*. The name *Calanus finmarchicus* s.l. is used here to designate a form of uncertain taxonomic status showing morphological resemblances with both *C. australis* (Brodski, 1959) and *C. pacificus pacificus* (Brodski, 1959). The various sibling species derived from the original *C. finmarchicus* stock appear to be concentrated (at least in the Southern Hemisphere) on and near shelf areas (Australia, Tasmania, New Zealand, Chile, Argentina, and Tristan da Cunha) but rare in the open ocean, as stated by Jillett (1971) in the case of New Zealand plankton. The Agulhas Bank form may well constitute a separate taxon, different from the varieties of *C. australis* recorded in similar latitudes off Australia, New Zealand and South America but, like these, falling into the *C. helgolandicus*-group.

*Candacia bipinnata* was found by Lawson (1977) in large numbers off the Somali coast and considered a good indicator of coastal upwelling conditions there. Unpublished data about the Benguela upwelling show that the latter opinion needs qualification if applied to southern African conditions: Unterüberbacher (1964) did not find the species during his year-round survey in the Walvis Bay upwelling area, whereas one single specimen was found in the same area by Stander & De Decker (1969) during the 1963 oceanographic anomaly.

An isolated occurrence of *Calanus finmarchicus* s.l. and *Candacia bipinnata* in two different, but close, neighbouring samples south-west of Madagascar supports the suspicion that the Madagascar shelf could harbour these species, whose appearance in the far north-eastern corner of the present survey area would be due to advection by the East Madagascar Current or by migrating eddies generated at its retroflexion. The presence of *Candacia bipinnata* in the waters around Madagascar has been reported by Binet & Dessier (1968) for the Nosy-Bé area and by Lawson (1977) for the Mozambique Channel and the southern tip of the island.



*Centropages chierchiae* appears to be more tolerant than the two previous species and is therefore a good indicator of advection. It avoids the cold upwelled water off the west coast and generally appears to be entrained by the mixed waters bordering the main stream of the Agulhas Current. The species starts following the ramifications of the Current from the moment the latter reaches the eastern flank of the Agulhas Bank. Along the east coast of South Africa it is found in the cooler inshore belt and is practically absent from the Agulhas Current proper, in the same way as can be seen in some other species, e.g. *Calanus finmarchicus* s.l. and *Calanoides carinatus*.

In the south *Centropages chierchiae* is advected along the southward branch of the Agulhas Current, whereas in the Atlantic it spreads in a manner similar to the Agulhas Current species *Macrosetella gracilis*, but further west and north.

The distribution of *C. chierchiae* is clearly dictated by the dynamic effect of the various branches of the Agulhas Current on the surrounding waters, although it does not belong to the fauna of that Current. Its areas of higher concentration are also clearly different from those of *Macrosetella gracilis*. A similar effect on the distribution of species not belonging to the Agulhas Current community is seen in cases such as *Calanoides carinatus*, *Candacia ethiopica*, *Centropages brady*, *Eucalanus attenuatus*, *Labidocera minutum*, *Rhincalanus cornutus*, *R. nasutus*, and *Temora turbinata*.

In the literature *Centropages chierchiae* is considered a tropical and subtropical Atlantic species (Vervoort 1965). Its distribution pattern in South African waters suggests that it is a form of mixed water, preferring higher temperatures than its congener *C. brachiatus*, which lives inside the colder belt of coastal upwelling. Available literature data about *C. chierchiae* convey the impression that the species is essentially neritic (see Bainbridge 1972), like many other *Centropages* species, but the distribution pattern emerging from the present survey suggests that it can withstand advection over considerable distances, as do some other neritic forms, e.g. *Temora turbinata* (Bradford 1977; De Decker & Coetzee 1979).

The small patch of *C. chierchiae* off Walvis Bay could be an outpost of a northern population of the species extending from the Moroccan coast (Furnestin 1957) southward along the coast as far as Angola (Marques 1953, 1958; Bainbridge 1960a, 1960b; Vervoort 1965; Neto & Paiva 1966; Corral 1970, Corral & Corral 1970) and occasionally carried towards the vicinity of Walvis Bay by the warm Angola Current (Unterüberbacher 1964; Stander & De Decker 1969). Several years' unpublished data at the author's disposal do not show a single instance of continuity between the west African and the South African populations of *C. chierchiae*.

#### *Benguela Current patterns*

*Centropages brachiatus* is most typical of the Benguela Current System and one of its most abundant copepods. Its world distribution is limited to certain areas of coastal upwelling, mainly in the Southern Hemisphere: it is a dominant species in the Peru Current (Björnberg 1973) and is also present, but less abun-



dantly, over the Atlantic shelf of South America (Ramirez 1966, 1969; Björnberg 1963).

Like most *Centropages* species, it is essentially neritic and, contrary to *C. chierchiae*, it thrives in the cool upwelling belt hugging the shoreline between the Cape and the northern outskirts of the Namib Desert. The sinuosity of its main distribution boundary to the west reflects the general trend of the depth contours, as in the case of *Calanoides carinatus* (see below). Its scattered occurrences west of the thermal front may be the expression of cool frontal eddies spawned by the Benguela System. The 500 nautical miles-long extension of the distribution area west of Cape Town is difficult to explain: it appears to be connected with some dynamic process as a similar westward trend can be seen to a variable extent in that area in the patterns of *Acrocalanus gibber*, *A. gracilis*, *Calanus finmarchicus* s.l., *Centropages chierchiae*, *C. furcatus*, *Euterpina acutifrons*, and *Temora turbinata*, and was observed mainly in samples collected during the TR cruise in March 1968. Two distribution maps of surface temperatures obtained by satellite in May–June 1966 and in 1970 have been published by Sze-kielda (1972). They show a cold patch centered about 300 nautical miles due west of Cape Town in approximately the same position as the westward extension of *Centropages brachiatus* and the other species named above. A similar hydrological configuration was found during March 1969 in the form of a cold-core, low-salinity anticyclonic vortex of about 200 nautical miles in diameter west of Cape Town, and on 9 February 1977 a similar feature in much the same position was detected on an infra-red image (Harris & Van Foreest 1977).

Apart from this isolated case of long-distance advection, *C. brachiatus* does not seem to withstand distant transport: the massive southward advection shown by *C. chierchiae* is indicated only faintly by *C. brachiatus*, whereas the penetration into the Indian Ocean, conveying a number of west coast species up the Natal coast by way of the inshore upwelling cells dotting the south-eastern coastline, is attested in the case of *C. brachiatus* merely by its occurrence off Durban in a single sample.

Northwards *C. brachiatus* does not appear to reach as far as Angola: neither Marques nor Neto & Paiva recorded it. Its only mention further north is by Rose (1929)—Mauretania, Canaries, Azores (authorities not named). The record from the Gulf of Guinea by Scott (1894) was proved erroneous by Bainbridge (Vervoort 1965). Recent investigations in the north-west African Atlantic by Corral (1970, 1972), Corral & Corral (1970) did not confirm the presence of *C. brachiatus* in these parts.

De Decker's (1962) suspicion that Cleve (1904) misidentified *C. brachiatus* as *C. typicus* in his South African material has been proved correct on examining Cleve's specimens in the collections of the South African Museum at Cape Town.

*Calanoides carinatus* is one of the main components of the zooplankton in the Benguela Current System, along with *Centropages brachiatus* (Unterüßbacher 1964; Hutchings 1979), but may be less abundant in the samples under discussion because of its preference for deeper levels; the gaps in its occurrence



along the west coast sampling track (HB cruise) are caused by diurnal vertical migration.

Like *Centropages brachiatus*, *Calanoides carinatus* proliferates in upwelling areas, but in the Benguela Current System it seems to occur at lower temperatures than those favoured by *Centropages brachiatus*. On a world-wide scale, however, it appears to be more eurythermic than *C. brachiatus*: in tropical coastal upwellings such as those in the Gulf of Guinea (Bainbridge 1972; Mensah 1974), along the south coast of Arabia (Vinogradov & Voronina 1962; Gapishko 1968; Grobov 1968), and off Somalia (Smith 1982), *Calanoides carinatus* occurs in water temperatures between 18 and 25 °C, which are the local minima. Such eurythermy may explain the extensive southward and north-eastward advection sustained by this species in the survey area, in contrast to *Centropages brachiatus*. The latter has never been recorded off Angola, whereas Marques (1953, 1956, 1958) established the presence of *Calanoides carinatus* in sizeable quantities along the whole Angolan coast as far north as Cabinda. Neto & Paiva (1966) found it practically all year round in Baía Farta (12°36'S). Data of the occurrence of *C. carinatus* along the whole Atlantic coast of Africa have been summarized by Thiriot (1977).

The near-continuous occurrence of *Calanoides carinatus* along the southern leg of the 1968 WS cruise is puzzling. In this connection it may be noted that the author, having examined large numbers of *Calanoides* specimens taken at various depths all around southern Africa, has serious doubts about the taxonomic homogeneity of the representatives of this genus in the area concerned, apart from the seasonally occurring *C. macrocarinatus*. The still problematic *C. natalis* Brady comes to mind in this context.

*Metridia lucens*, another abundant form in the Benguela Current System, differs fundamentally from both species mentioned above in that its surface distribution appears to form a direct link between the west coast upwelling and the Subantarctic. Its presence in the Marion–Crozet region agrees well with the findings of Seret (1979) around the Crozet and Kerguelen islands, those of Hardy & Gunther (1935) around South Georgia, and of Ealey (1956) at Heard Island. Although more cryophilic than *Calanoides carinatus* and *Centropages brachiatus*, the occurrence of *M. lucens* in surface samples off the west coast of southern Africa extends further into the warm surface water beyond the Benguela front. This can be explained by the extensive diurnal vertical migration of *Metridia*: whenever the thermocline lies at a depth within the migratory range of this organism (i.e. a few hundred metres), *Metridia* may be found near the surface at night.

The isolated occurrence of *M. lucens* near Durban is another instance where east-coast upwelling manifests itself. Other species showing a similar occurrence are *Calanus finmarchicus* s.l., *Candacia bipinnata*, *Centropages brachiatus*, *Clytemnestra scutellata*, *Ctenocalanus vanus*, and *Euchaeta wolfendeni*. The biological effects of the east-coast inshore upwelling seem to be regular, more intense, and longer lasting in the Durban area than elsewhere along this coast. One may draw attention, in this connection, to the phenomenon



called 'Natal pulse' by Lutjeharms (1981a), whereby large deflections of the Agulhas Current away from the coast appear to be initiated in the Natal Bight, inducing corresponding dynamic upwelling inshore.

Seret (1979) distinguished two size groups of *M. lucens* in her material from Kerguelen. Size measurements were not made on the material discussed here, but the author did notice some subtle differences among the specimens taken in the southern part of the survey area; the lateral profile of the head and the shape of the fifth thoracic segment were closer to *M. gerlachei*. A detailed account of this difference will be rendered elsewhere.

The three species discussed above, although dominant members of the zooplankton assemblage of the Benguela Current System (Unterüberbacher 1964; Hutchings 1979), have little else in common biogeographically in the eastern Atlantic. *Centropages brachiatus* is limited to the coastal upwelling belt and its close vicinity between the Cape and the northern part of South West Africa; it is neritic epiplanktonic. *Calanoides carinatus* stretches along the whole length of the African Atlantic, living in mesopelagic depths, probably along the slope, and migrating to the surface and inshore during the upwelling season (Thiriot 1977, 1978). *Metridia lucens* extends northward from the Subantarctic to south of Angola; its abundant North Atlantic population extends southward along the African coast and tapers out in the latitude of Gambia (Kornilova 1967; Thiriot 1978).

#### *Subantarctic patterns*

*Calanus simillimus* and *Clausocalanus laticeps* have a clearly Subantarctic distribution, but they display great discrepancies between their occurrences during successive cruises.

Along the eastern leg of the AM cruise (April 1963), they were found 300 to 400 nautical miles further north than the neighbouring western leg of the MC cruise (June 1962), apart from an isolated northern patch along the latter leg. A similar difference in latitudinal position existed between both legs of the MC and AM cruises.

During the SA cruise (March 1964) both species were completely absent from the survey area, which extended beyond 44°S, but the TR cruise (March 1968) showed their presence in the same area even to a point slightly further north than the position of the warm core of the large anticyclonic eddy found in 1964 at 40°S.

These discrepancies can be explained by the existence of planetary waves of the same order of magnitude along the Subtropical Convergence and by the transient character of the eddies generated at the retroflexion of the Agulhas Current (see *Remarks on the hydrology* p. 307).

*Scolecithrix glacialis* occurred at the southern outskirts of the survey area only in water temperatures below 12°C; between Marion and Crozet islands, in water temperatures below 6°C, it was somewhat more abundant than elsewhere. Near the upper limit of its temperature range the species was found in night catches only.



The neritic Subantarctic species *Drepanopus pectinatus* shows an amazing oceanic dispersal extending over 300 nautical miles to the north of its normal occurrence on the shelf of the Crozet Islands: it was found in a continuous series of fourteen samples, in quantities of up to twenty specimens per sample, as against several hundred per sample in the neighbourhood of the islands. According to Orren (1966), a northward current was observed at stations between the Crozet Islands and latitude 41°S. An isolated record of *D. pectinatus* still further north, and around 39°30'S, coincides with an upwelling mentioned by Orren (1966: 7, figs 8, 11).

The complete absence of this species from the surroundings of Marion and Prince Edward islands is the more intriguing as it also failed to turn up in the material of Grindley & Lane (1979), who examined fourteen samples taken near these islands by vertical WP II-net hauls between 300 m and the surface in March and November 1976. This record of absence appears to be unique among the Subantarctic islands investigated to date (Bayly 1982).

#### *Notal patterns*

*Clausocalanus ingens*, although widespread, ostensibly avoids temperate extremes. It is absent both from the coldest inshore part of the west coast upwelling and from the warm southern branch of the Agulhas Current. In the eastern part of the Indian sector it shows a zonal trend in the middle latitudes (approx. 35 to 42°S) corresponding roughly to water surface temperatures between 10 and 20°C. In the Atlantic sector the isolines of temperature and salinity are deflected north-eastward against the continent (see Deutsches Hydrographisches Institut *Monatskarten*) and so is the northern boundary of *C. ingens*; the small area in the south where the species was absent during the TR cruise lay slightly south of the 10°C surface isotherm (Henry 1972). The zonal, circumglobal distribution of this species is clearly shown by Frost & Fleminger (1968, chart 3), but dearth of samples from the south-eastern Atlantic prevented these authors from documenting a north-eastward trend in its distribution in that area.

*Calocalanus tenuis* shows a zonal pattern of a similar type to, but much more restricted than, that of *Clausocalanus ingens*; the Schmitt-Ott eddy disrupts the pattern. Hutching's (1979) intensive survey of the Cape Peninsula upwelling showed that *Calocalanus tenuis* is linked with frontal conditions and is most abundant in the presence of strong thermoclines.

Two more species have a pattern suggesting zonality: *Oculosetella gracilis* and *Undeuchaeta plumosa*. It should be kept in mind, however, especially in the case of the latter species, that the present records concern only near-surface patterns of distribution: *U. plumosa* is well known as an inhabitant of deeper water over vast areas of the oceans. Its zonal distribution at the surface, if confirmed, could be linked with some physical or biological factor as yet unidentified, e.g. the absence of a pycnocline between its deep habitat and the surface.

The pattern of *O. gracilis* is in perfect agreement with the map presented by Lang (1948, fig. 314) and the record of Vervoort (1957) south of Tasmania,



while confirming the notal distribution of this species over an added 1 500 nautical miles in the south-western Indian Ocean.

The remarks concerning the surface distribution of *Undeuchaeta plumosa* also apply in the case of *Calanoides macrocarinatus* and *Calanus tonsus*. Though scarce and widely scattered, their occurrences show a degree of similarity in that three out of the four or five patches of occurrence of the one species lie in close proximity to three of the other, viz. south-east of the Schmitt-Ott eddy, near or on the shelf off Port Elizabeth, and over the Madagascar Ridge in about 35°S latitude.

The distribution and life cycle of both species, as recorded in the literature and in unpublished documentation on the South African plankton, appear to have much in common.

Brodski (1972) is probably right in assigning *Calanoides macrocarinatus* to the Notal zone.

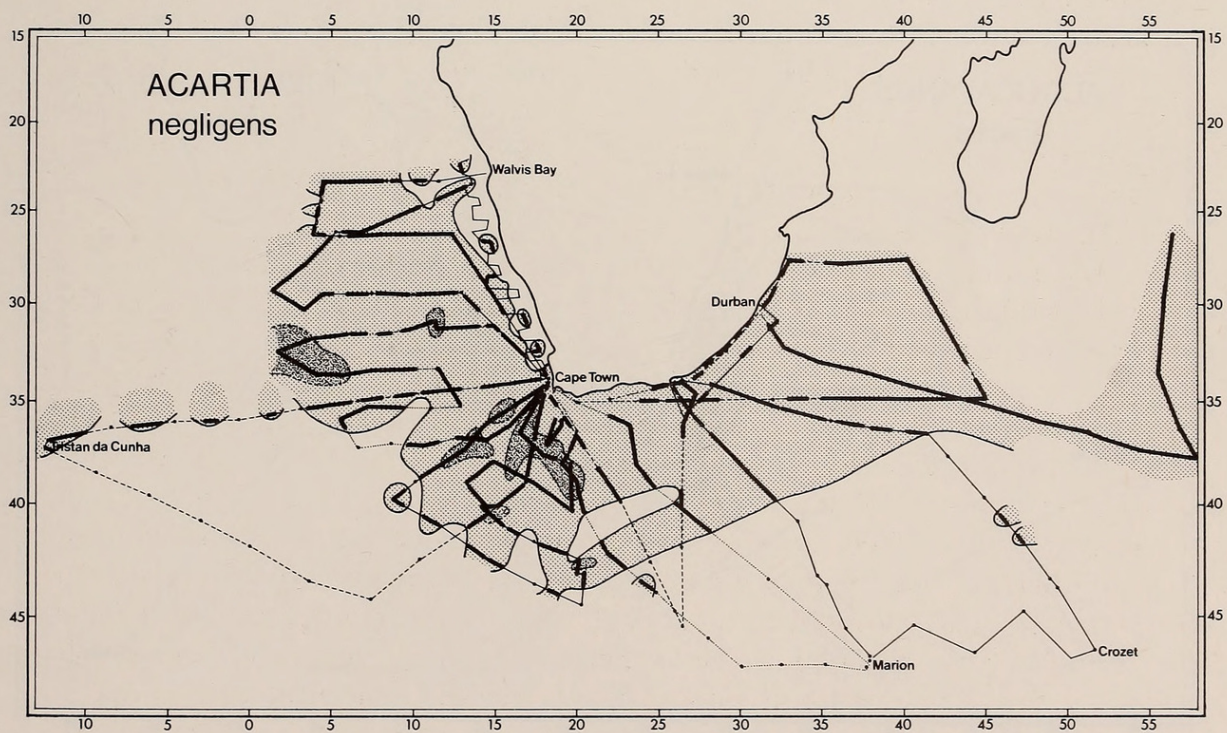
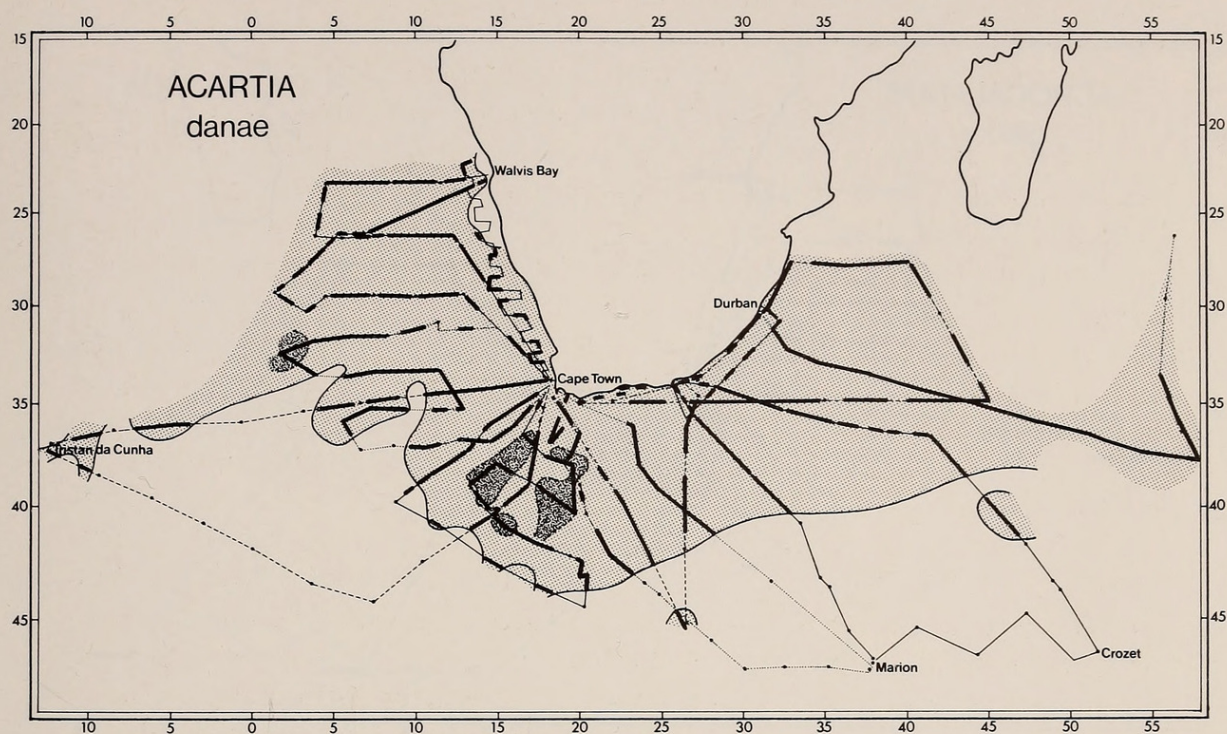
*Calanus tonsus* is typical of the Subantarctic Water (Vervoort 1957; Tanaka 1960, 1964; Senô *et al.* 1963a, 1963b). Jillett (1968), working in southern New Zealand waters near 46°S, noted that the species appeared closely associated with the Subtropical Convergence and that it executed extensive seasonal vertical migrations, appearing near the surface in large numbers from September to January. De Decker (1973), on the basis of unpublished data, mentioned the appearance of *C. tonsus* and *Calanoides macrocarinatus* in the surface water close to the south and west coasts of South Africa, also from September to January. Best (1967) found both species regularly in the stomachs of sei whales shot by shore-based catchers within 200 nautical miles from Cape Town as far as 32°30'S; they appeared from September onward, taking the place of *Clausocalanus ingens*, which the whales had eaten earlier in the year in the same area. (Best's paper antedates the original descriptions of *Clausocalanus ingens* Frost & Fleminger, 1968, and *Calanoides macrocarinatus* Brodski, 1972; these two species are mentioned in the paper as *Clausocalanus arcuicornis*, forma *major* and *Calanoides carinatus*, respectively.)

At Tristan da Cunha, Wiborg (1964) found *Calanus tonsus* in large numbers at the surface between 15 December and 2 February, but absent later in February and in March.

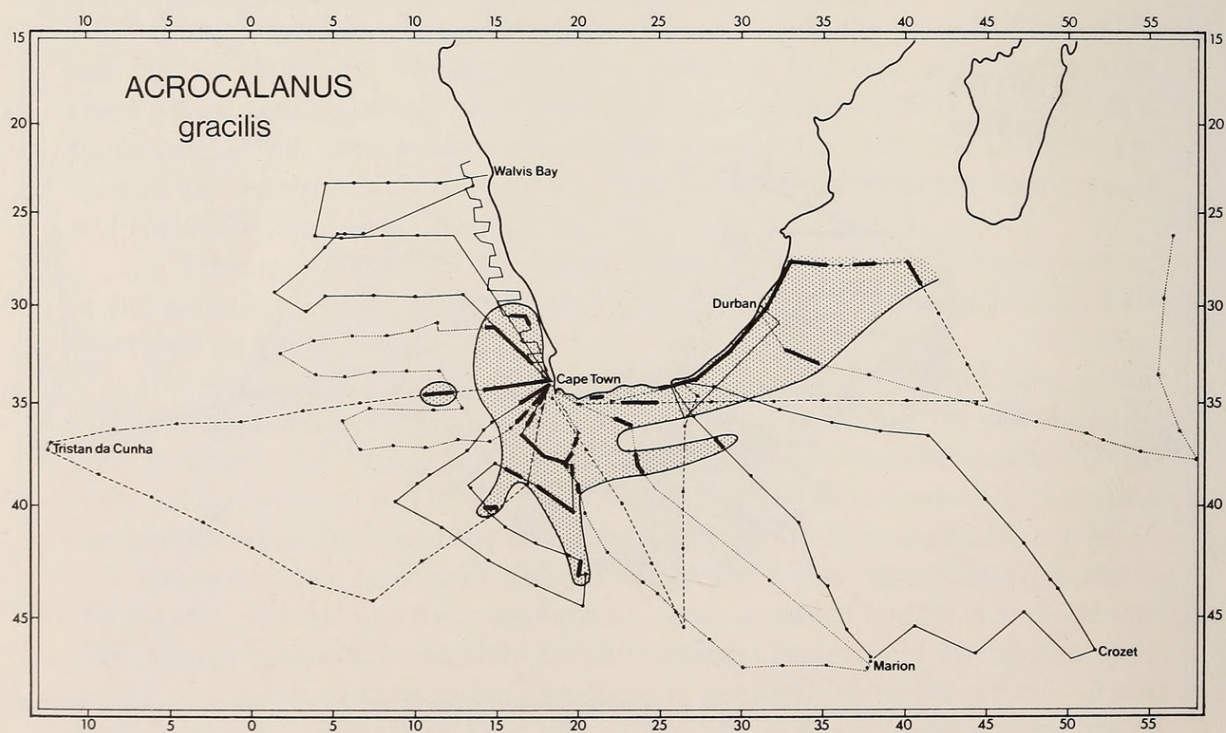
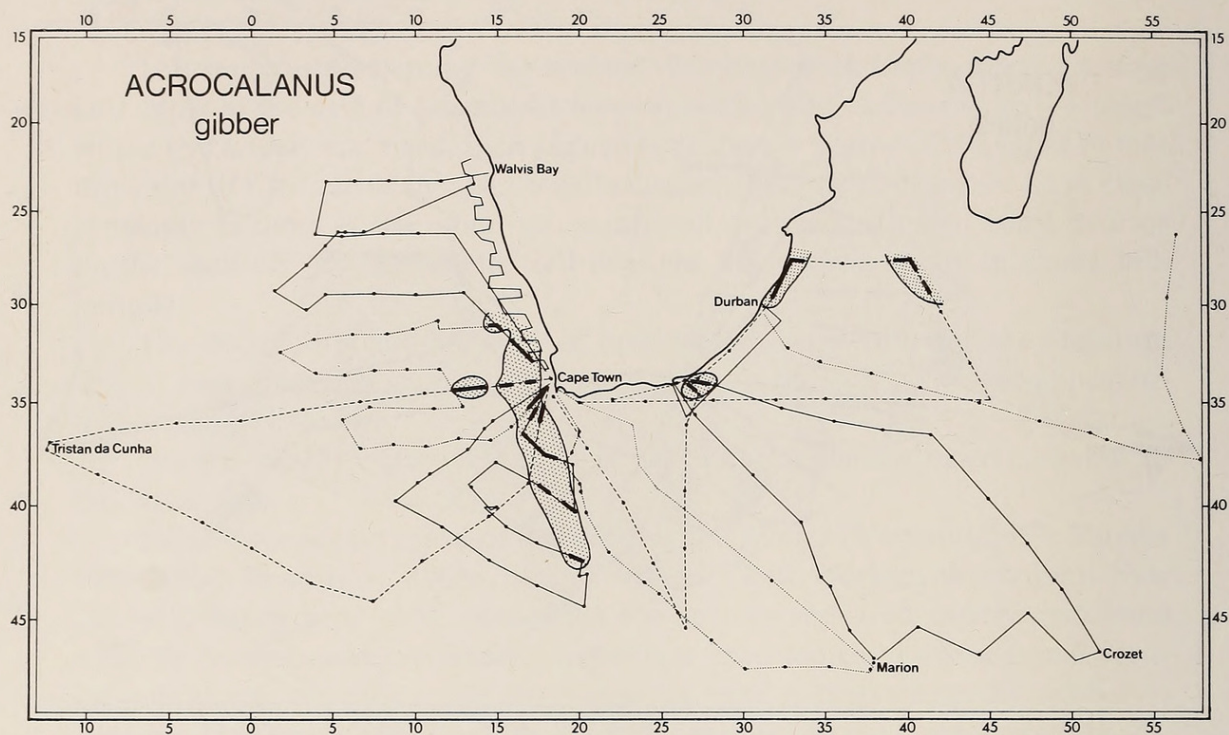
The record of *Calanus tonsus* in a single sample south-west of Madagascar (WS 50, September 1968) may appear suspect, considering the low latitude, 28°S; however, De Decker & Mombeck (1964) recorded a similar isolated occurrence of *C. tonsus* at a station only 60 nautical miles further north in a vertical net haul between 50 m and the surface, during the IIOE cruise in June 1961.

The occurrence pattern of *Calanus tonsus* and *Calanoides macrocarinatus* in the present material and their near-simultaneous seasonal appearance at the surface in large numbers far north of the Subtropical Convergence are another indication of a substantial intrusion of southern elements on to the South African shelf, apparently without relation other than vicinity to the inshore upwelling of the Benguela Current System.

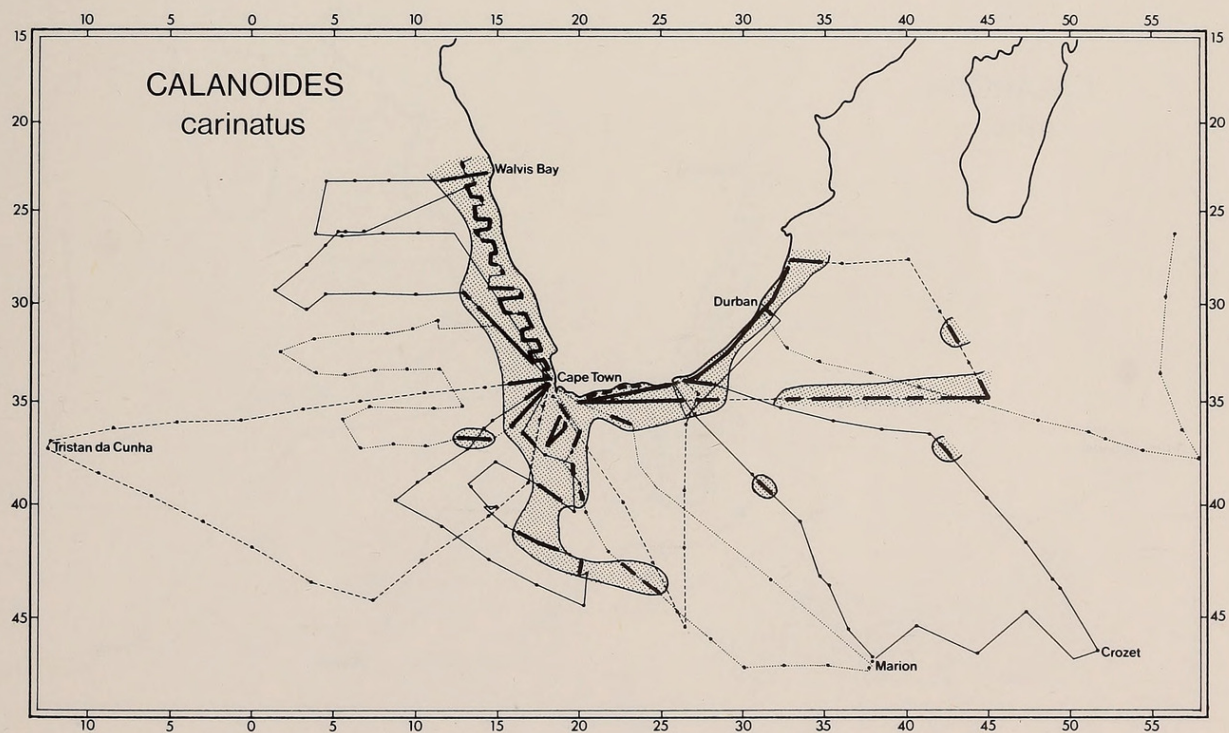
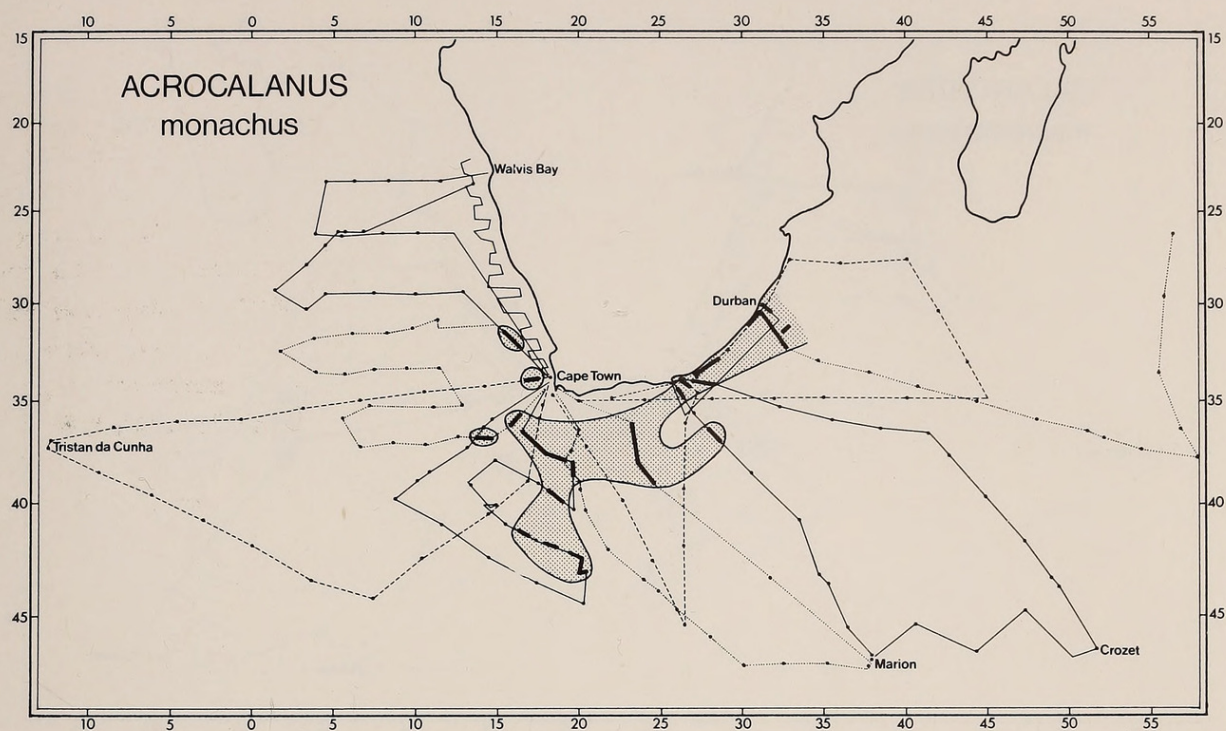




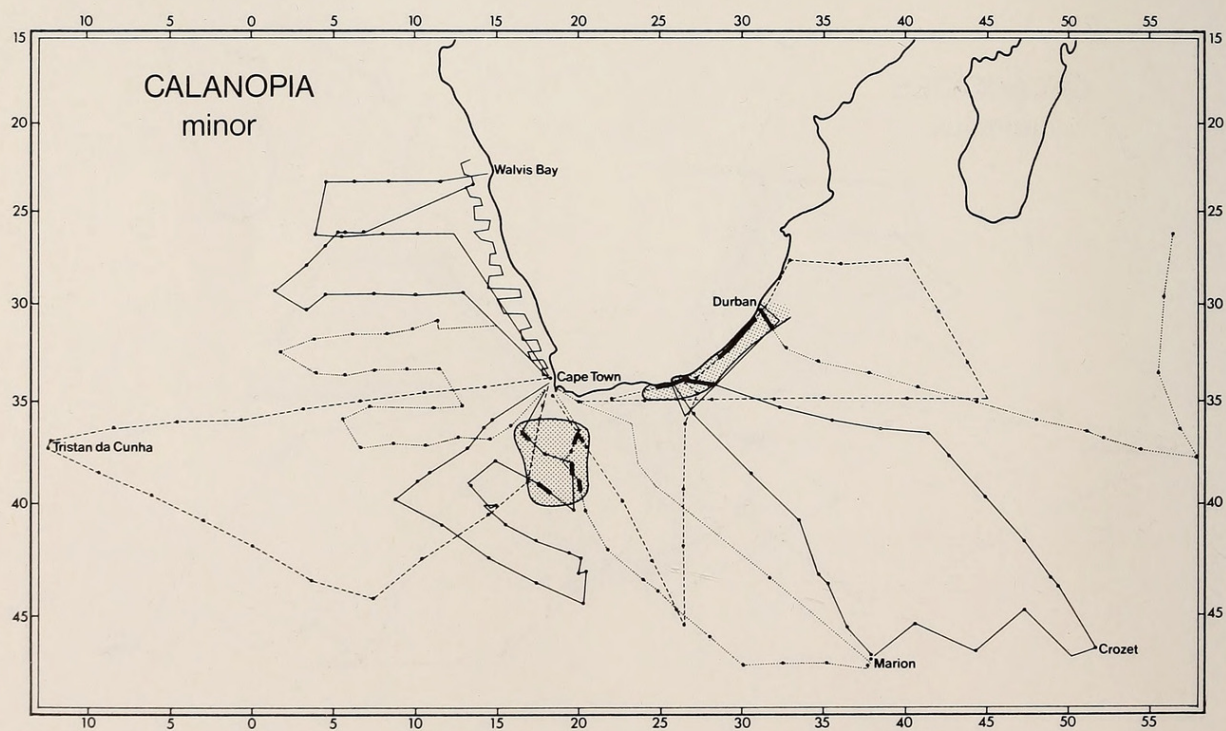
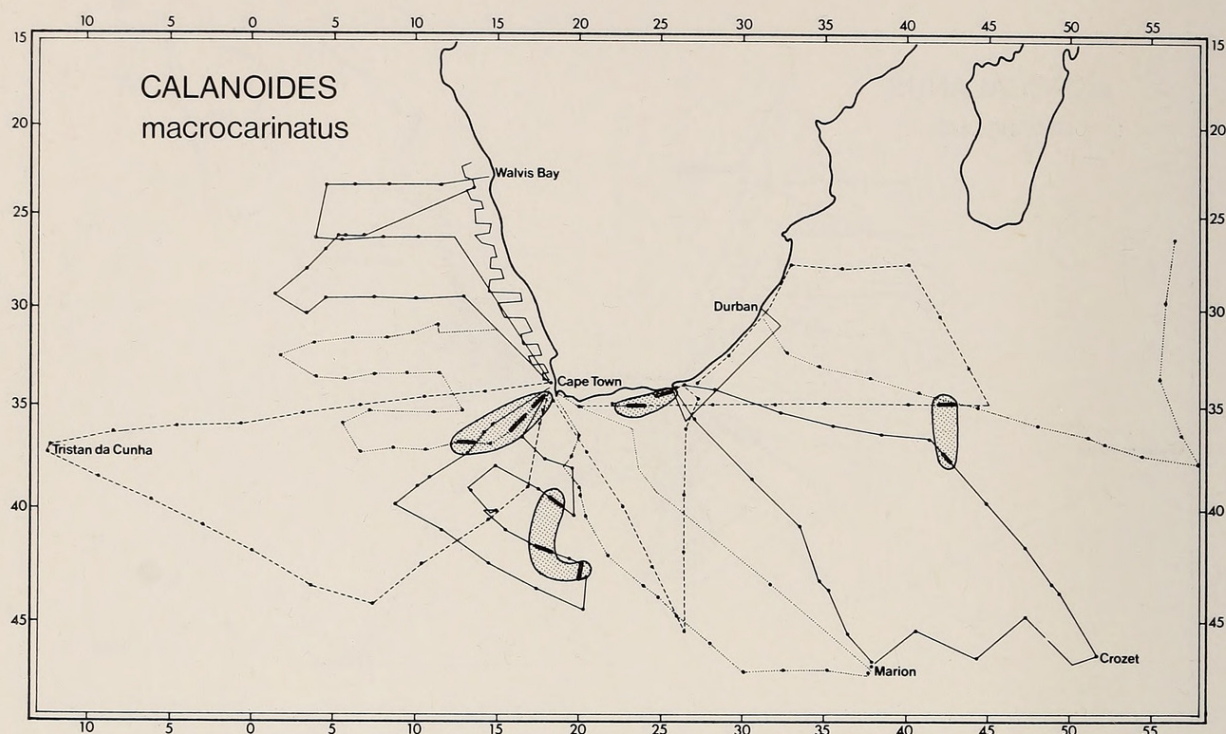




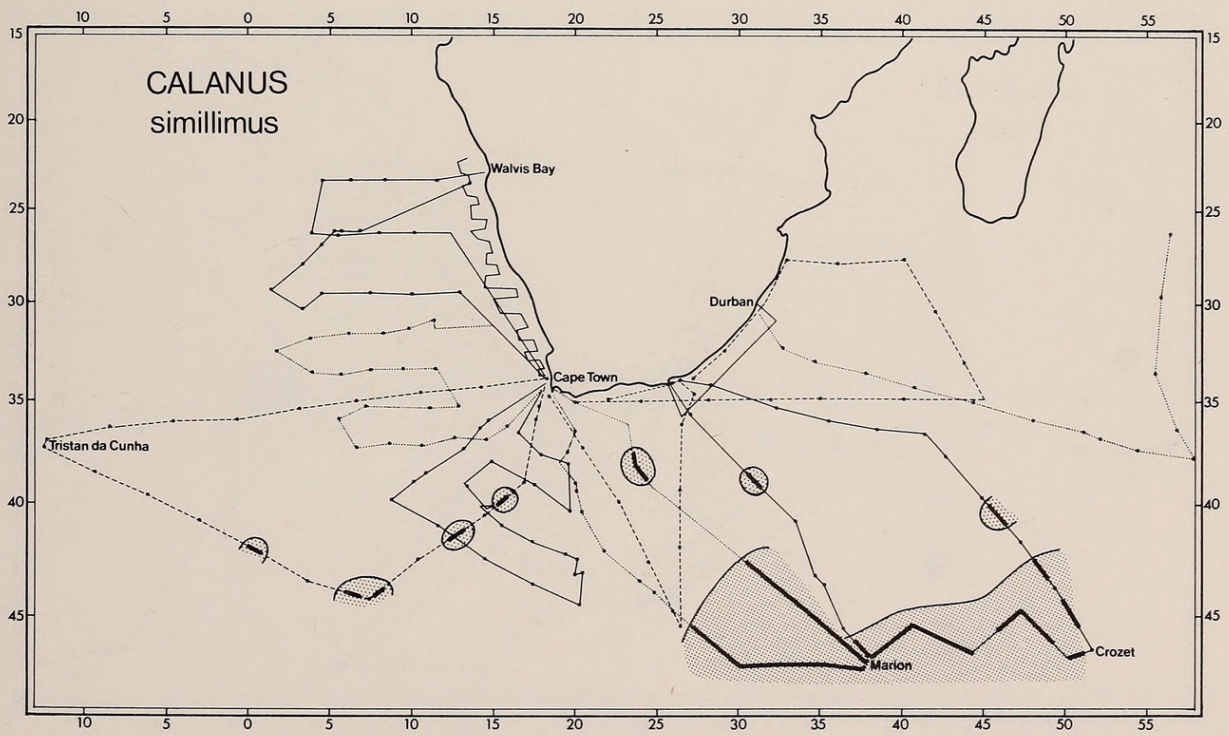
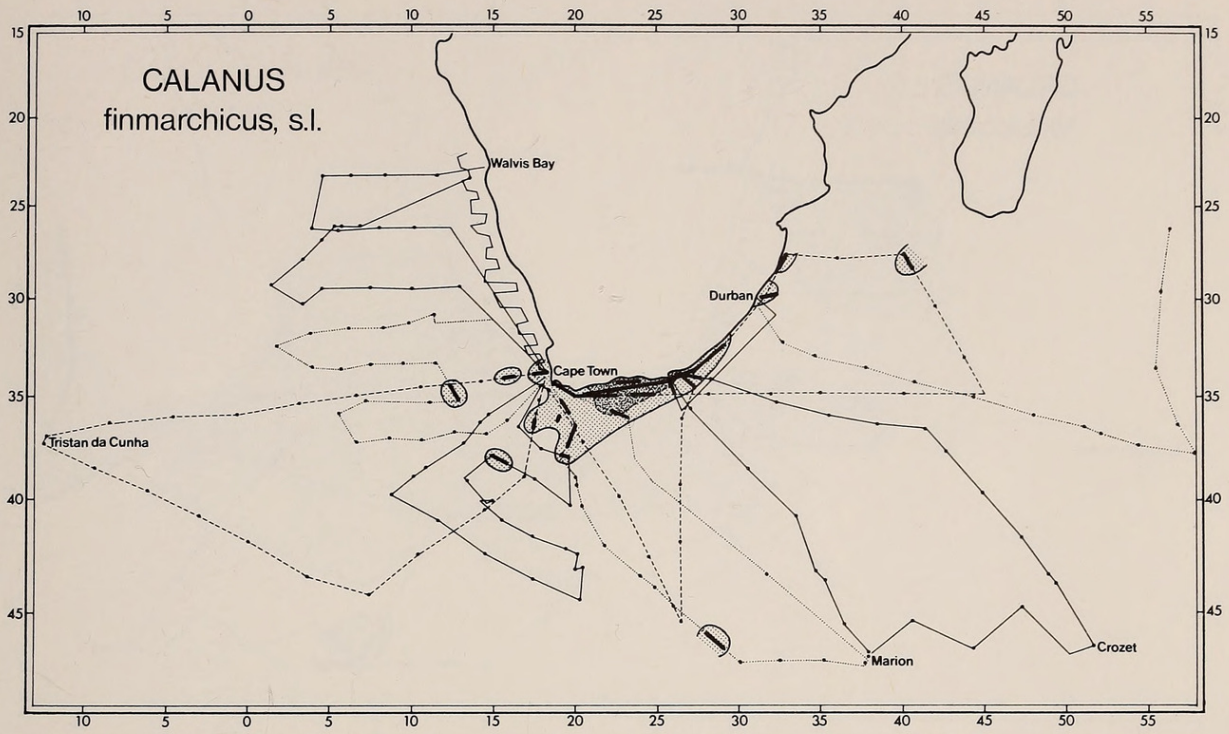




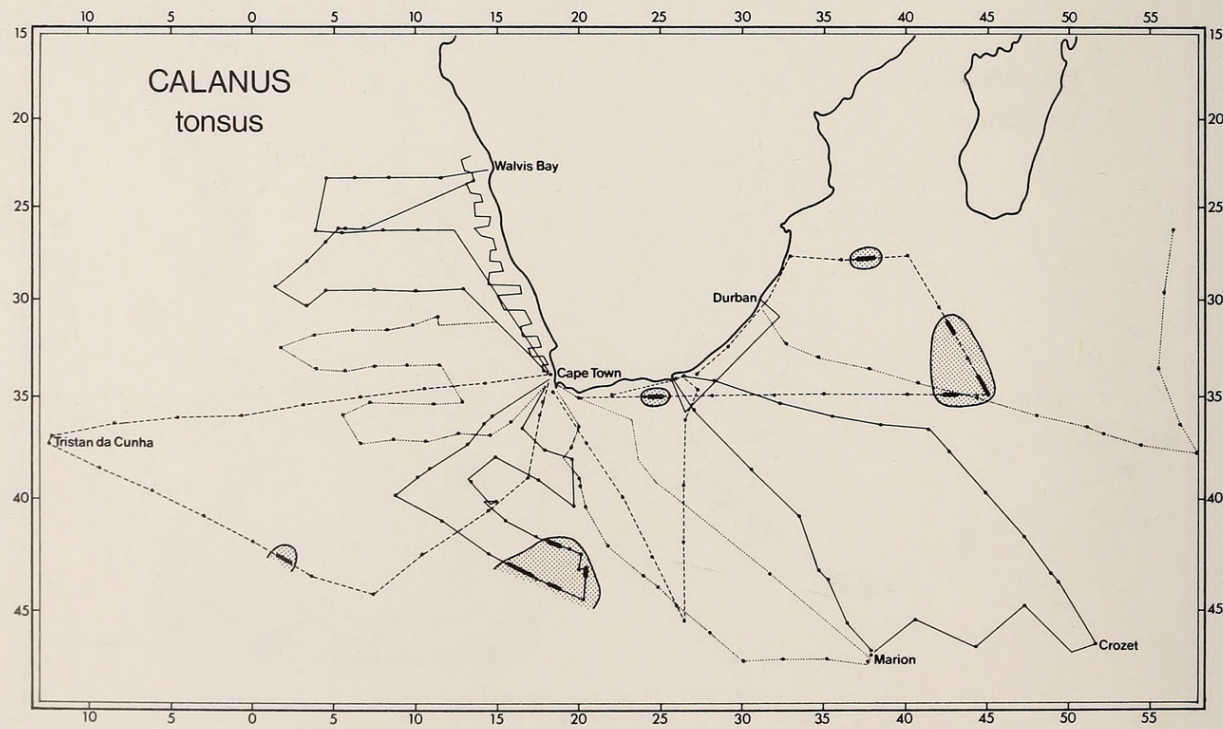
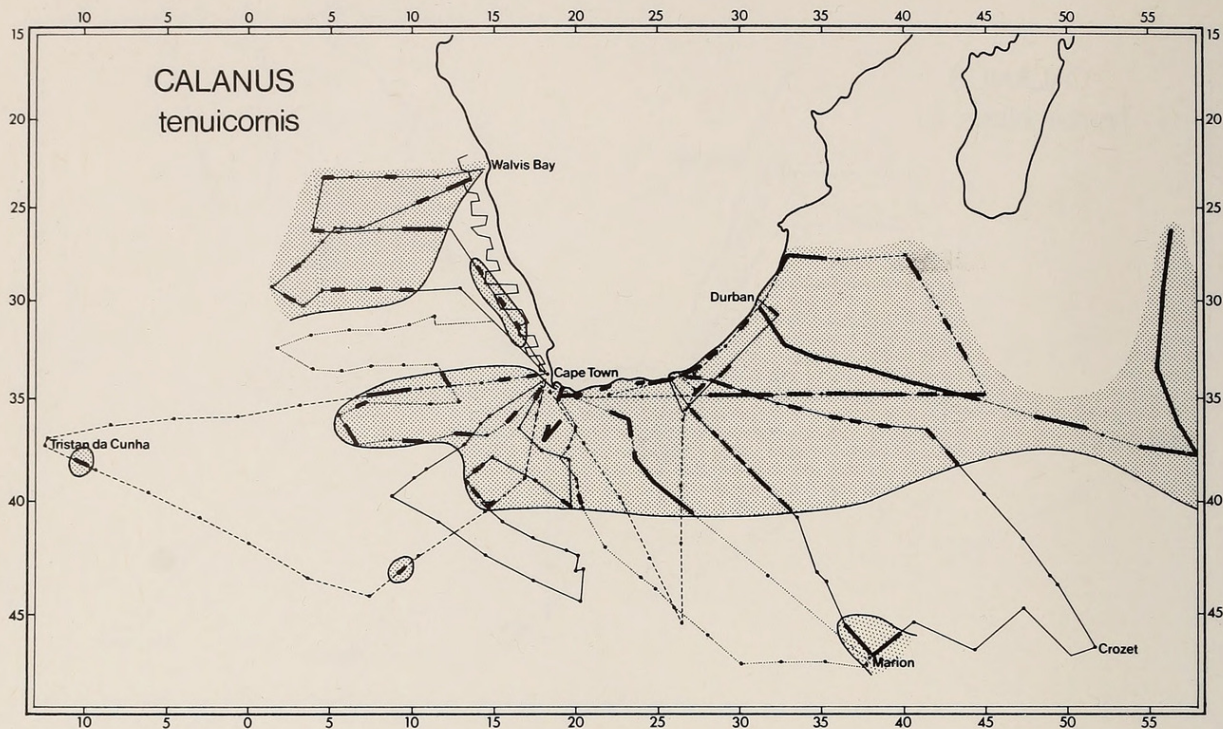




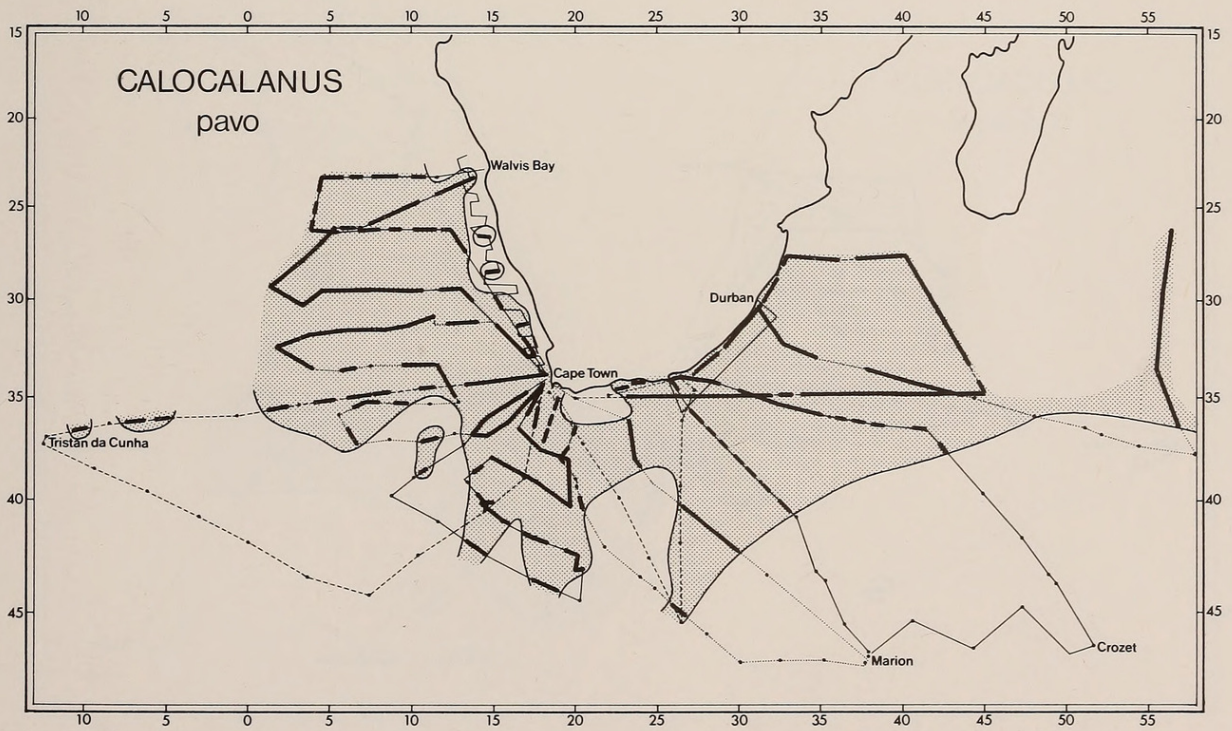
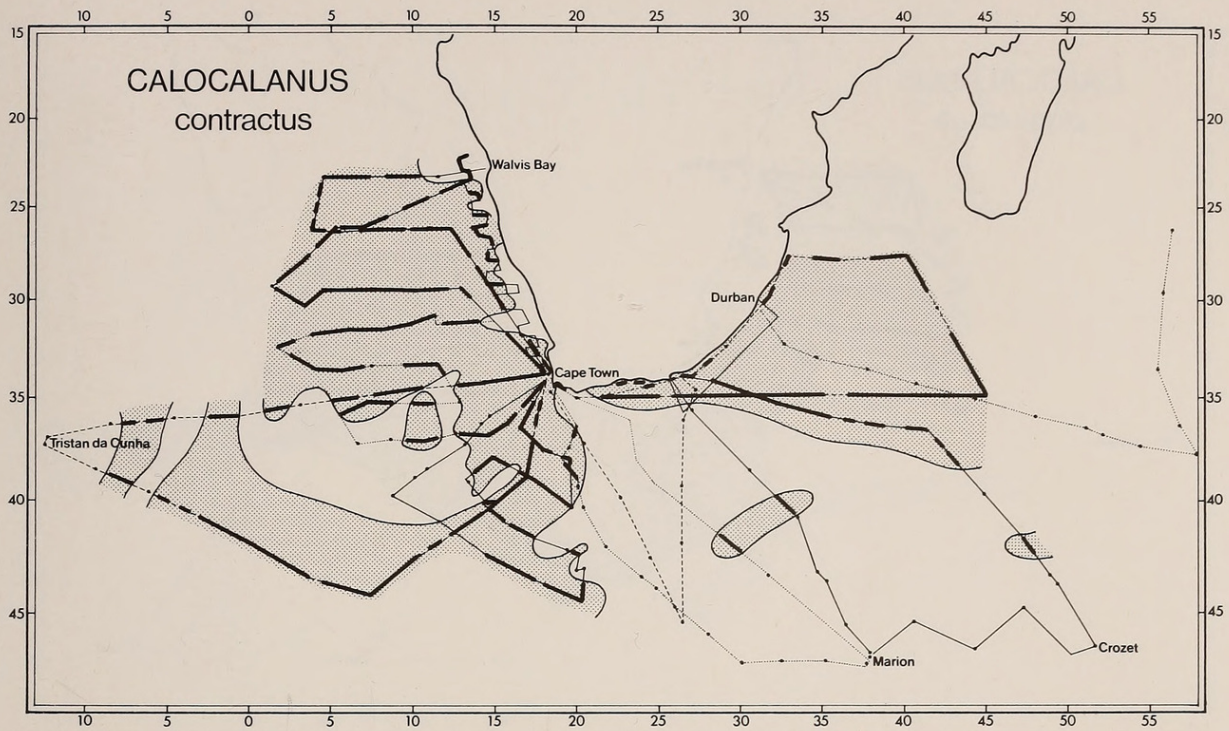




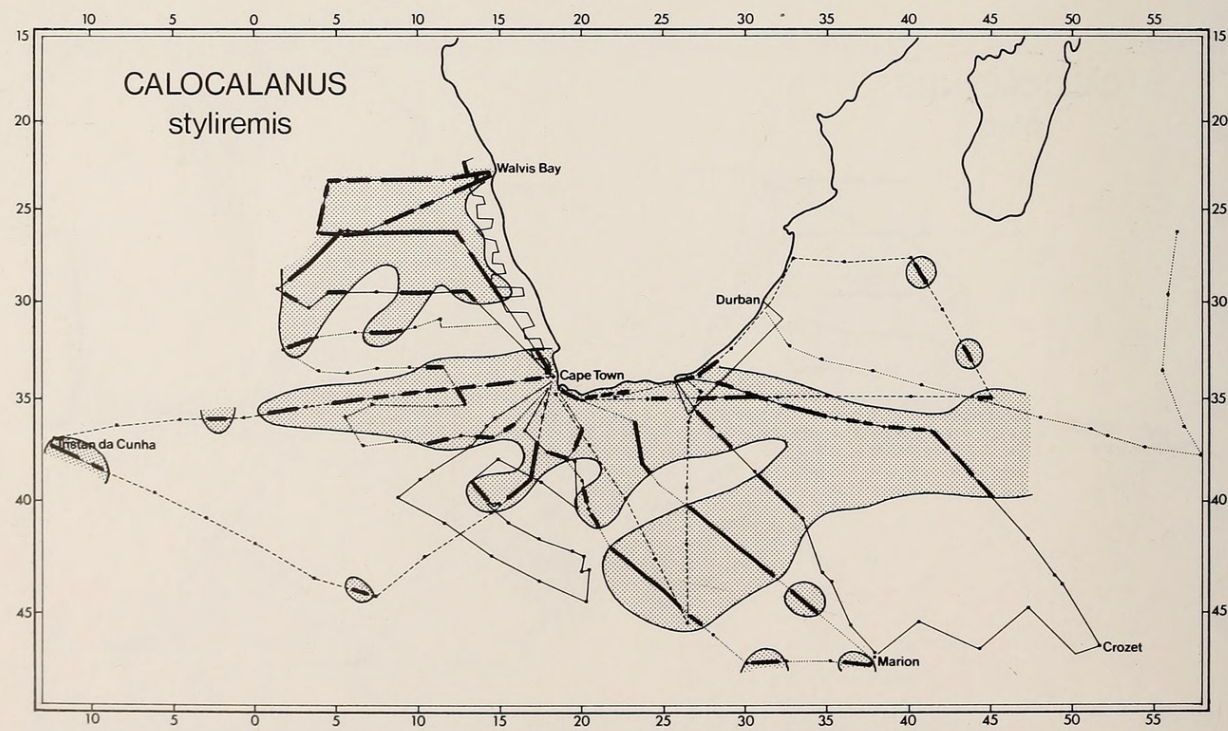
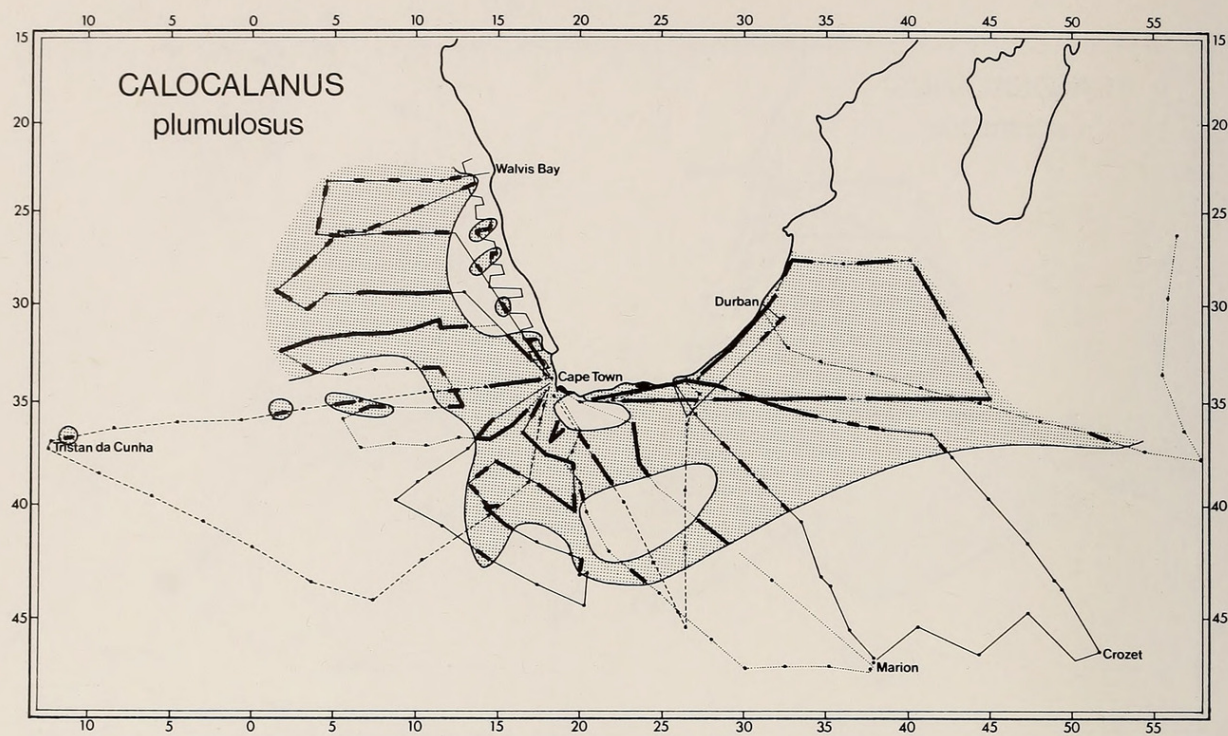




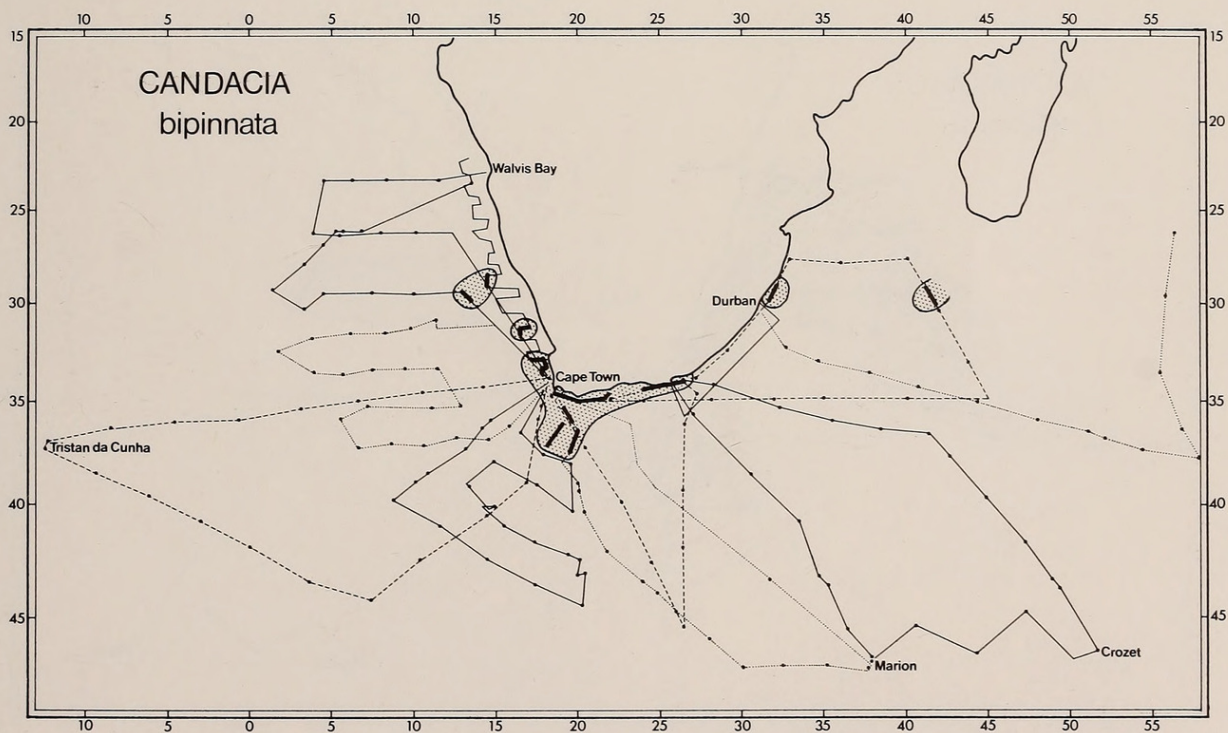
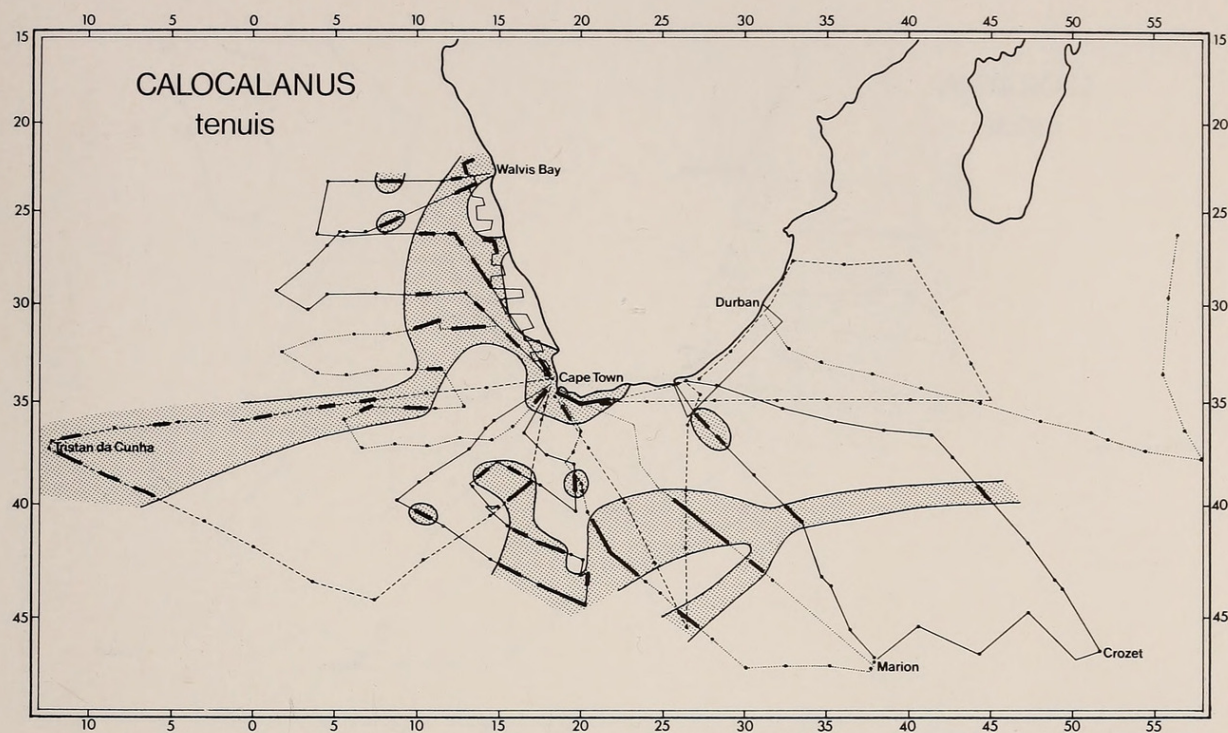




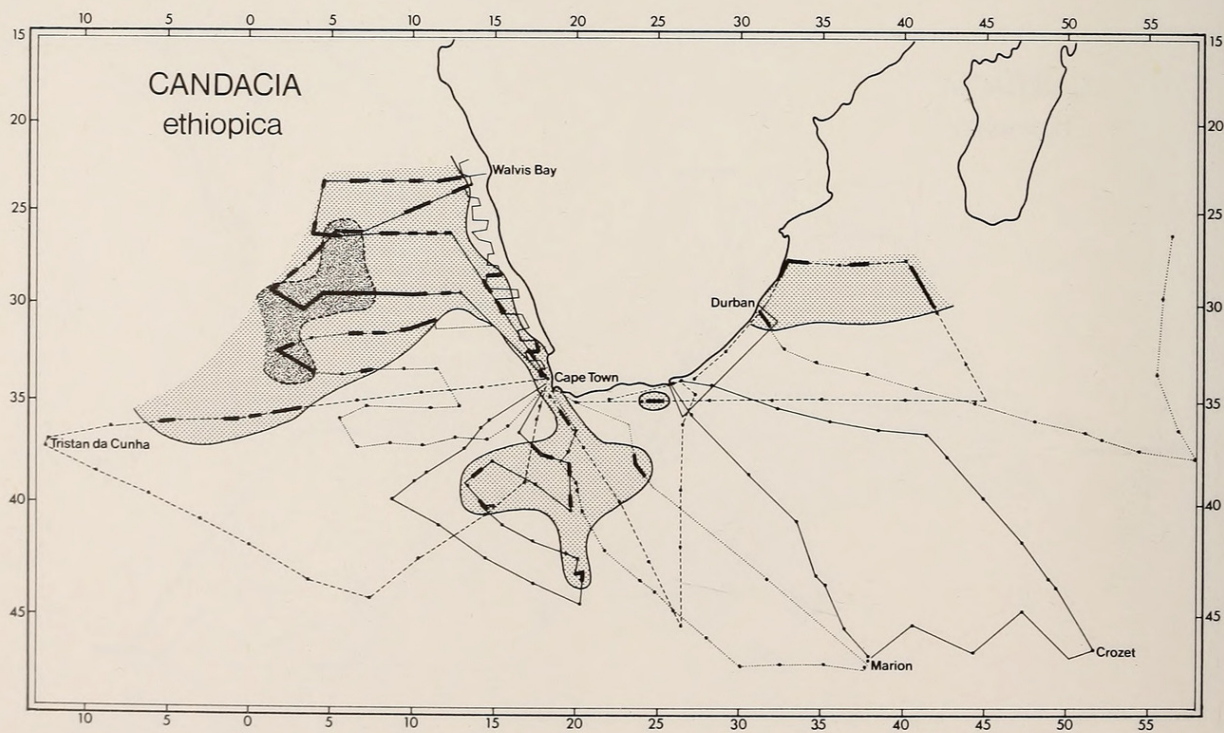
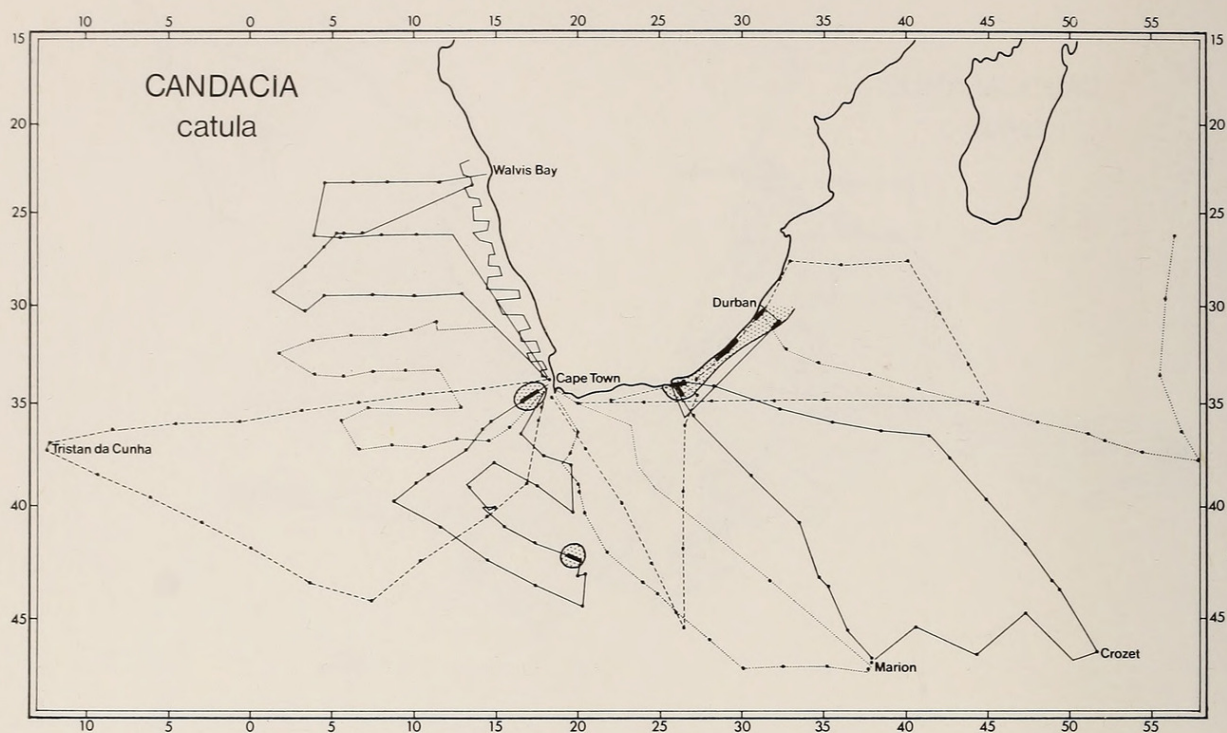




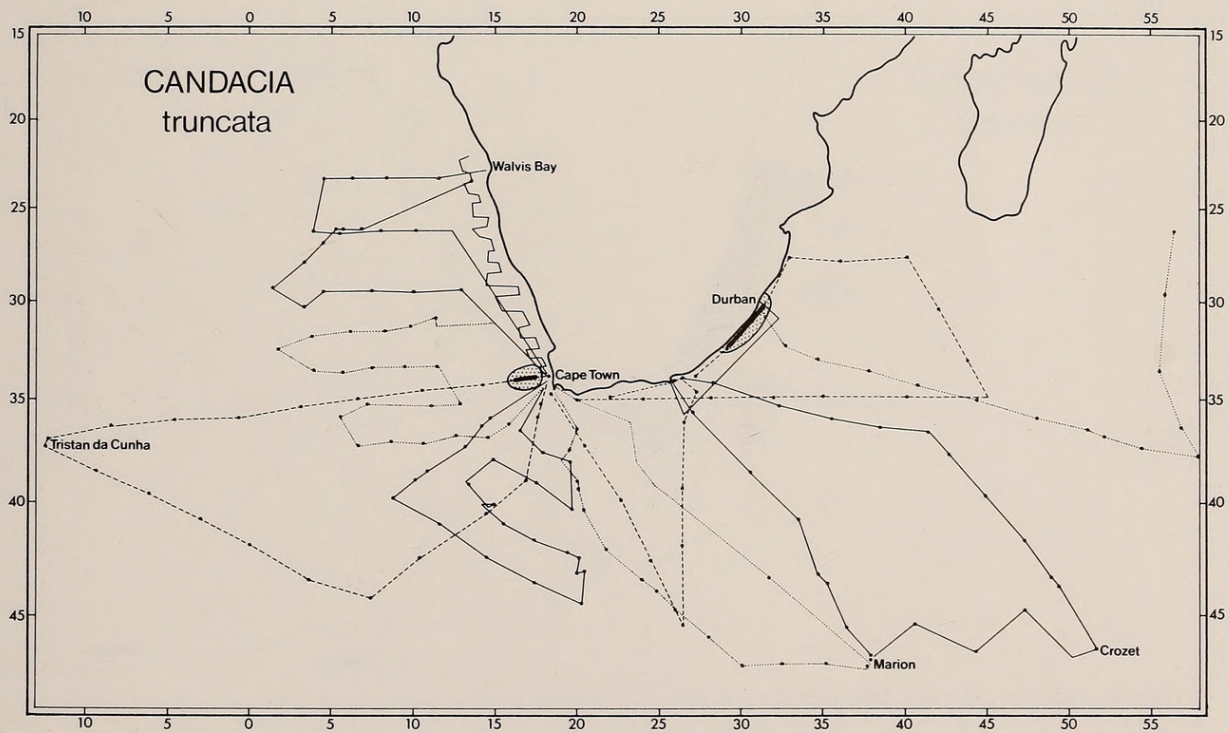
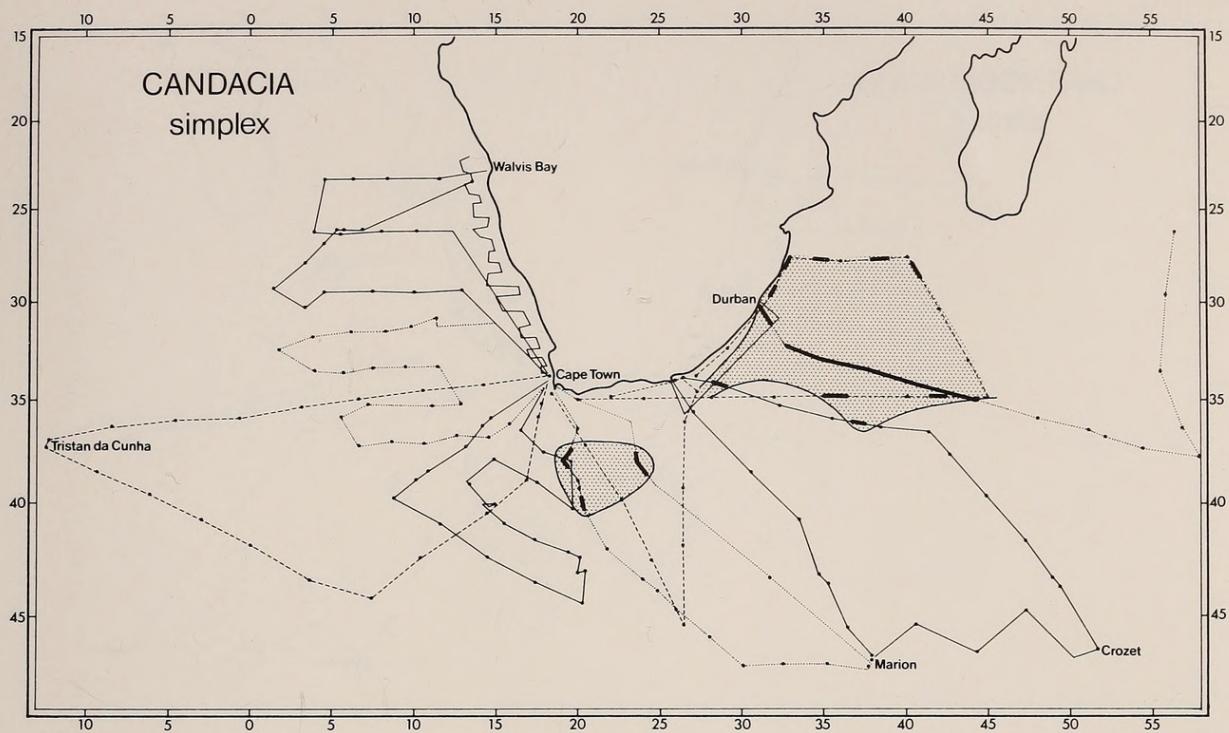




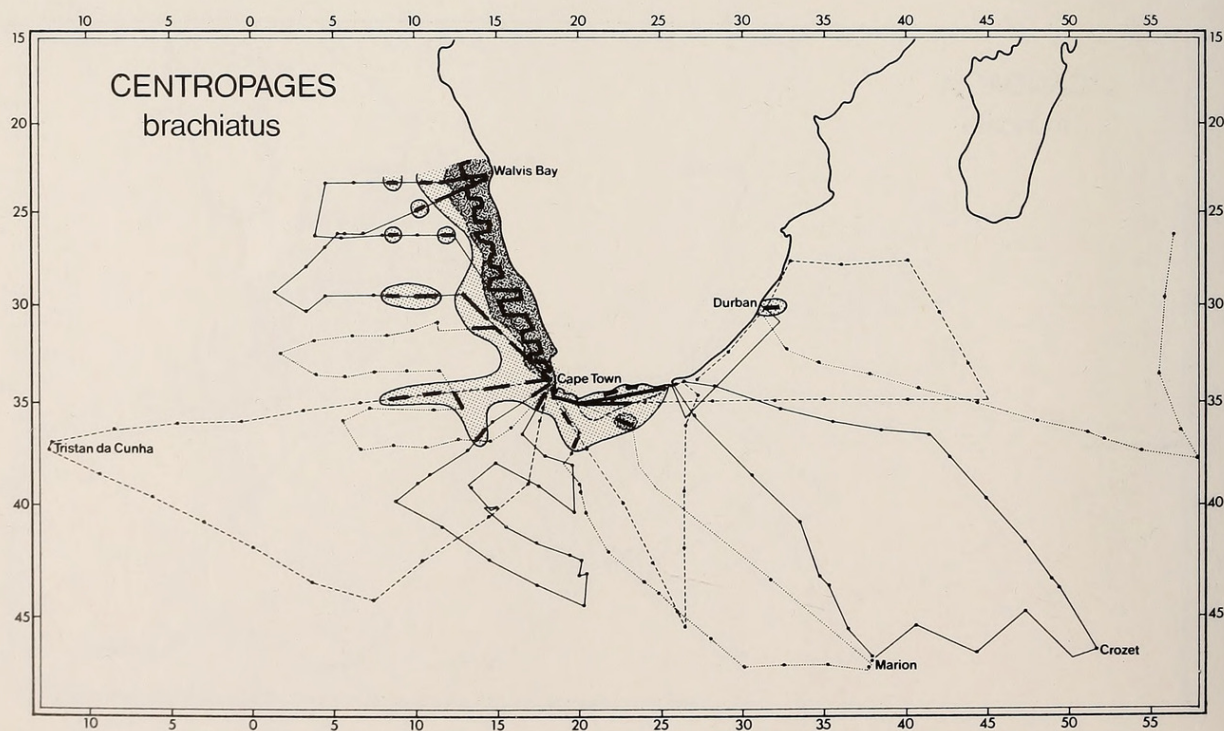
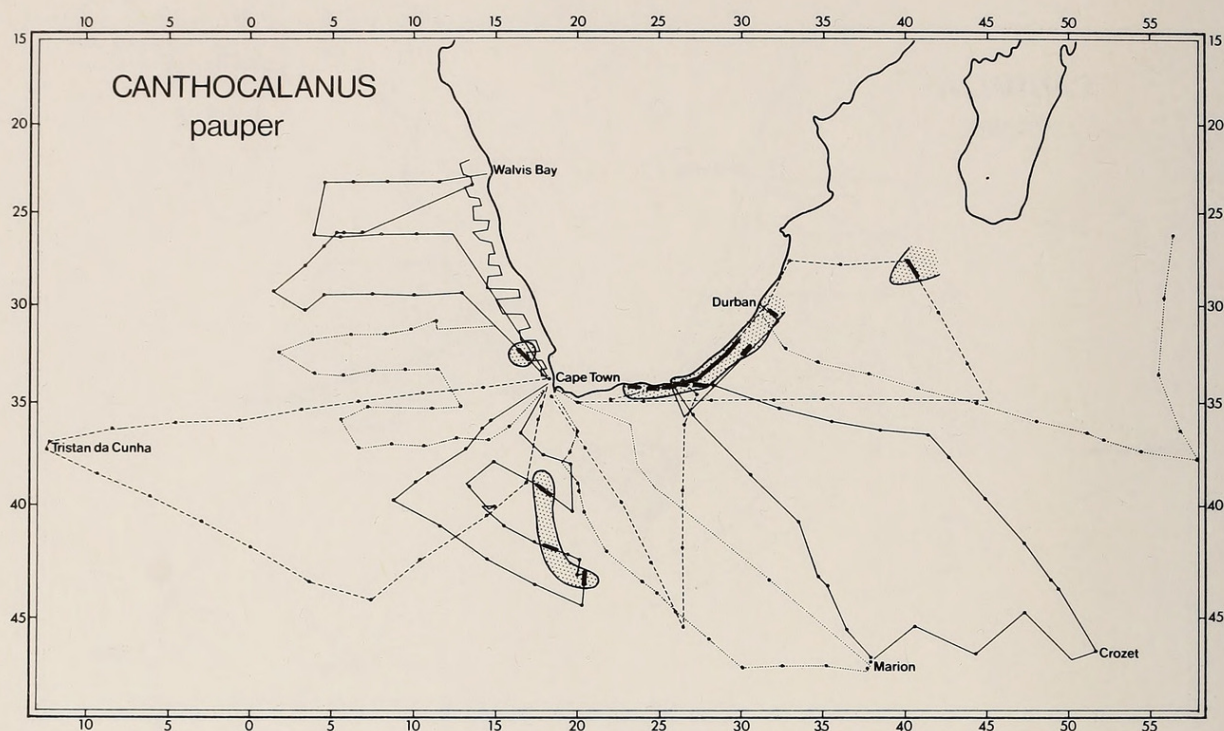




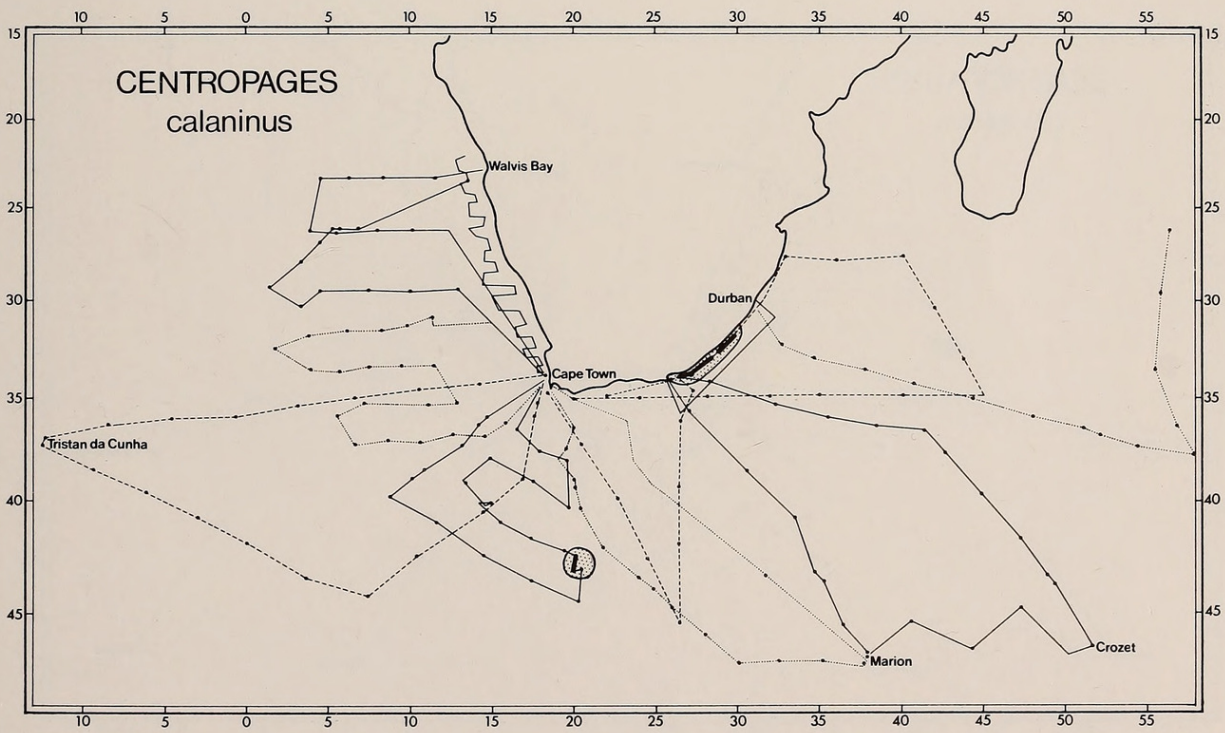
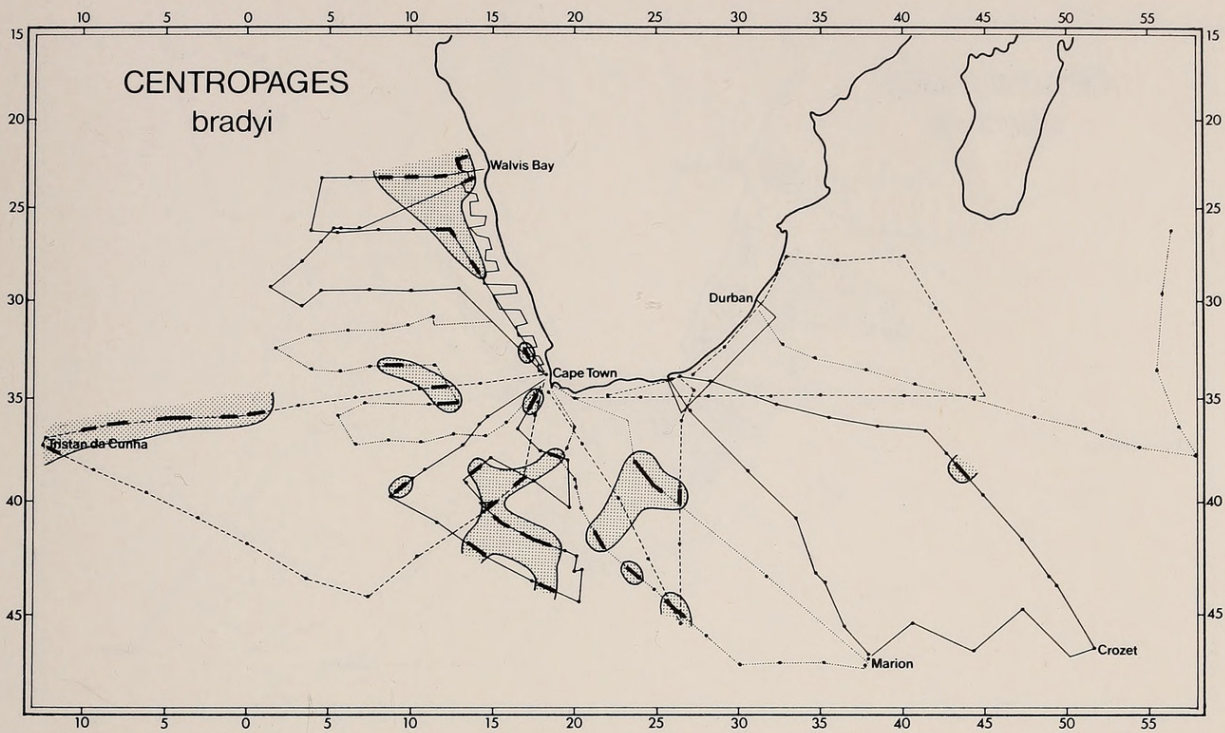




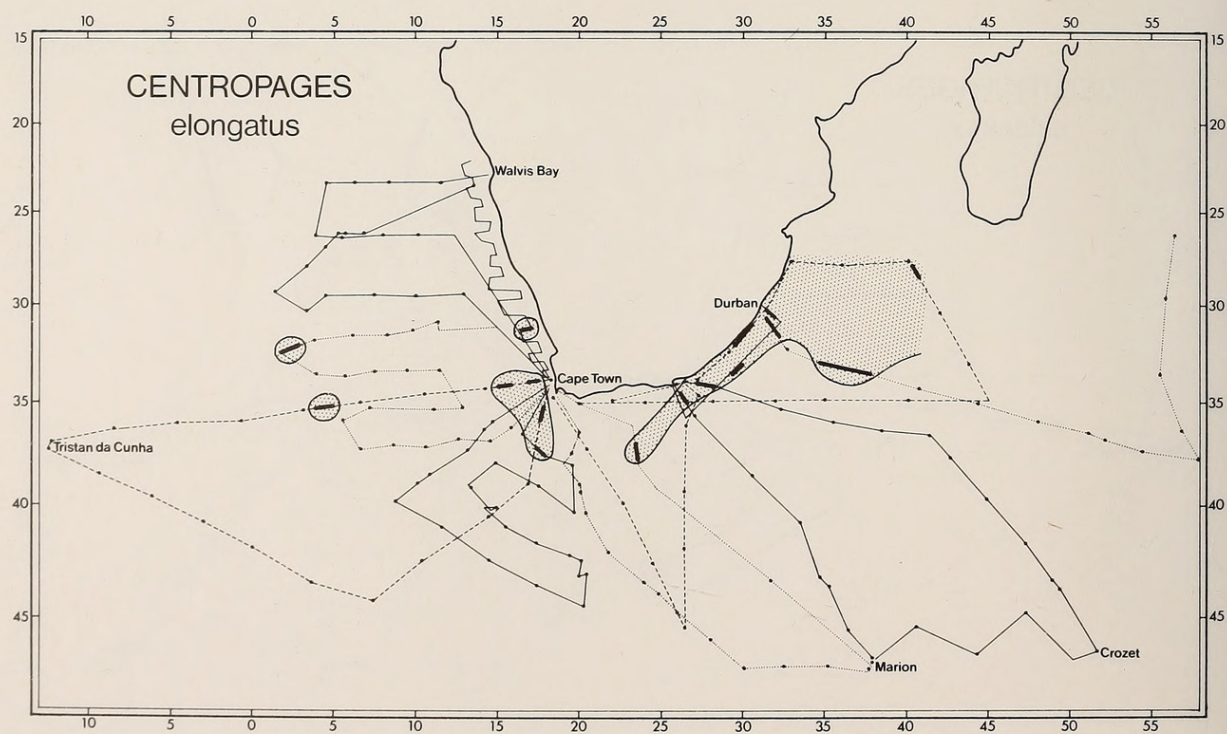
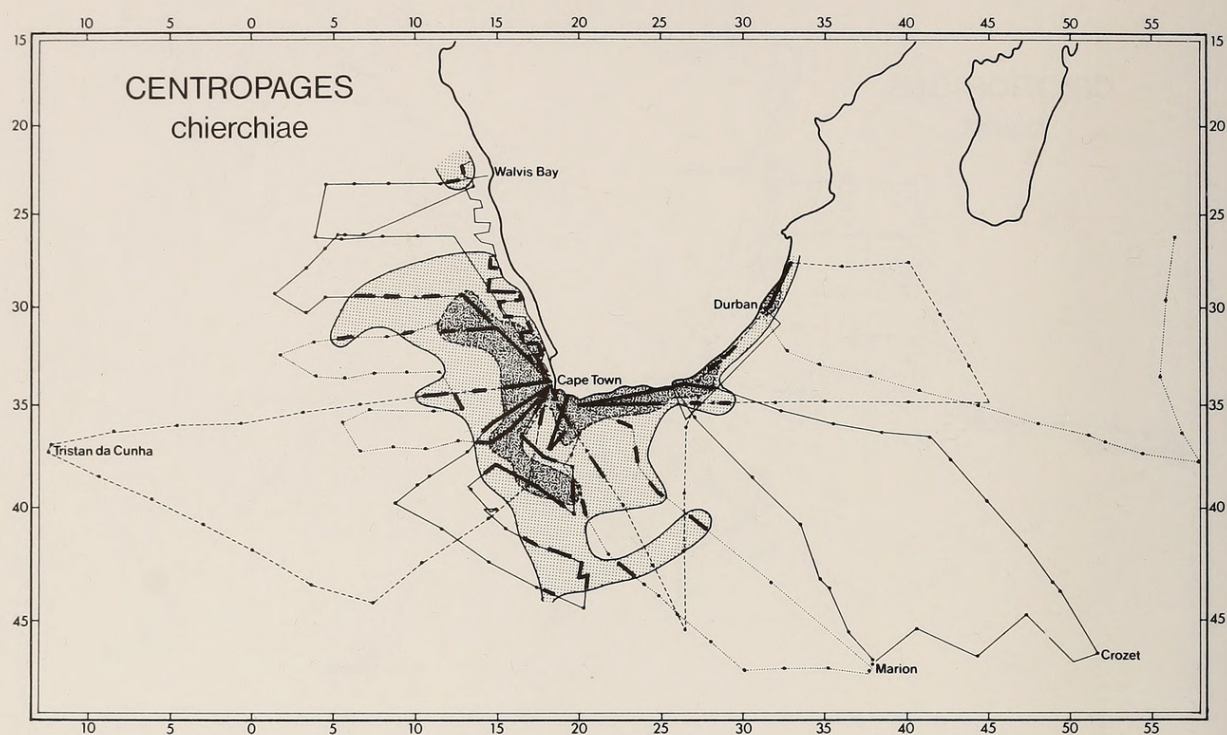




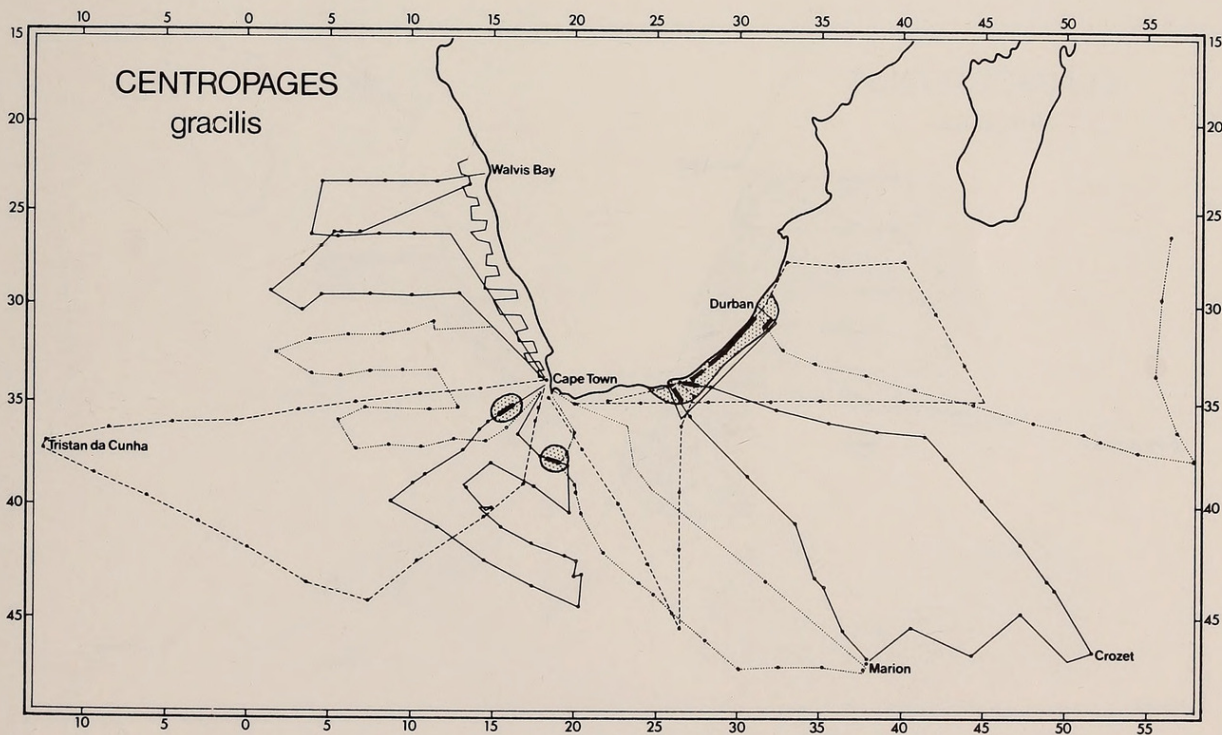
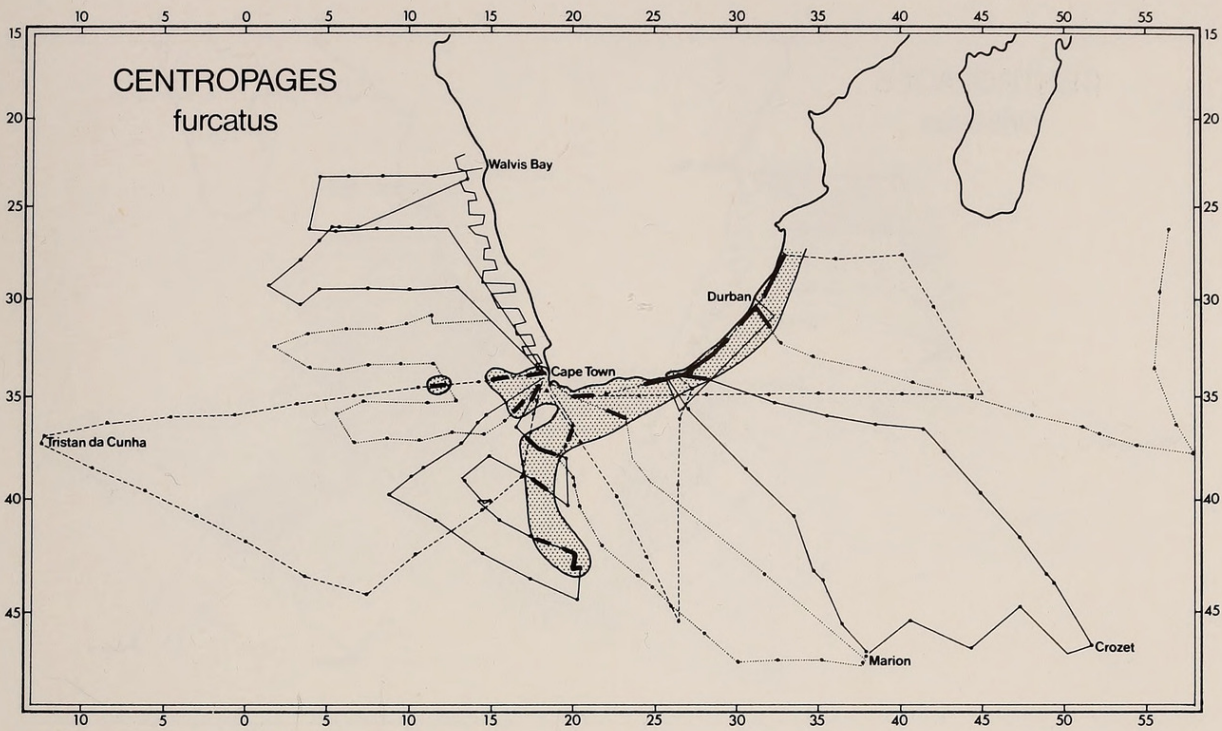




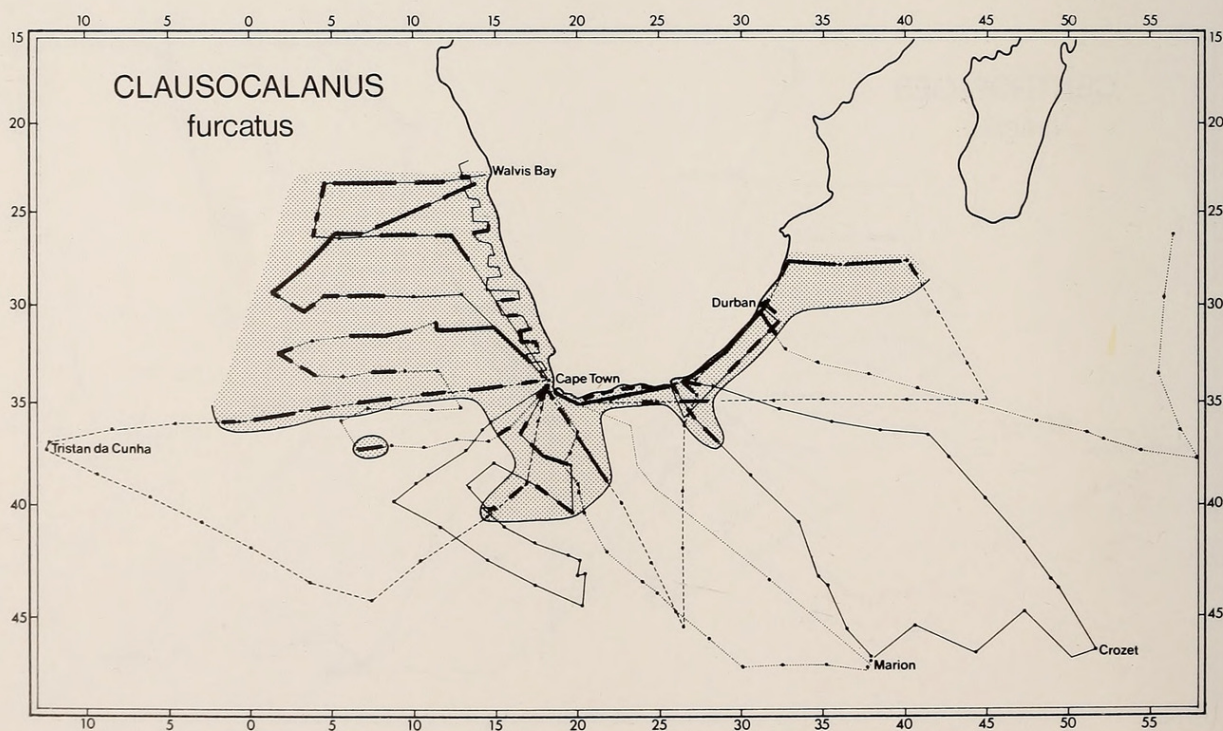
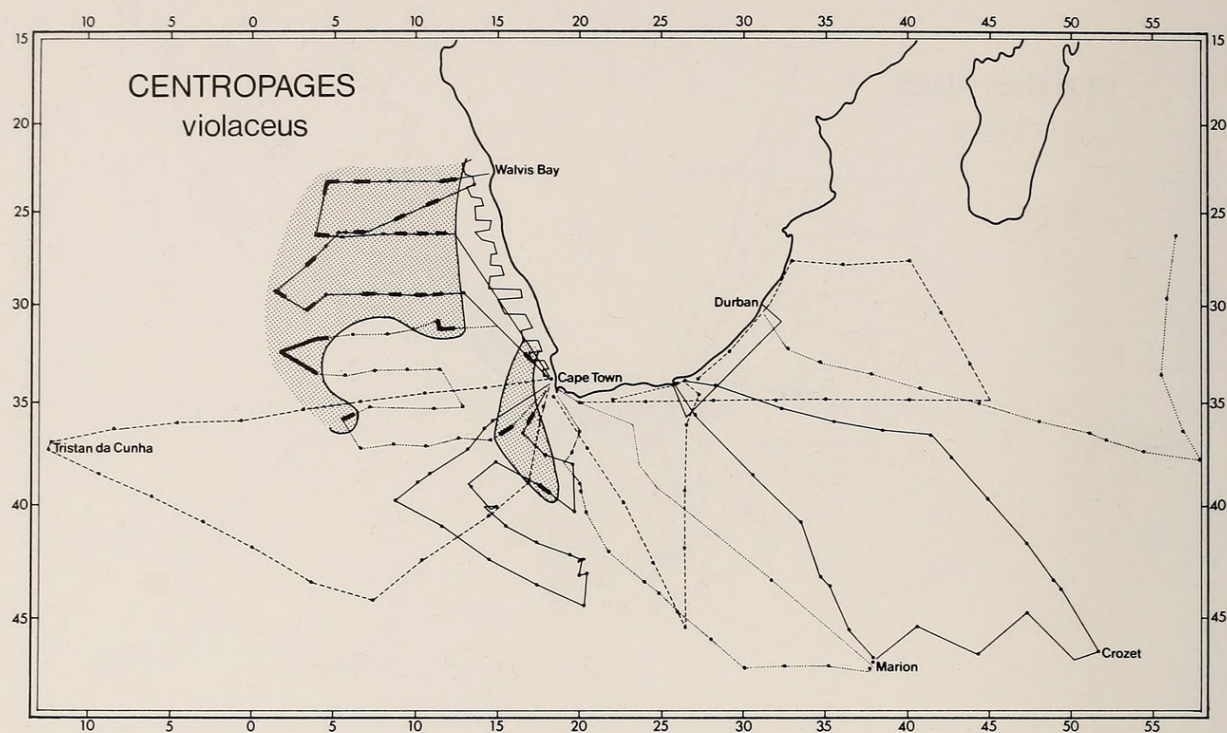




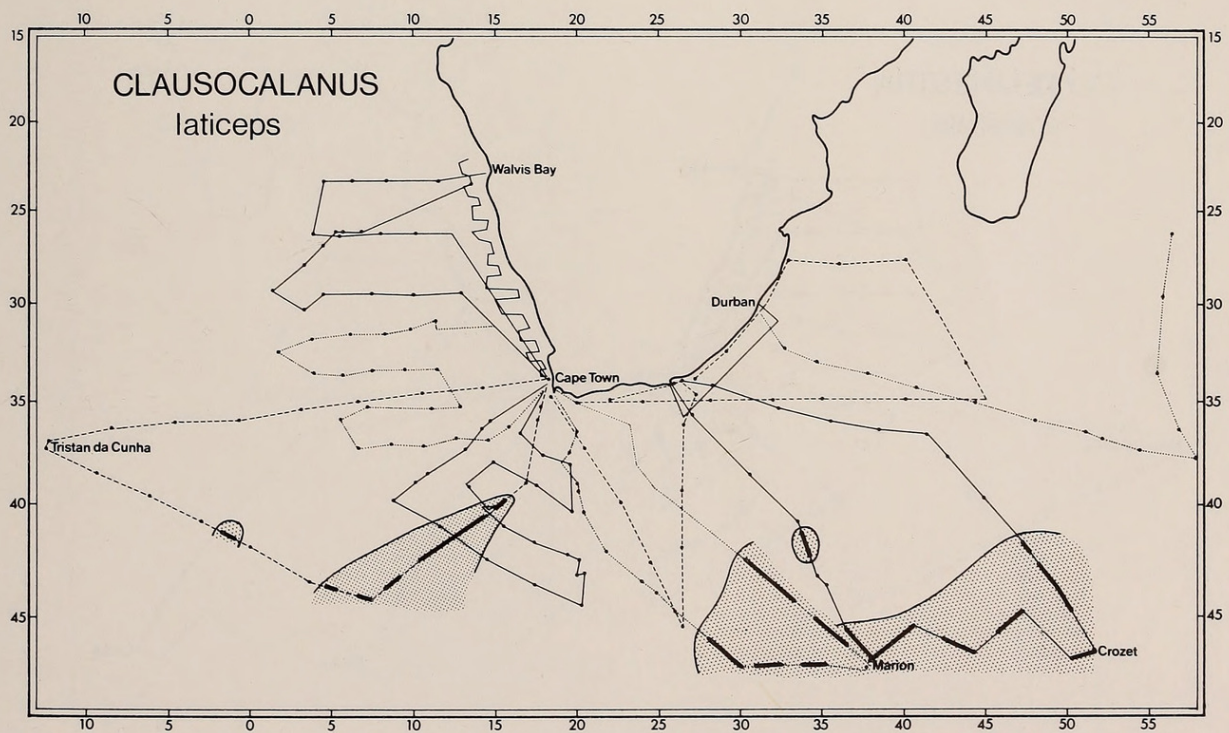
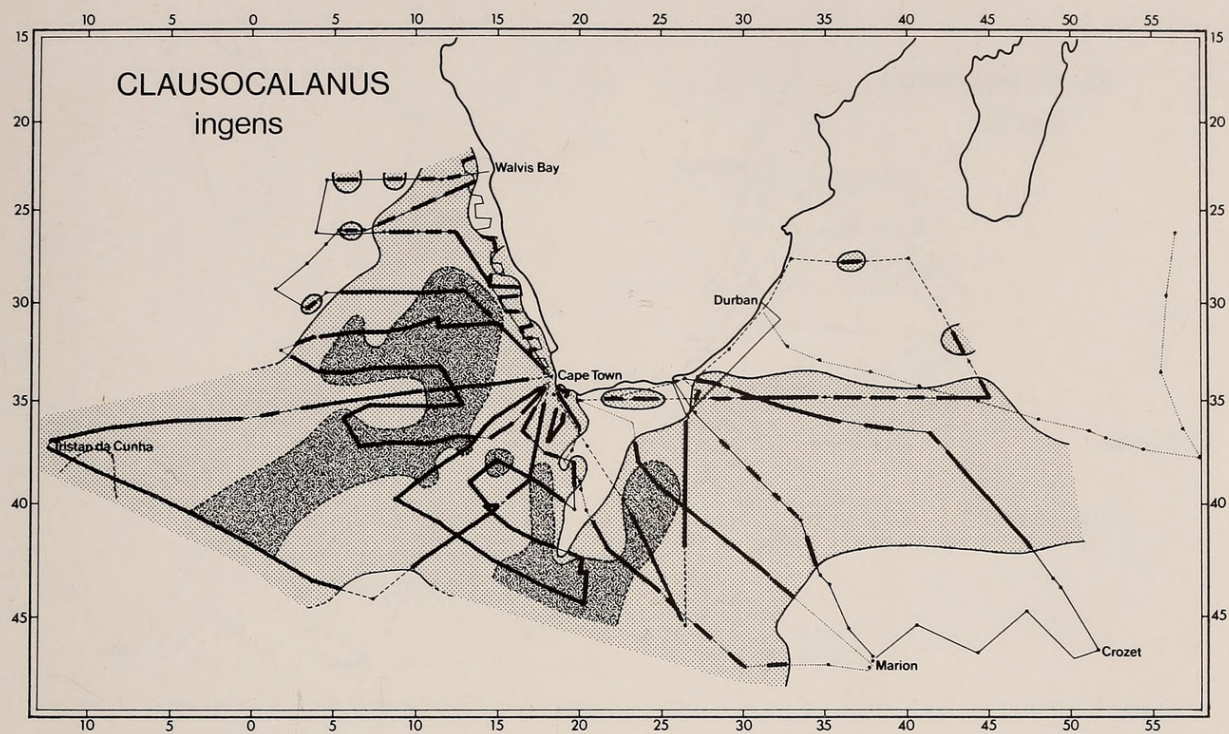




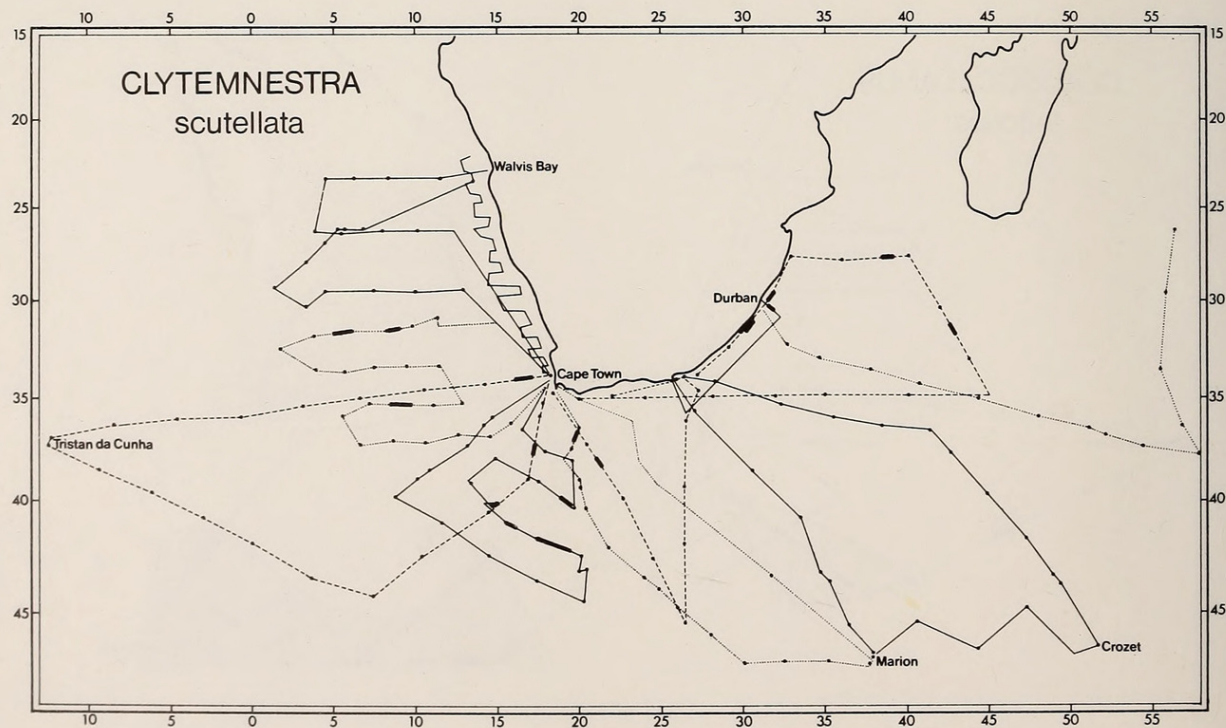
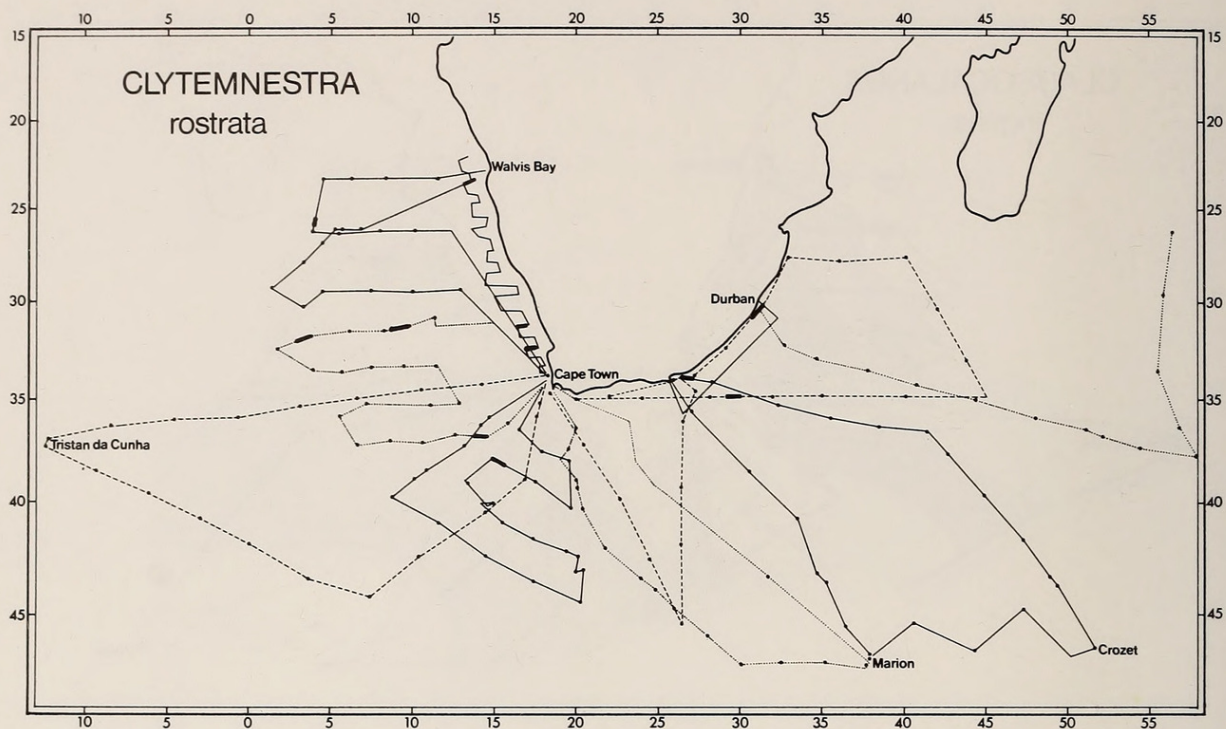




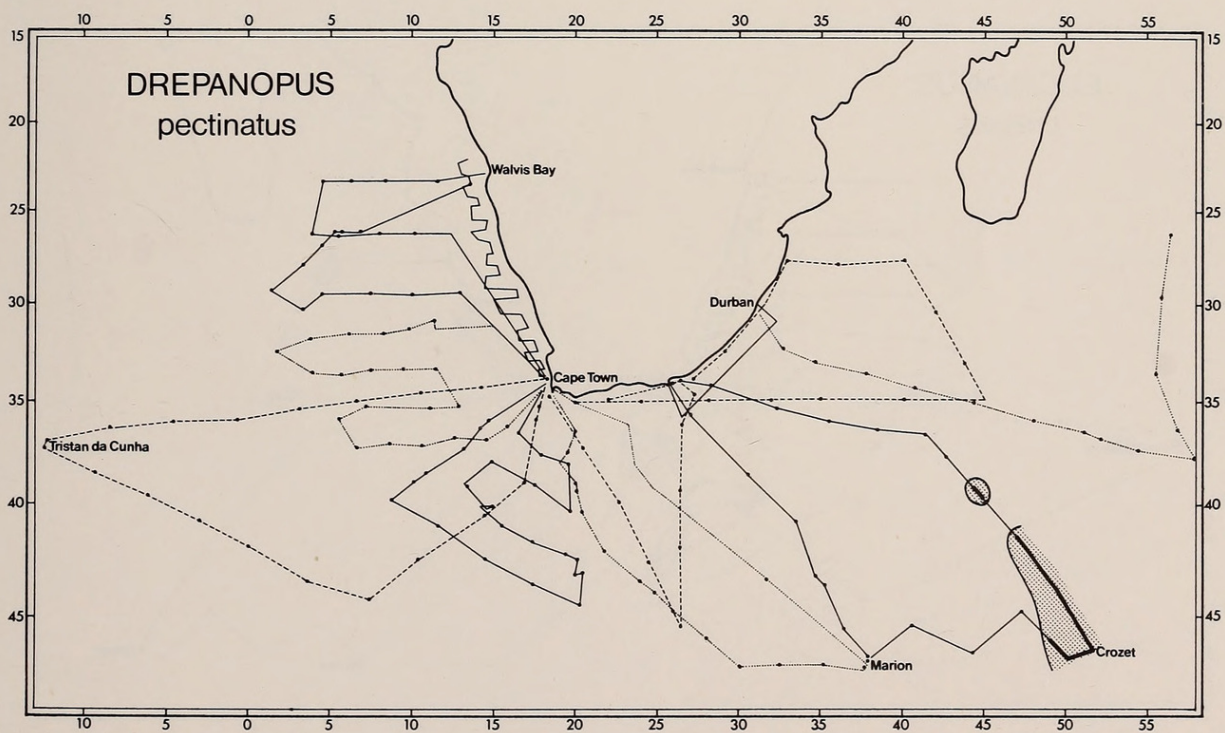
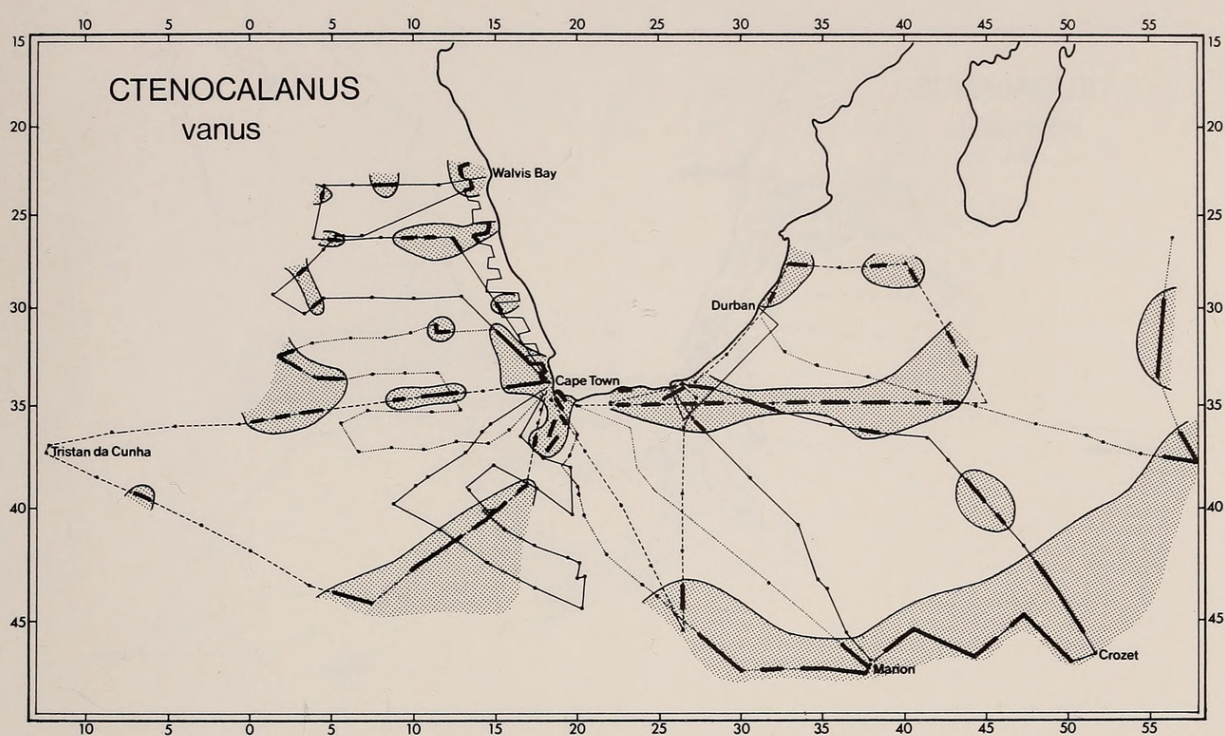




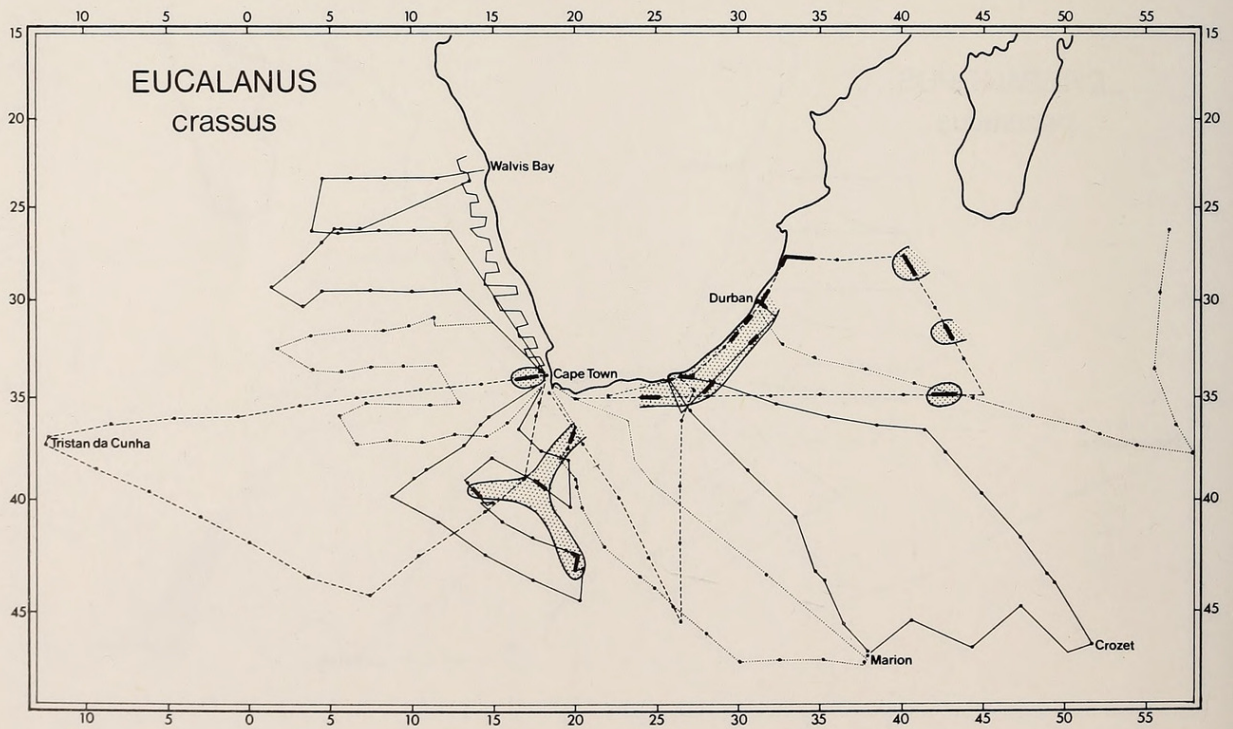
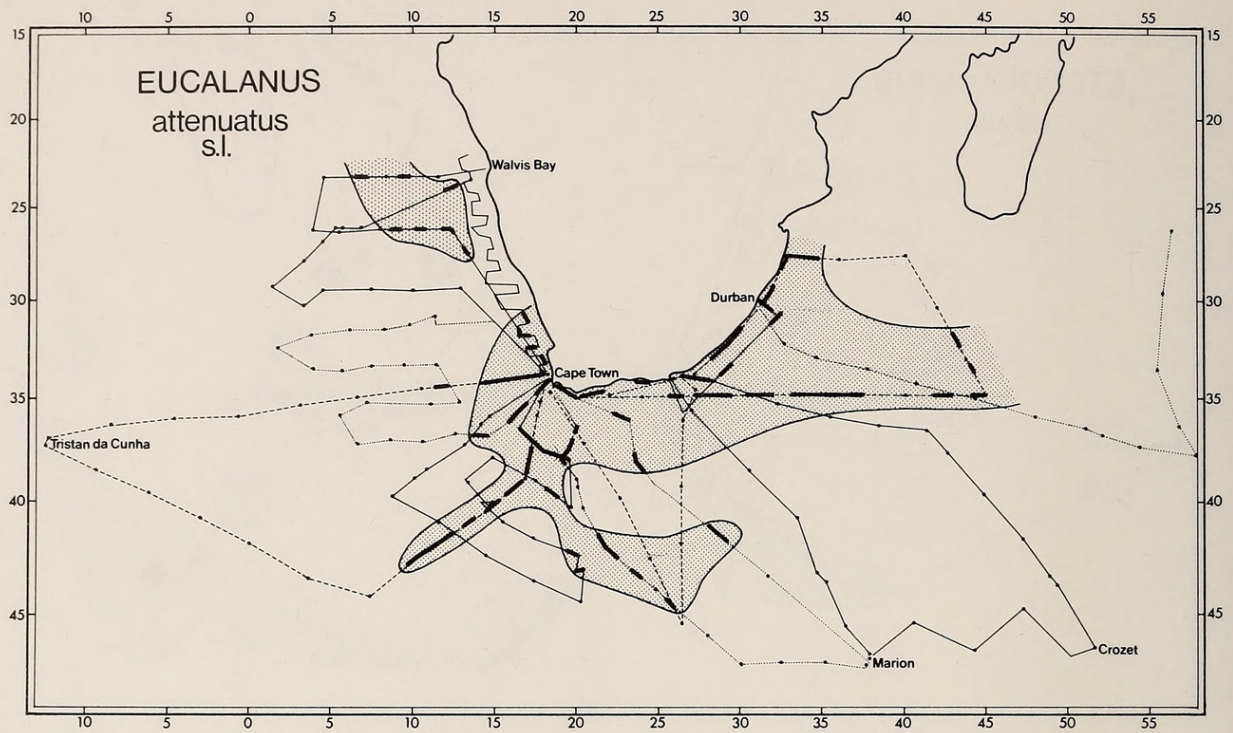




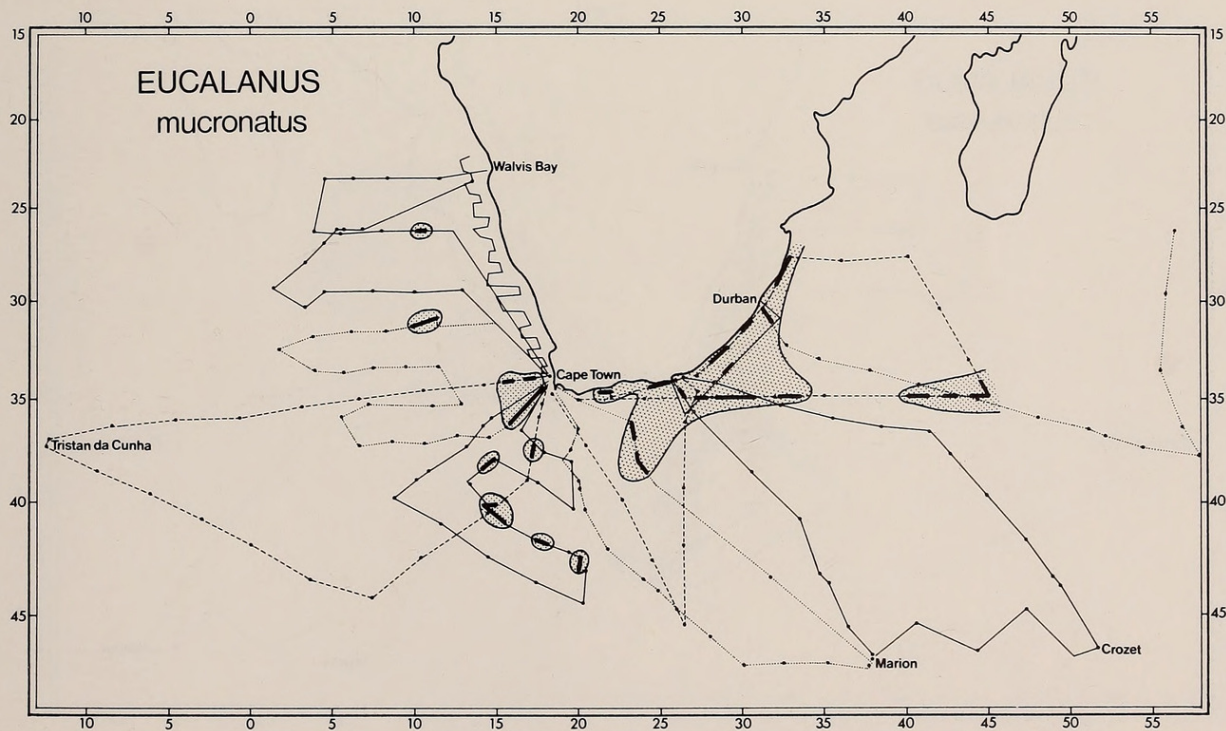
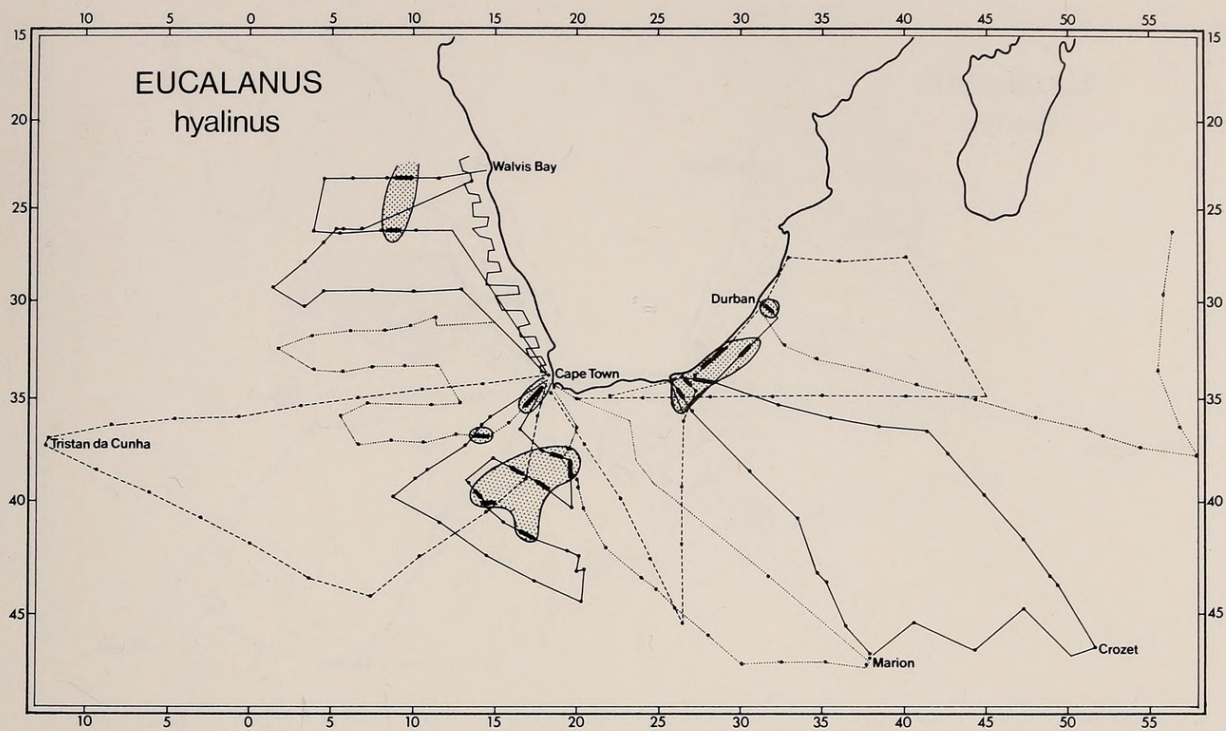




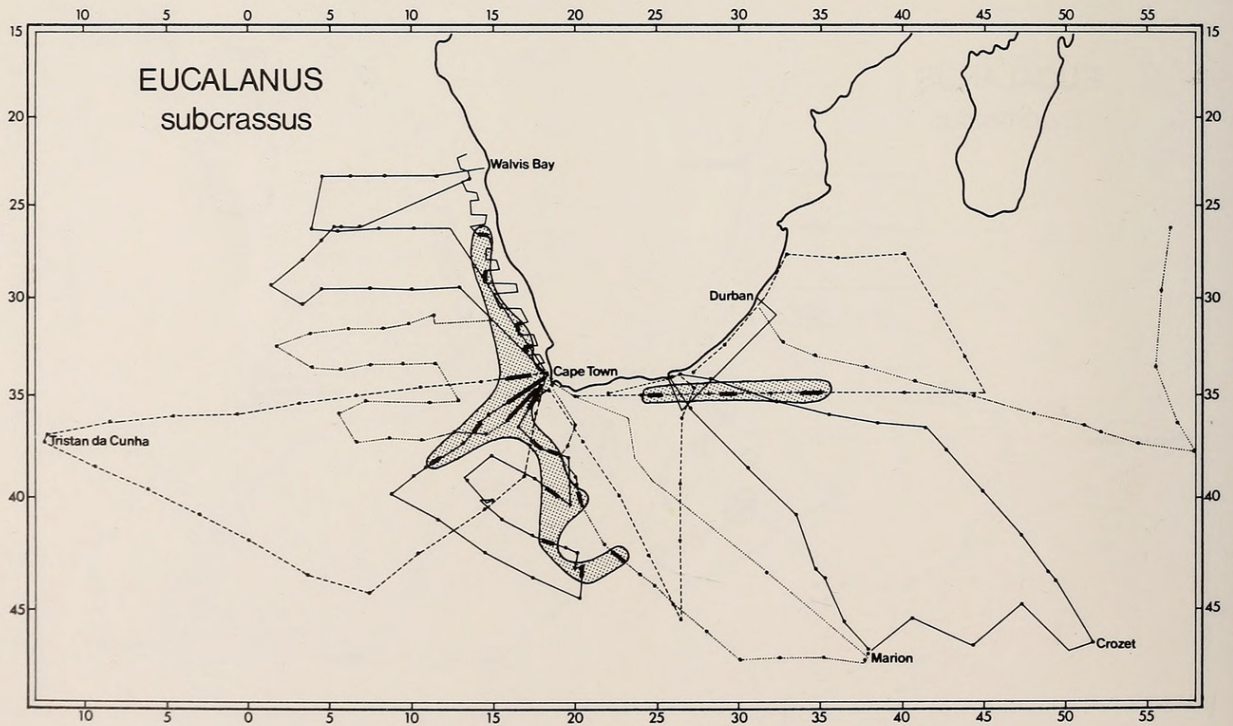
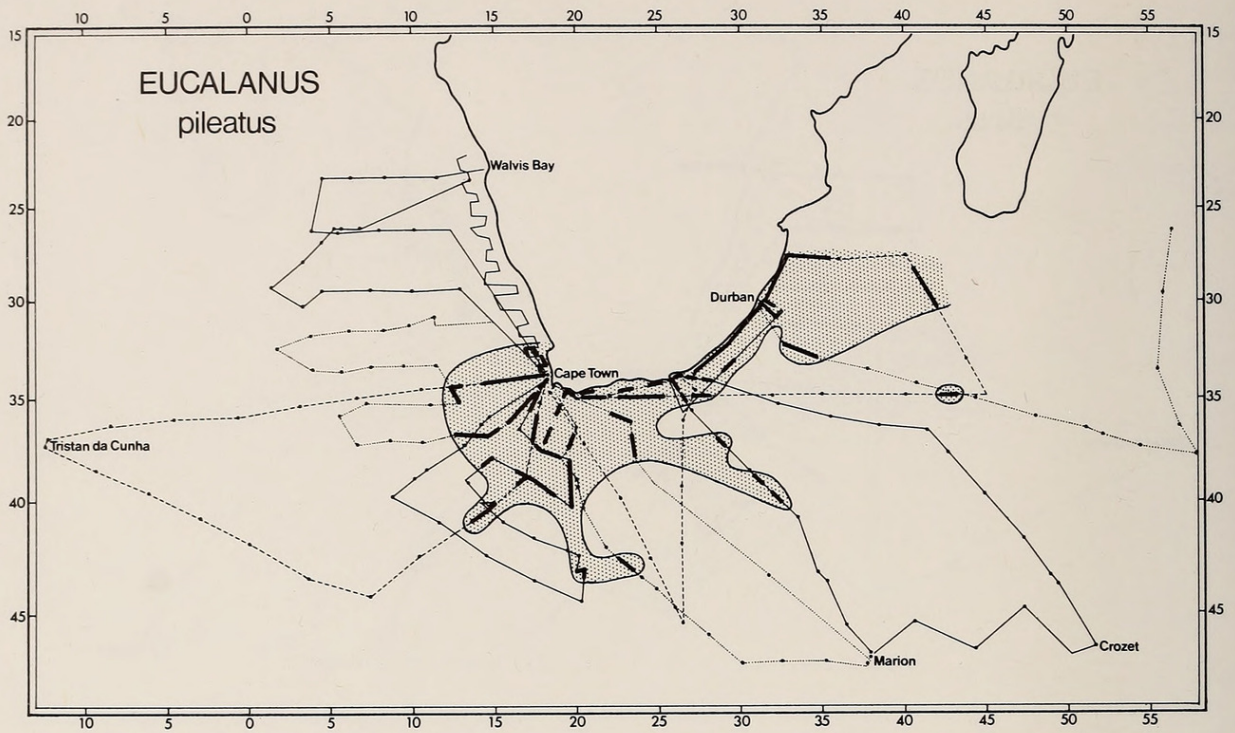




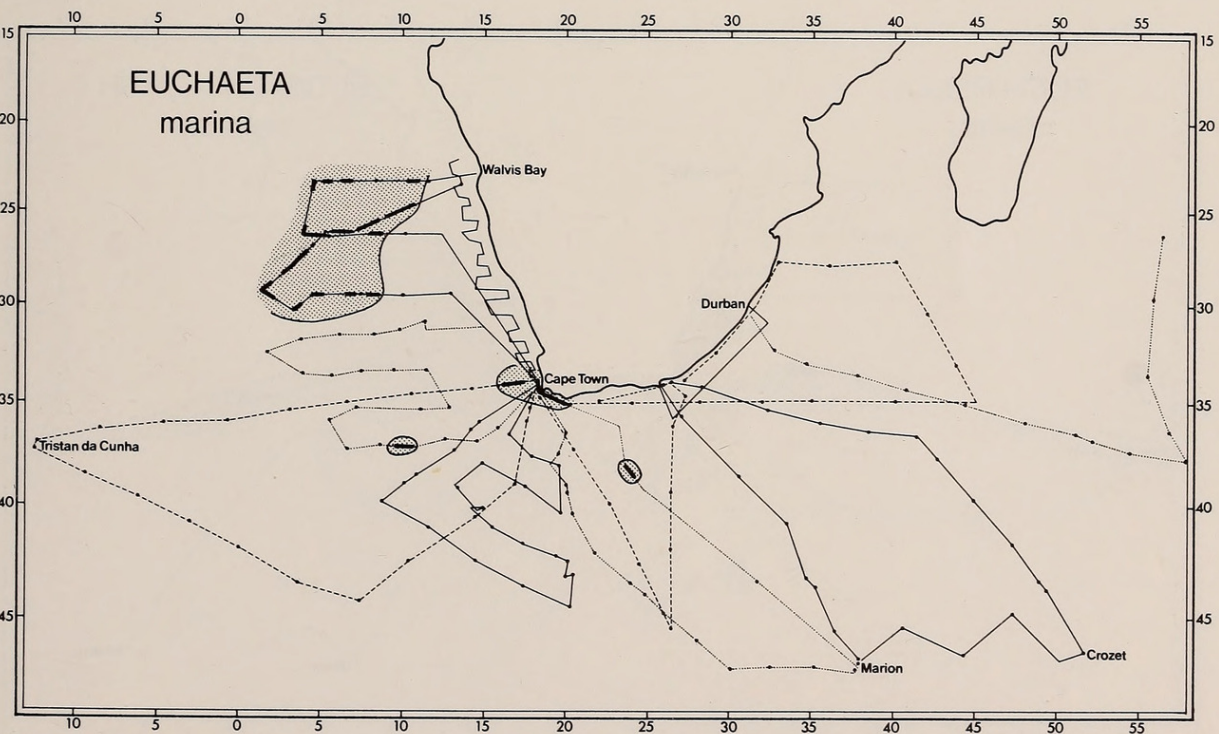
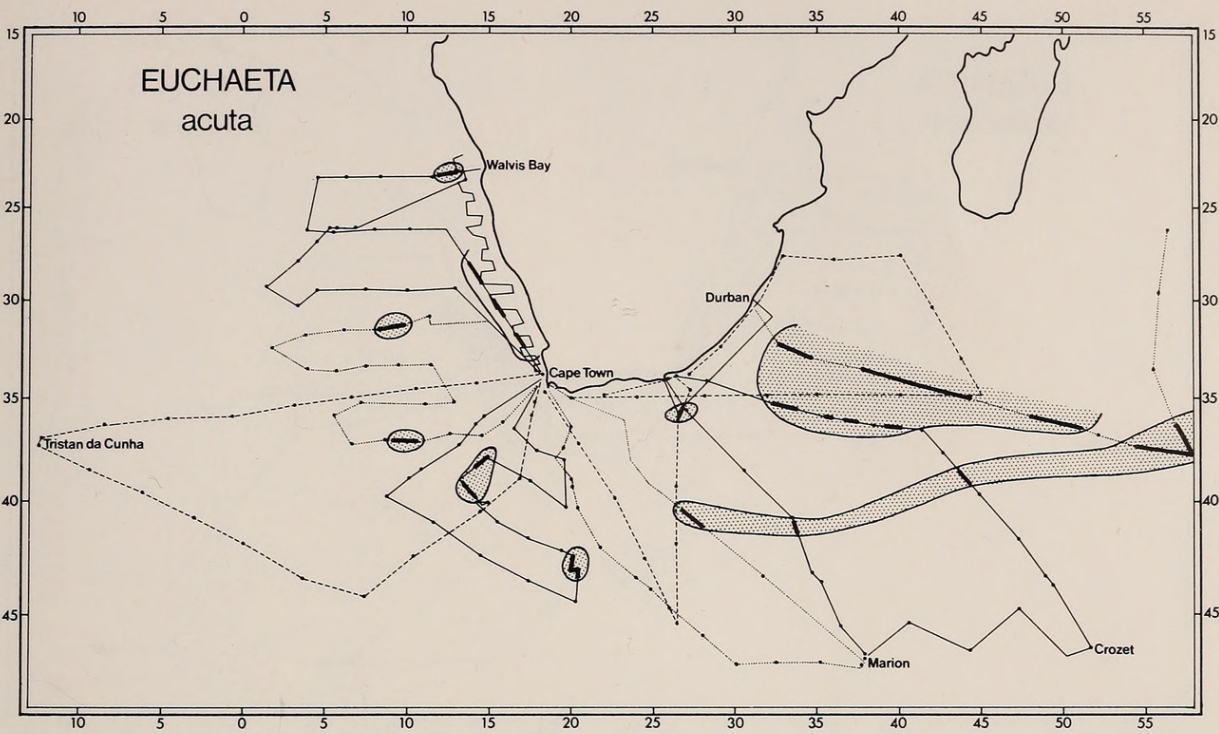




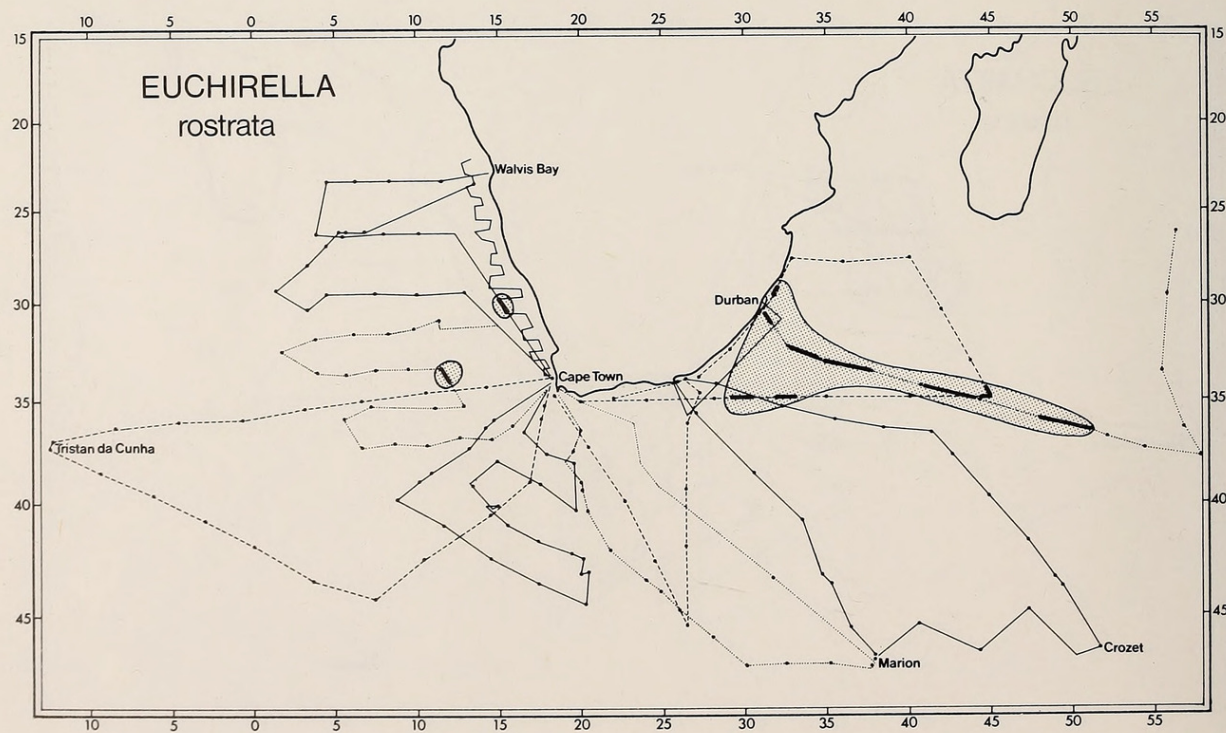
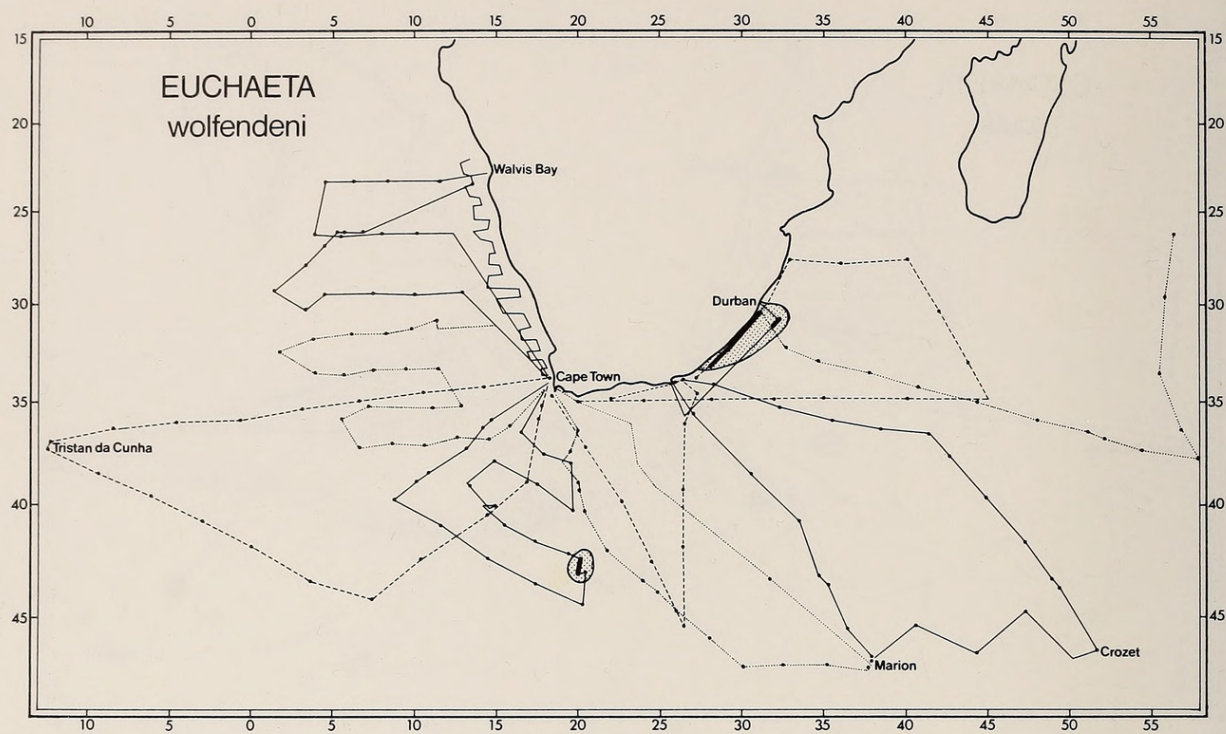




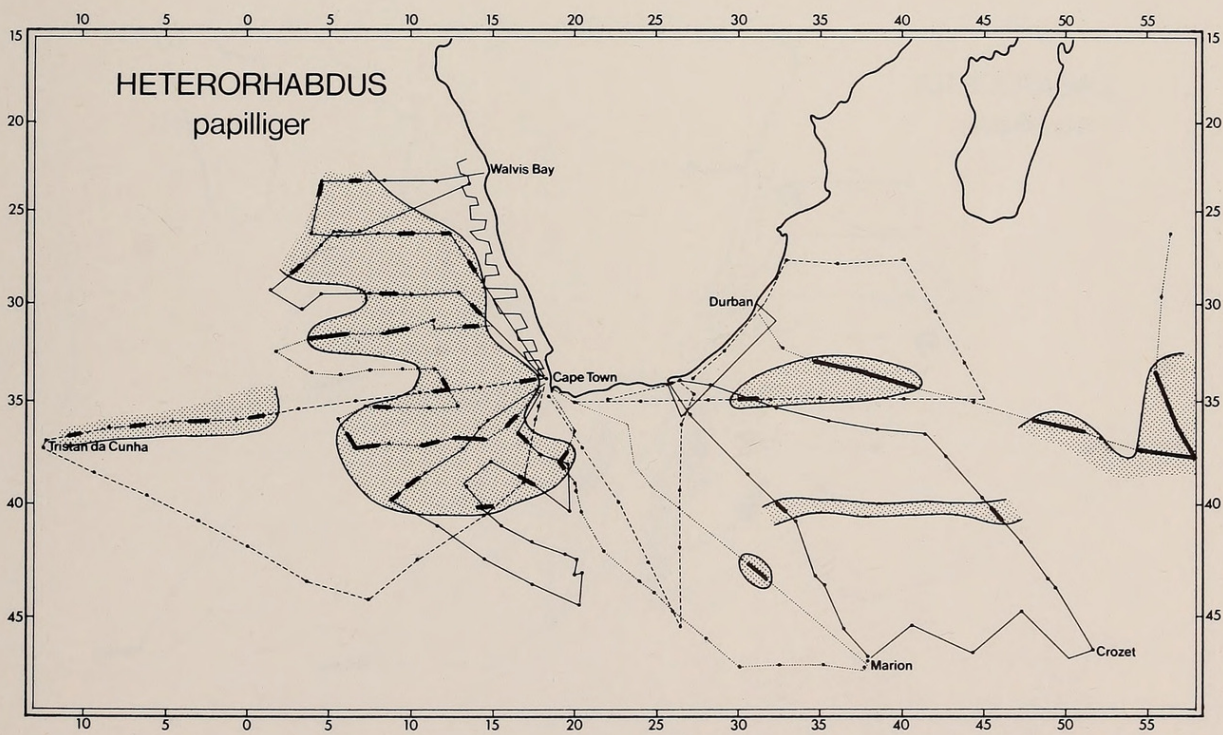
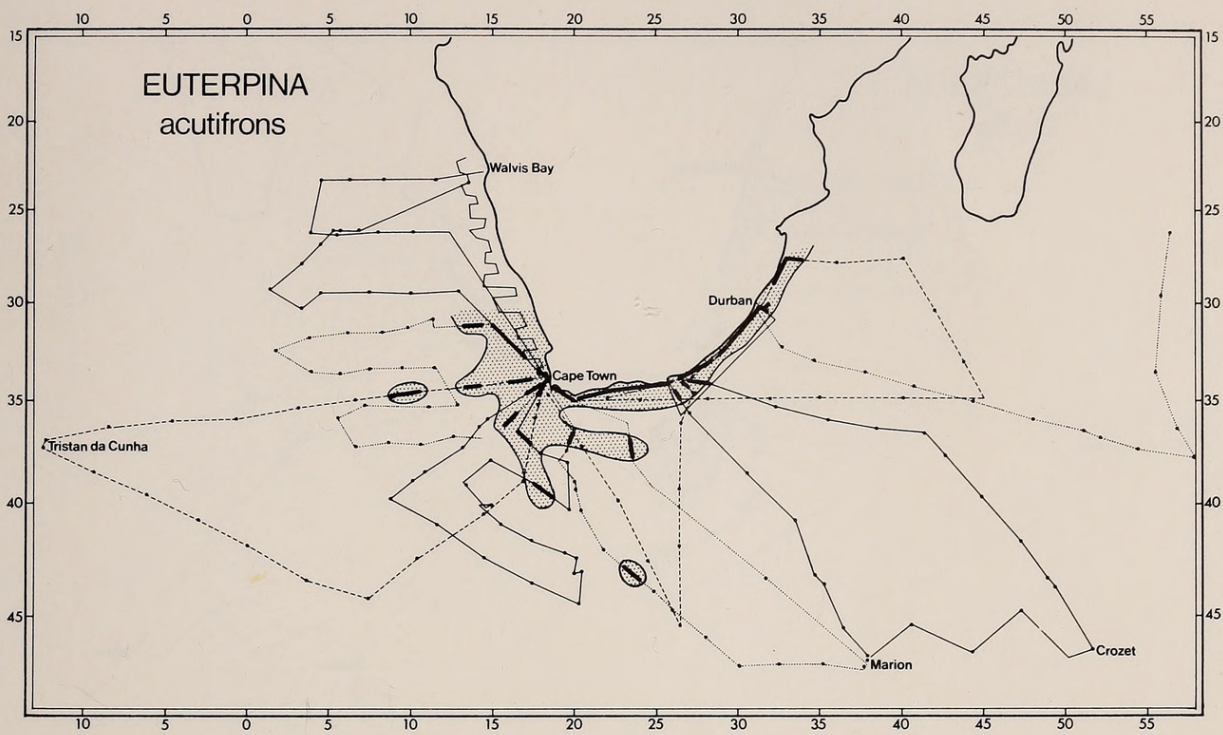




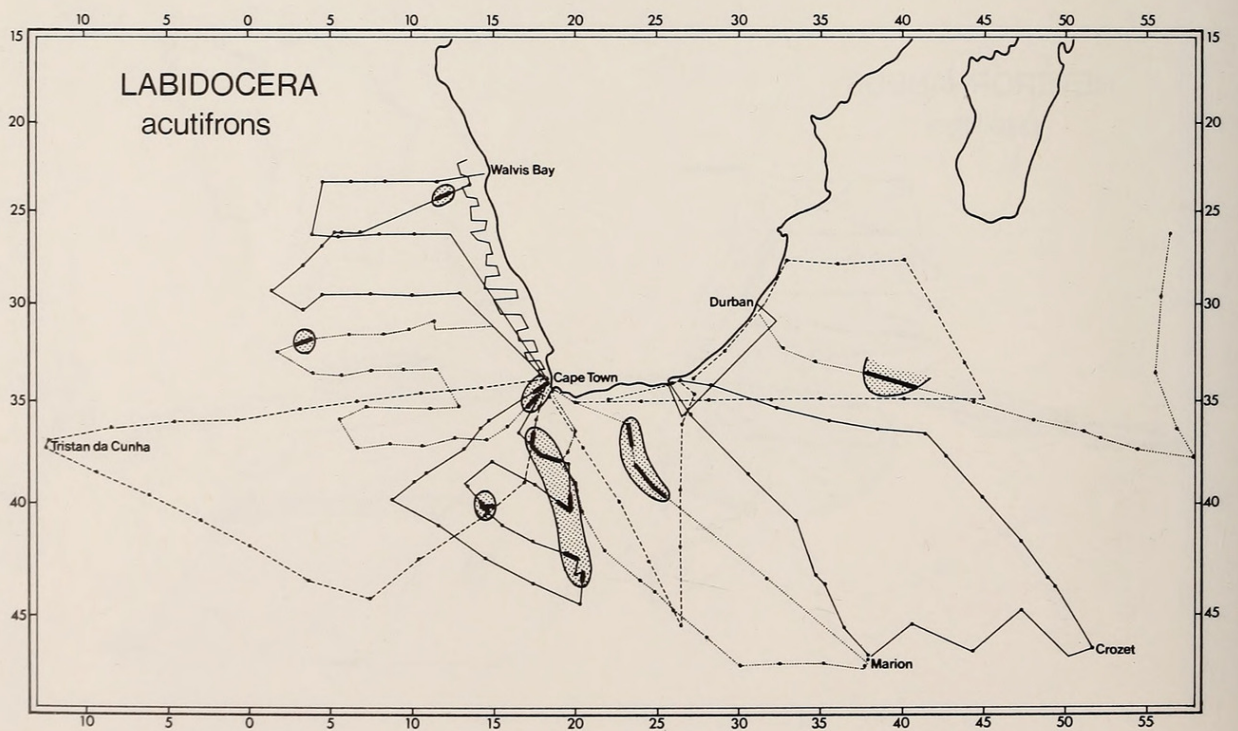
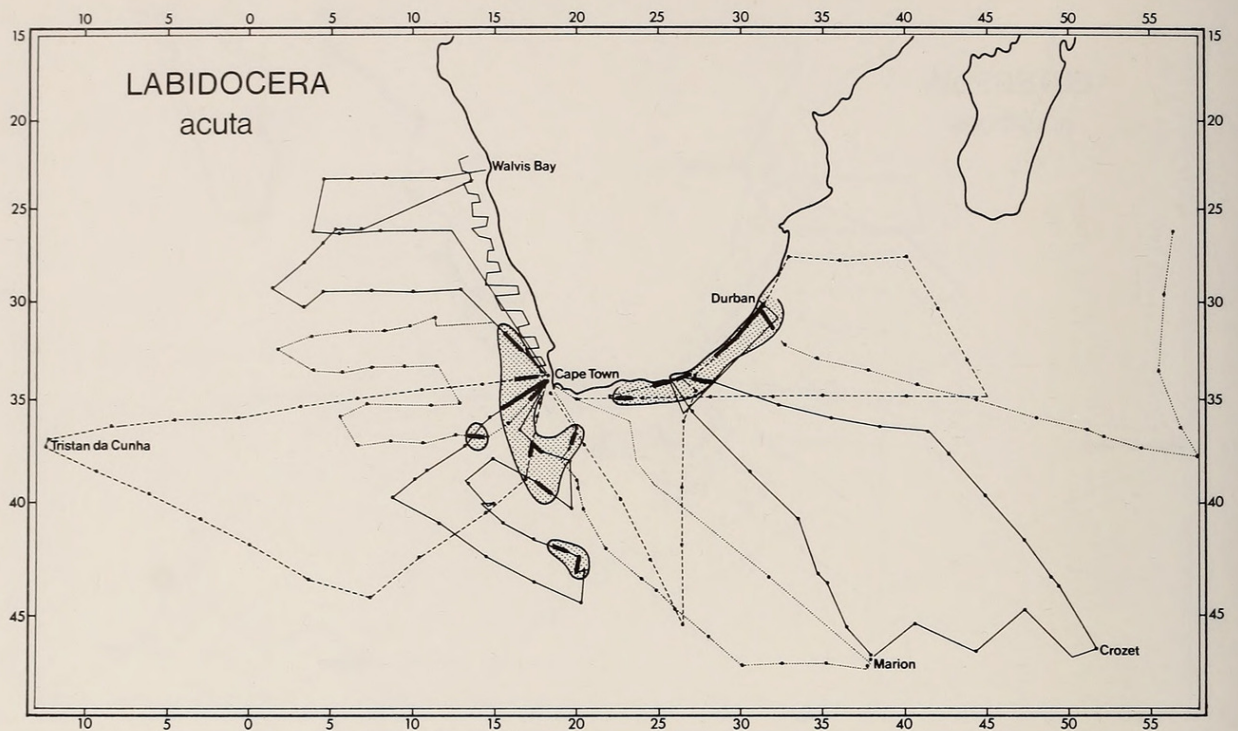




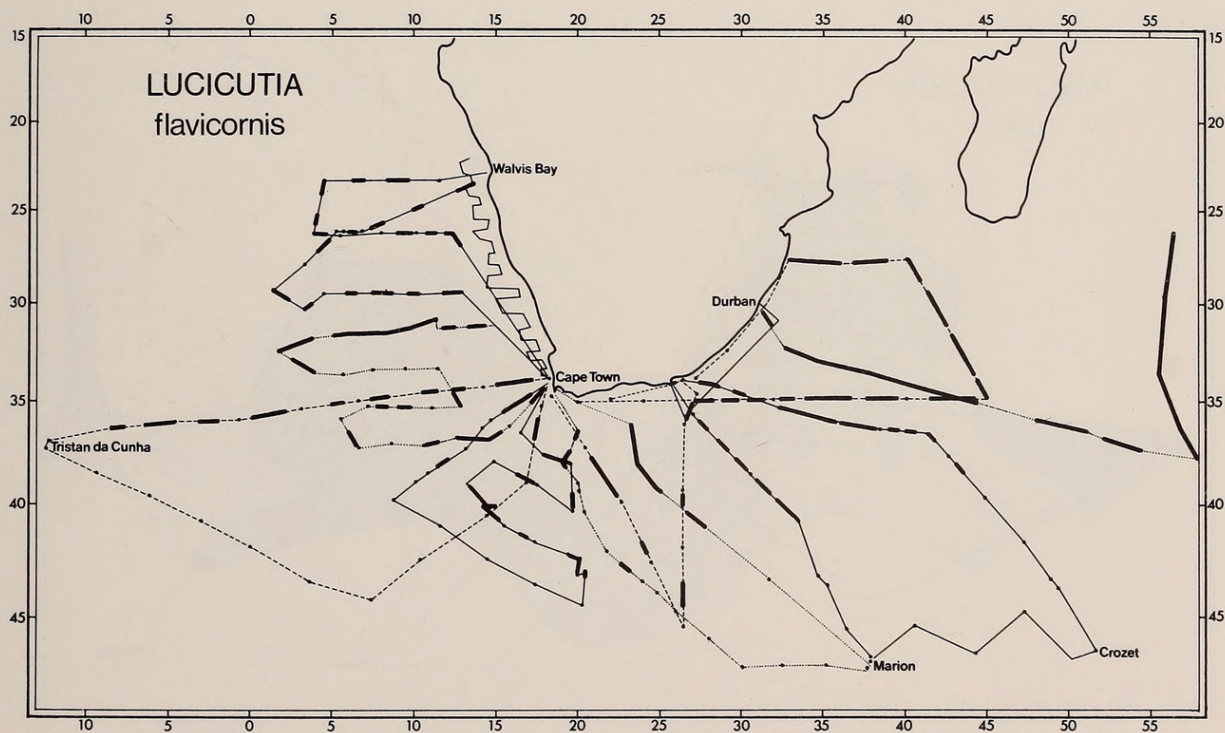
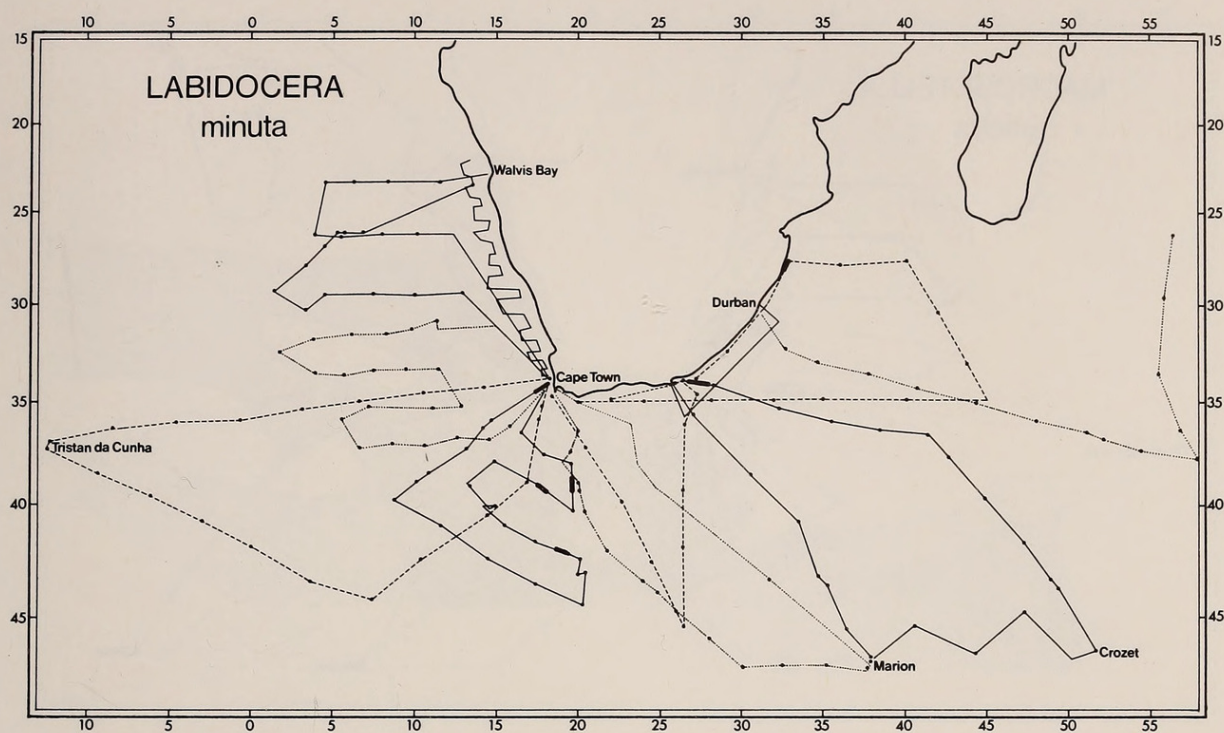




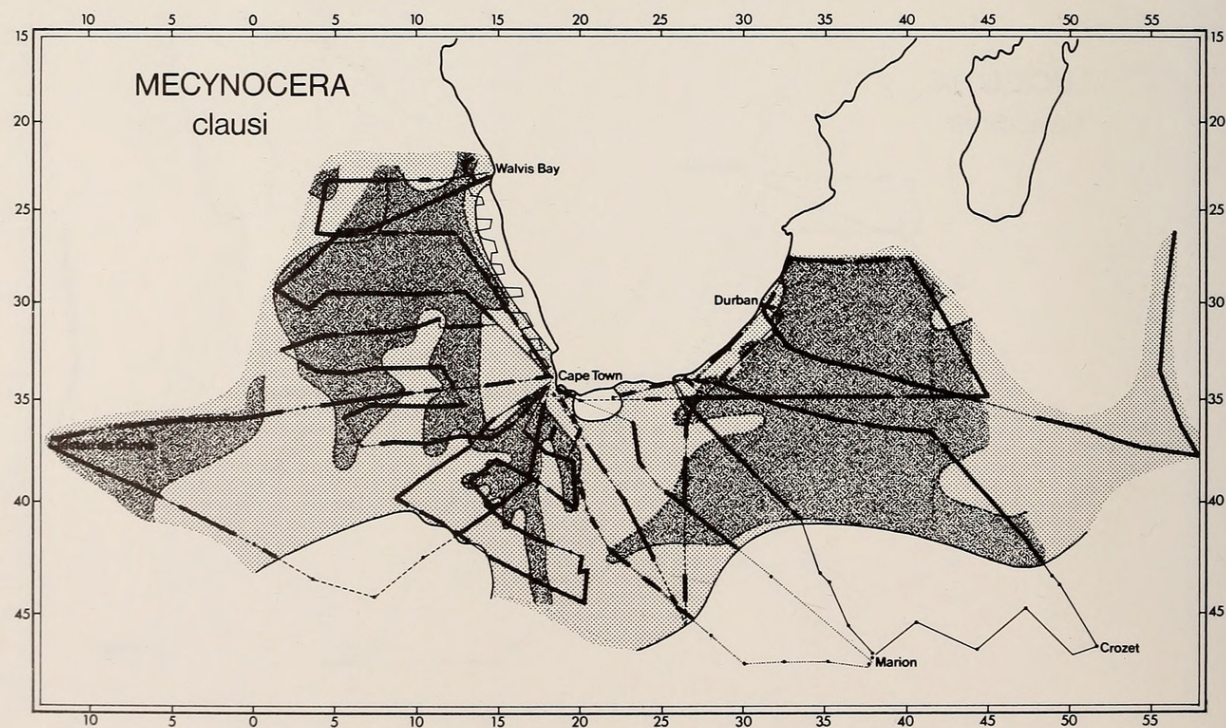
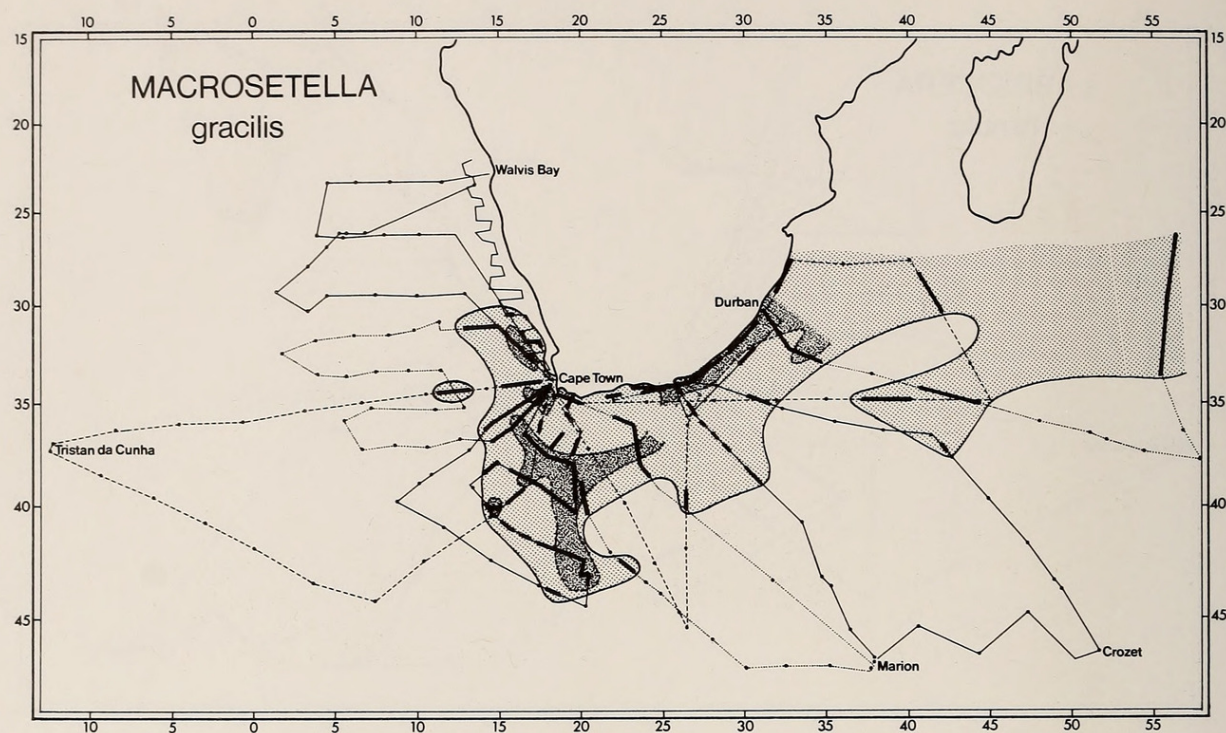




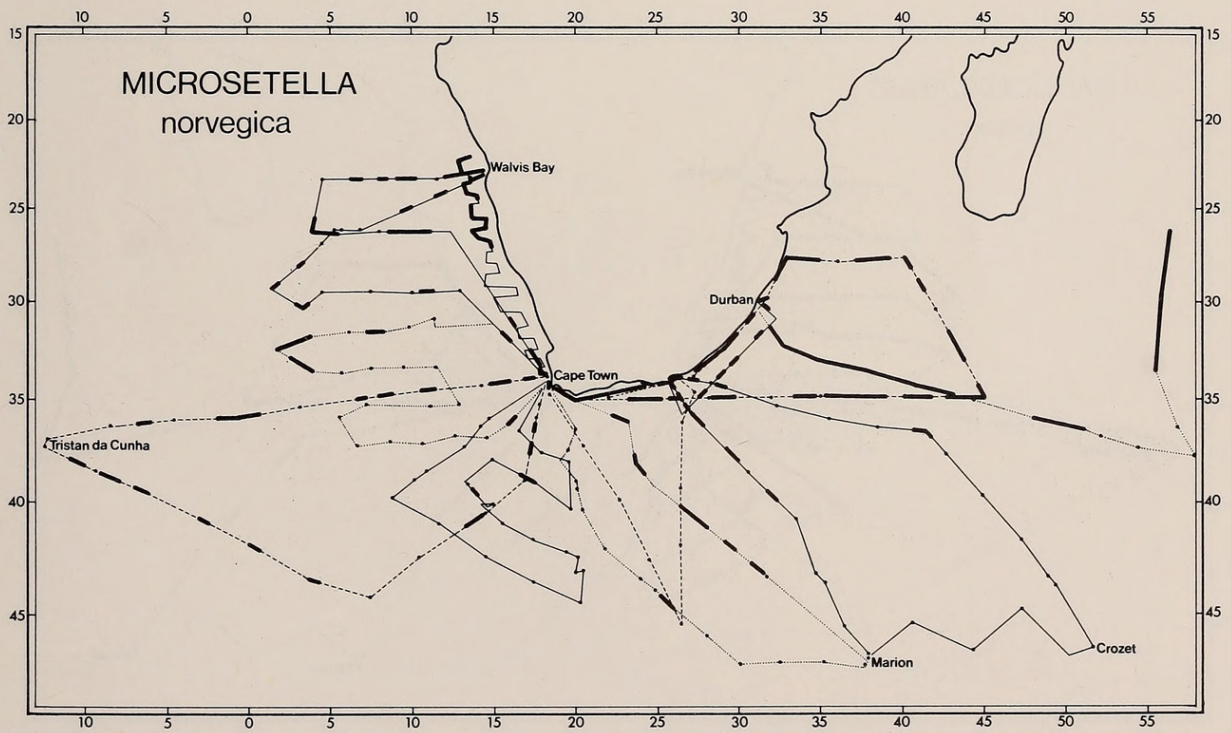
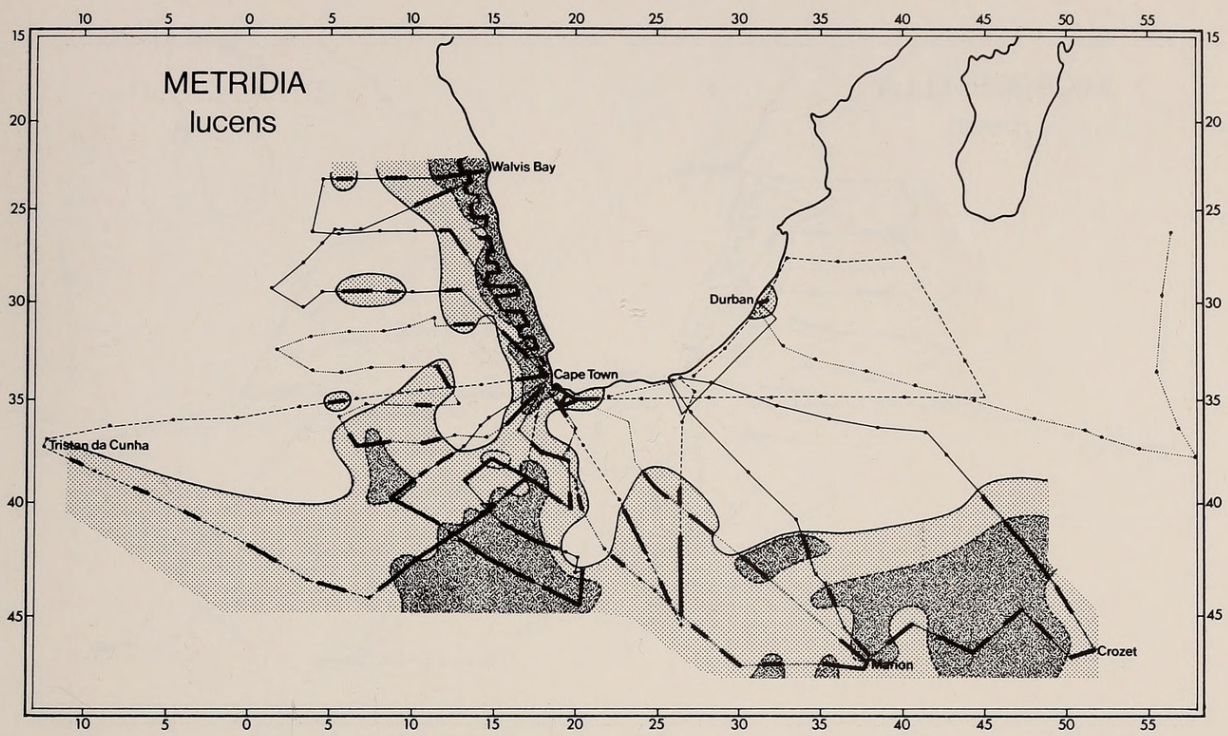




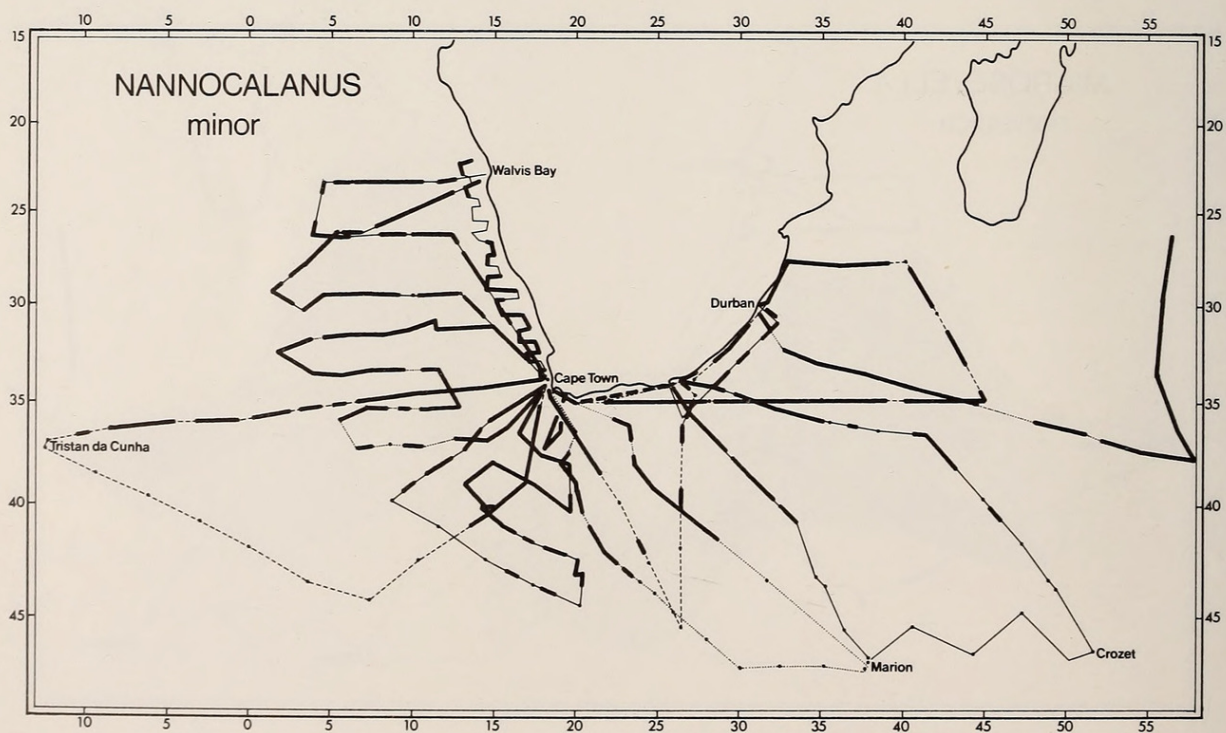
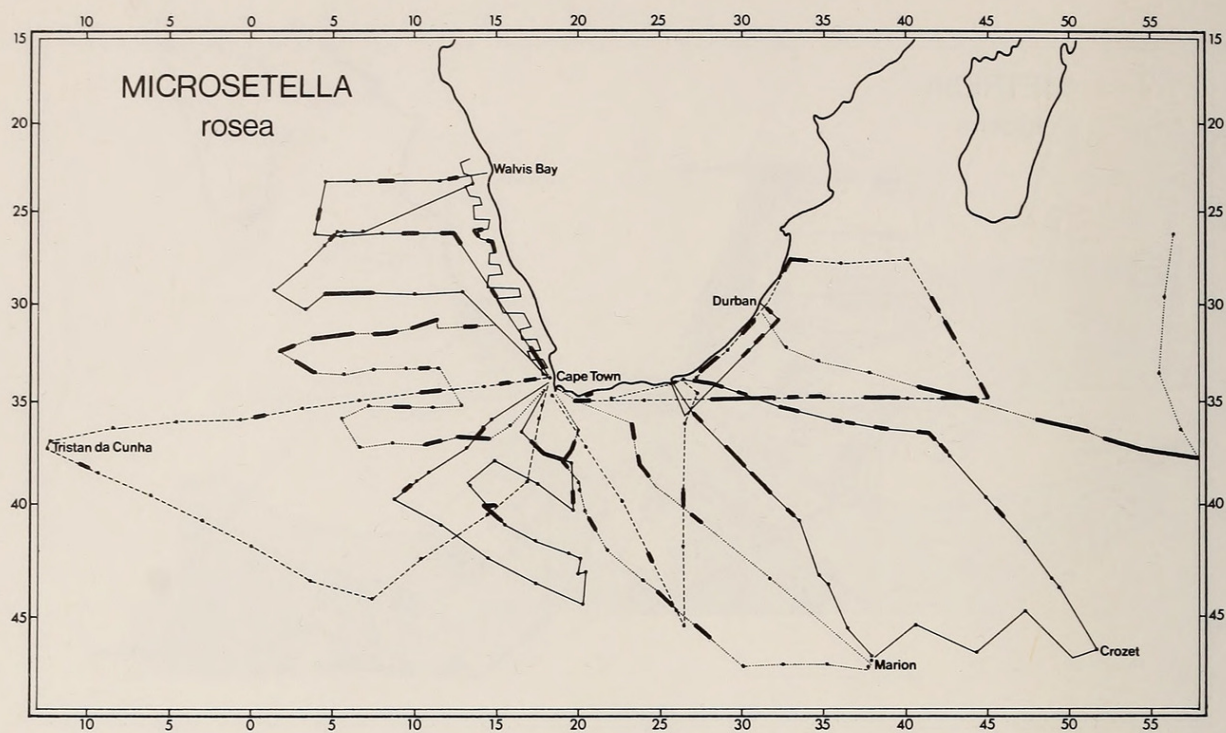




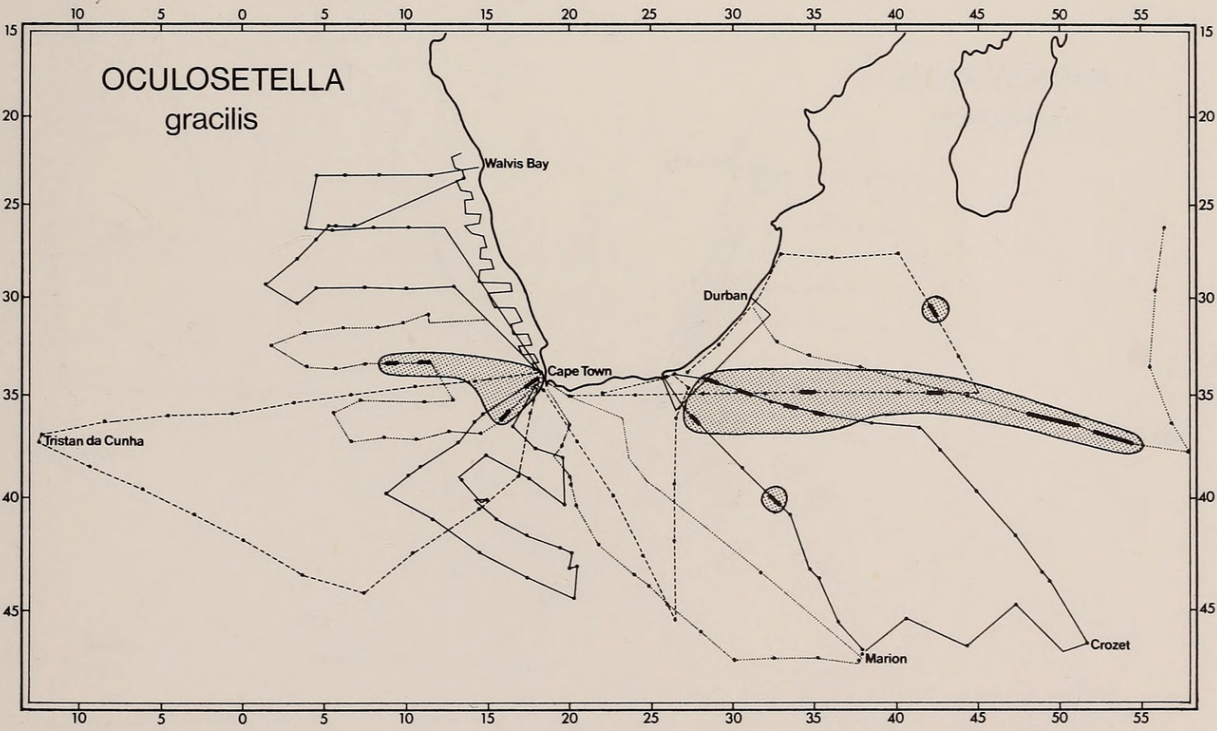
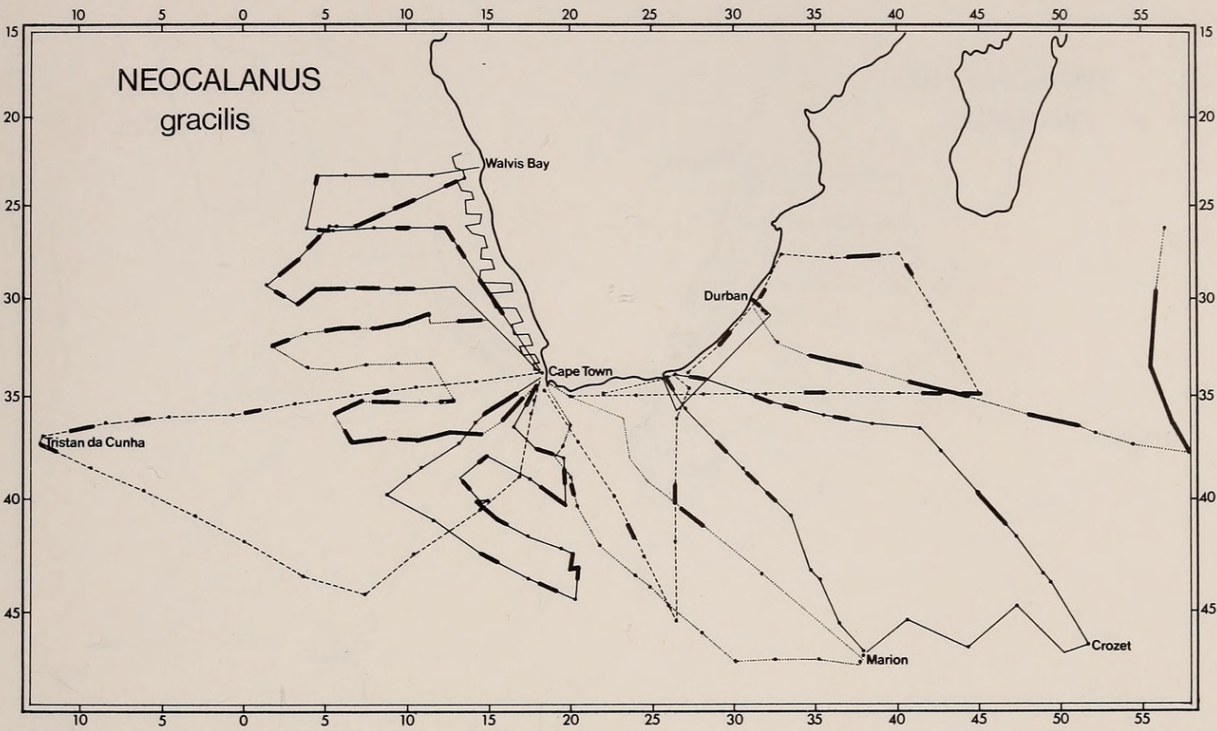




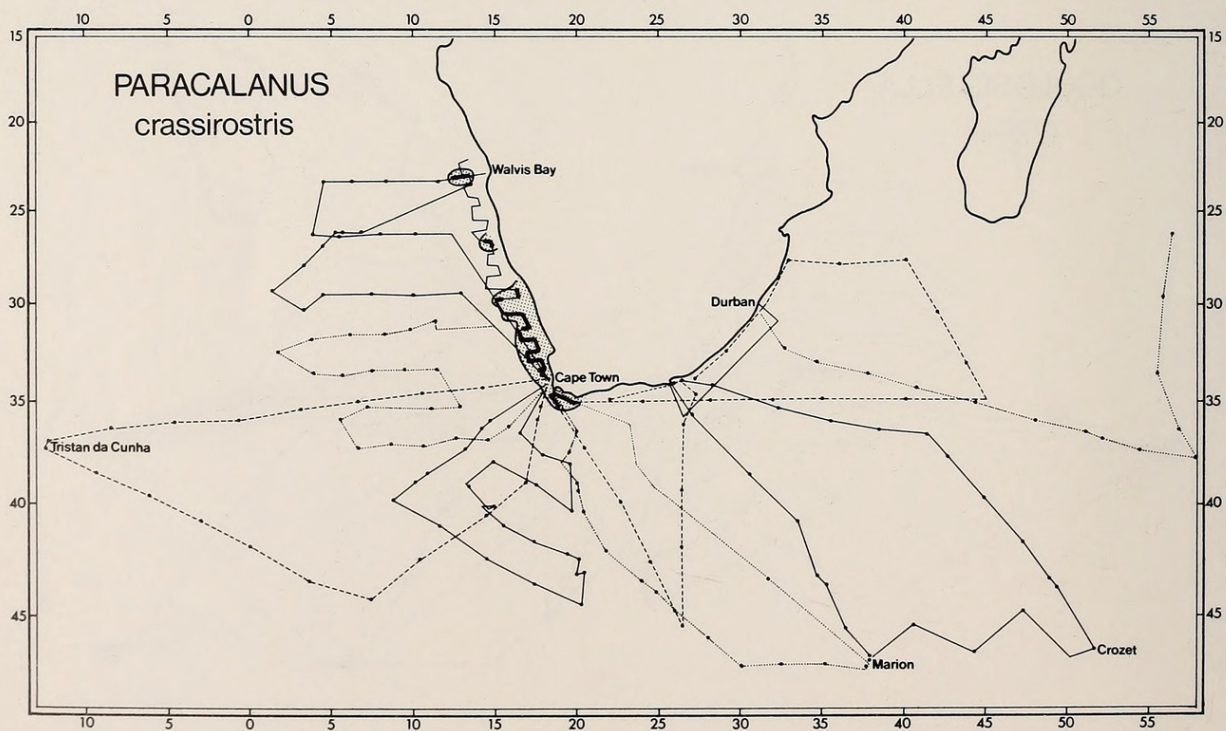
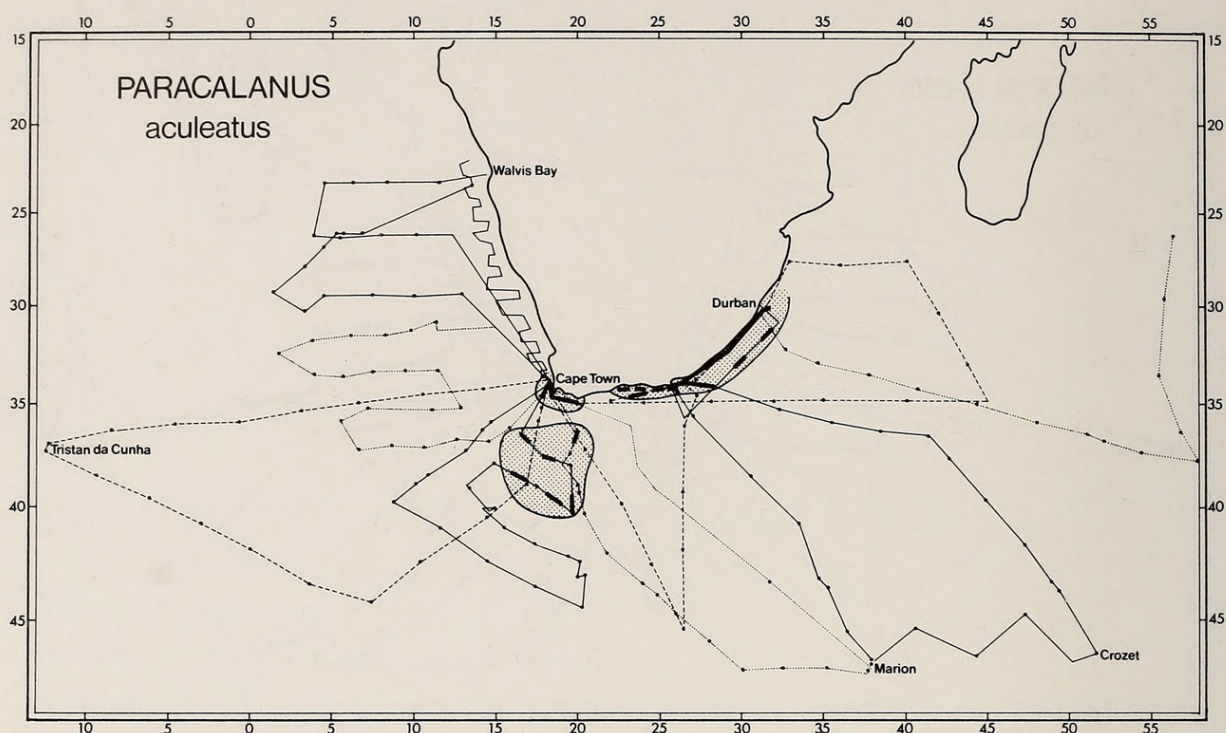








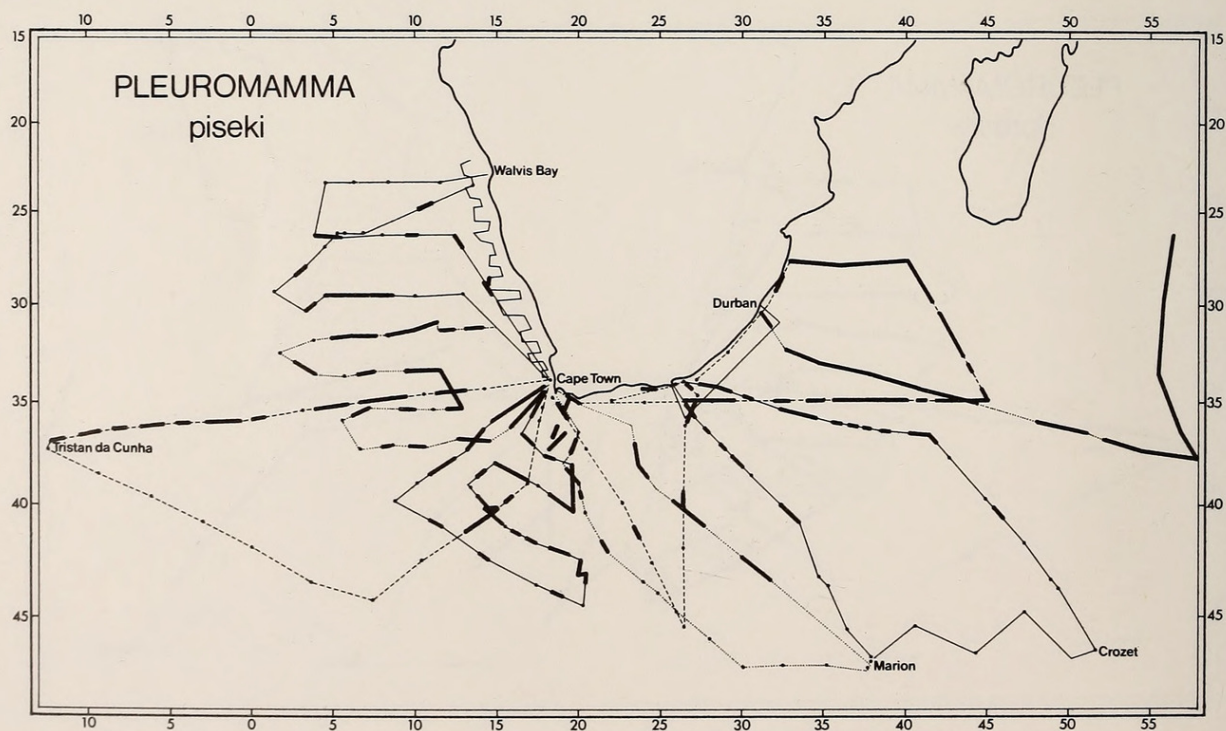




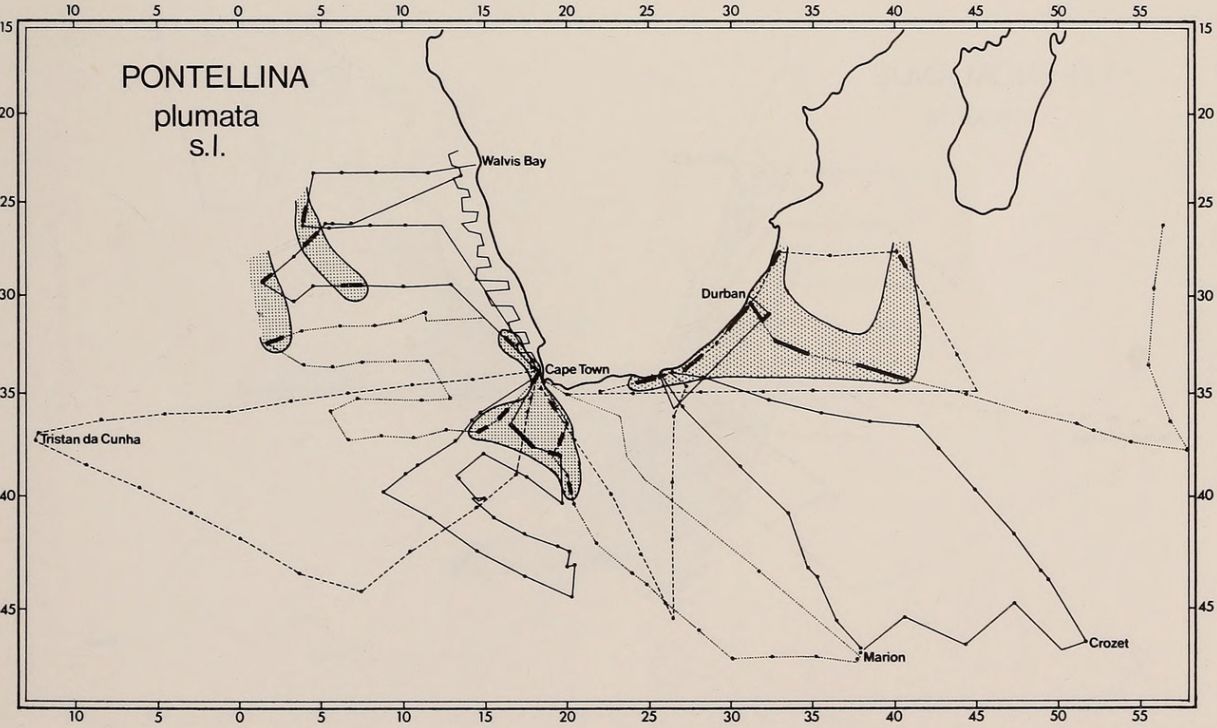
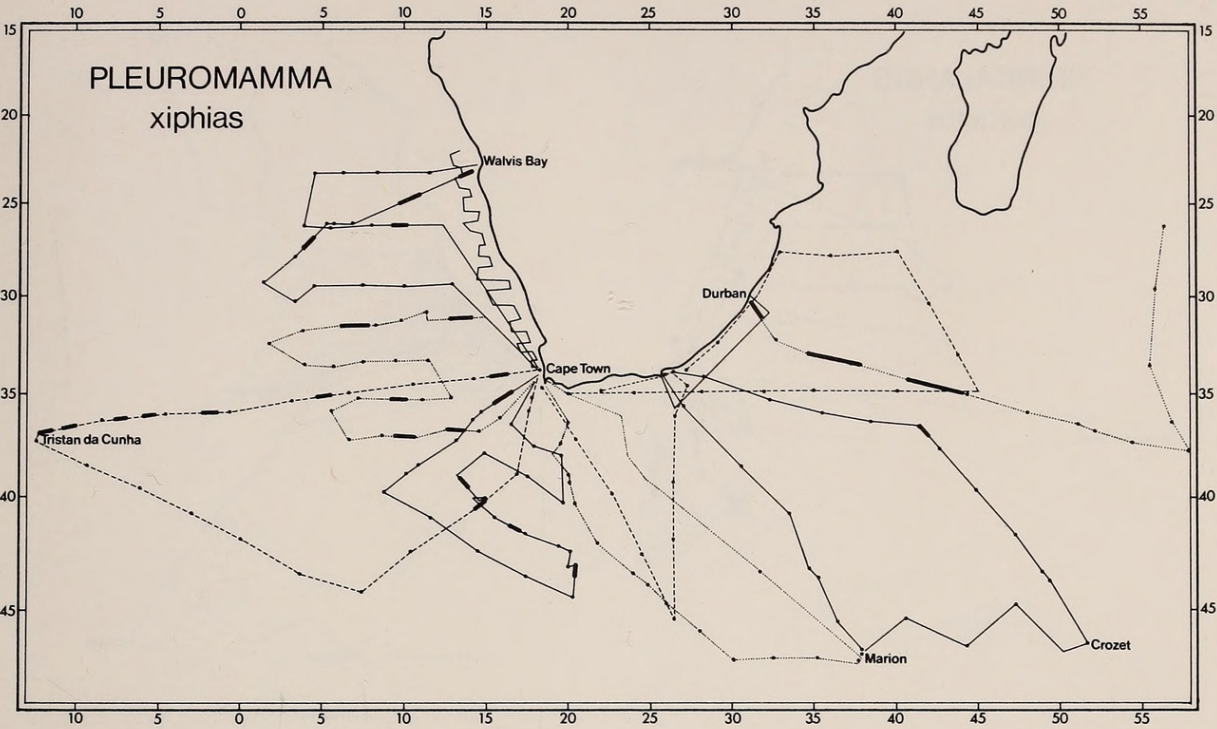




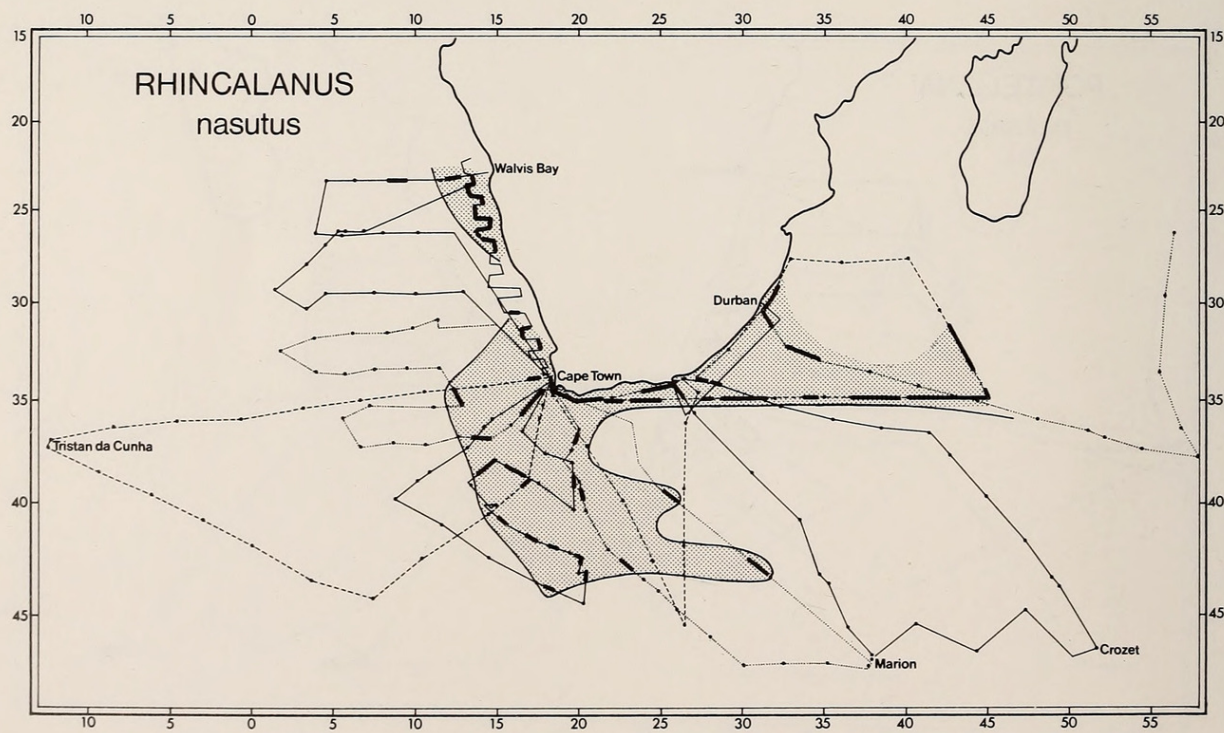
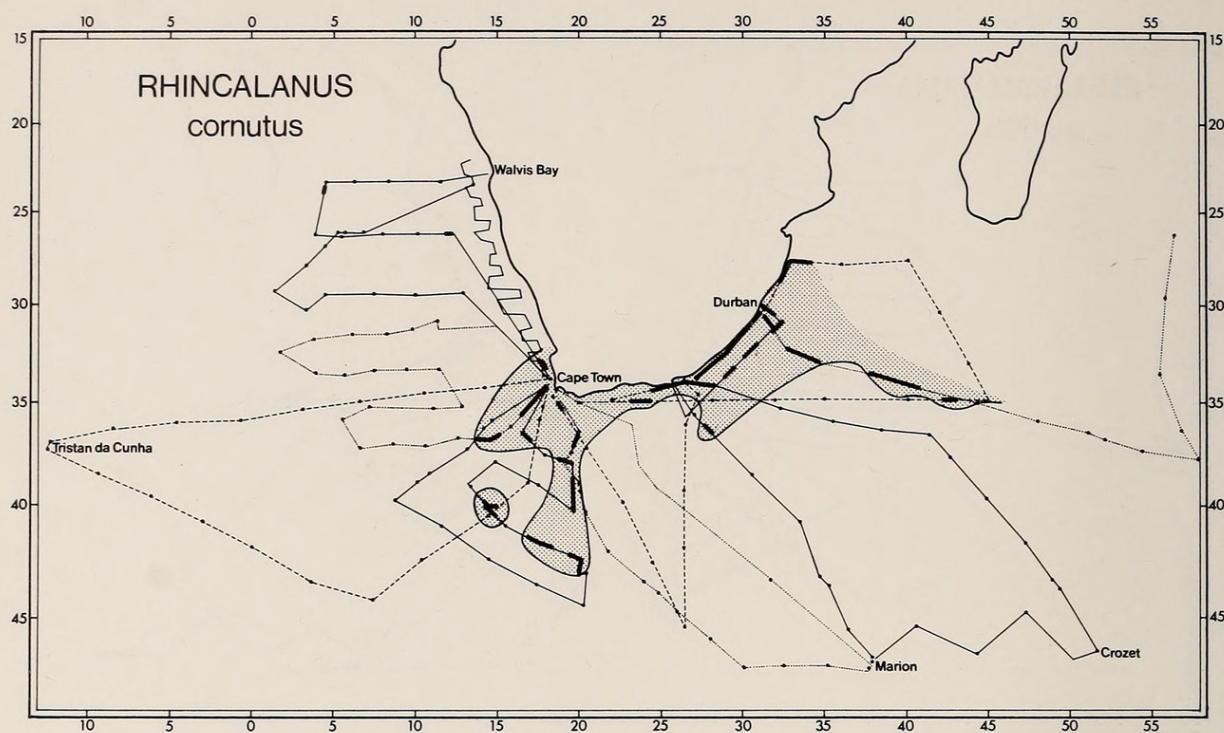




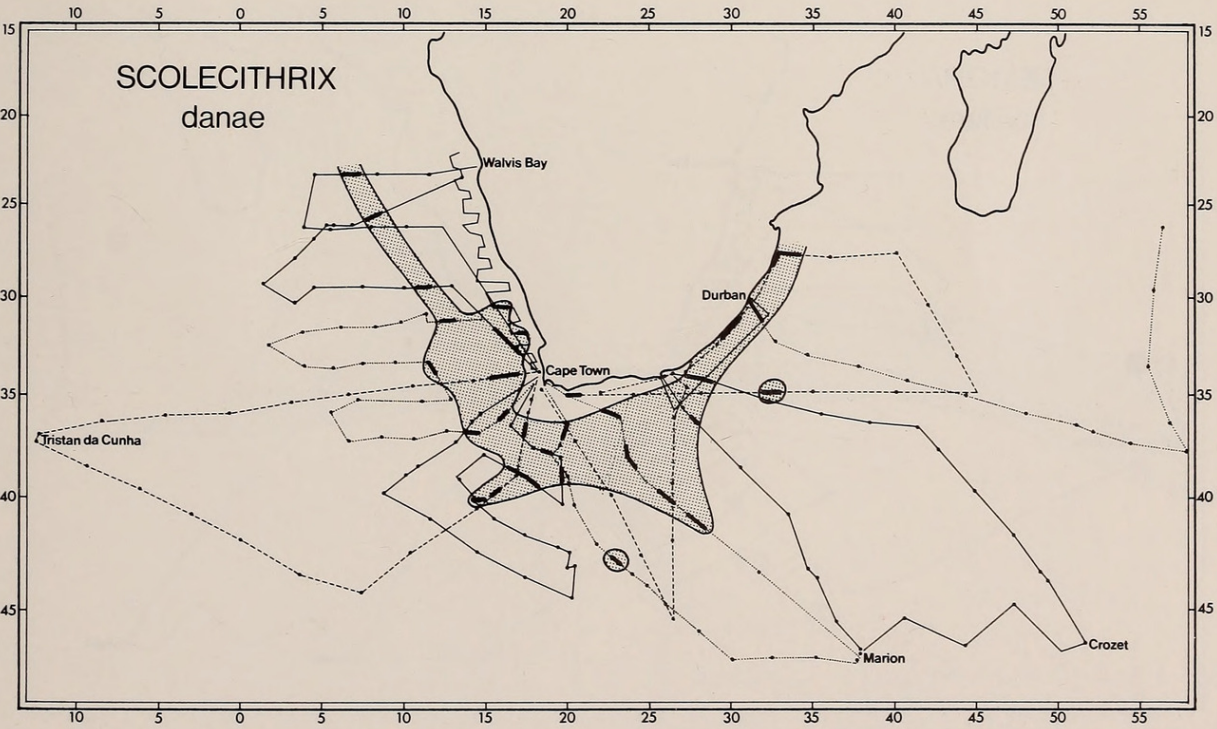
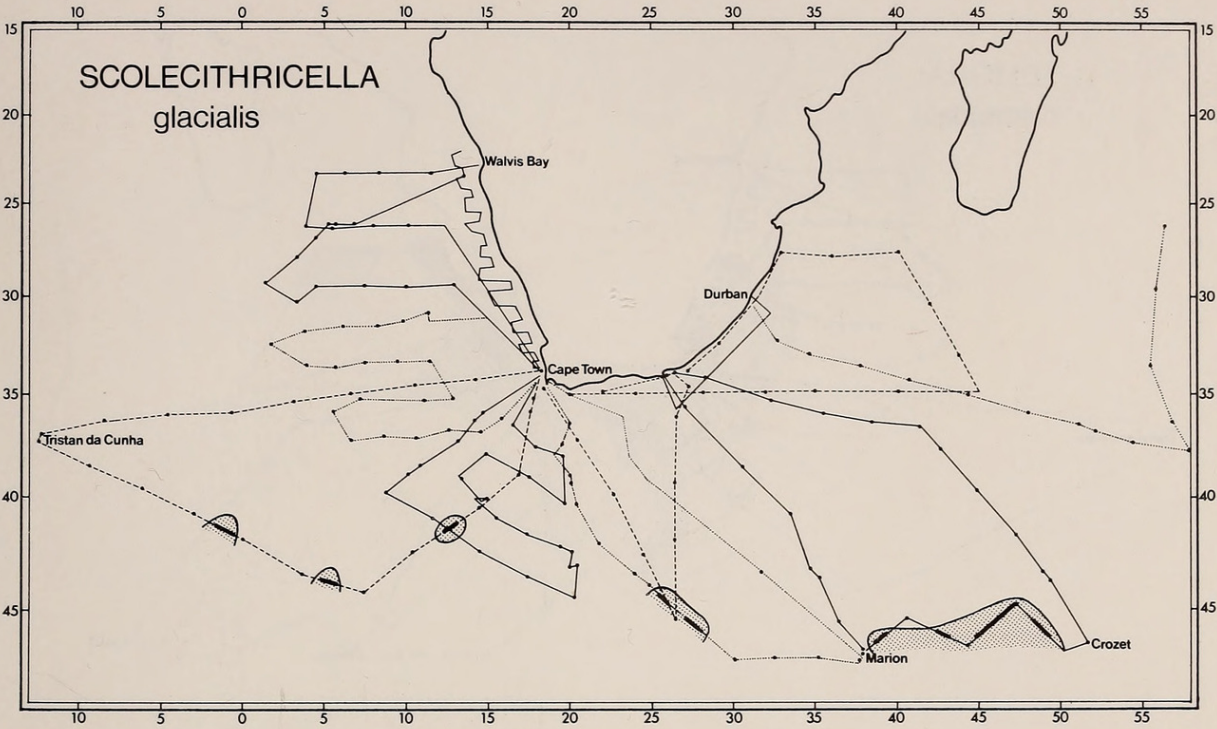




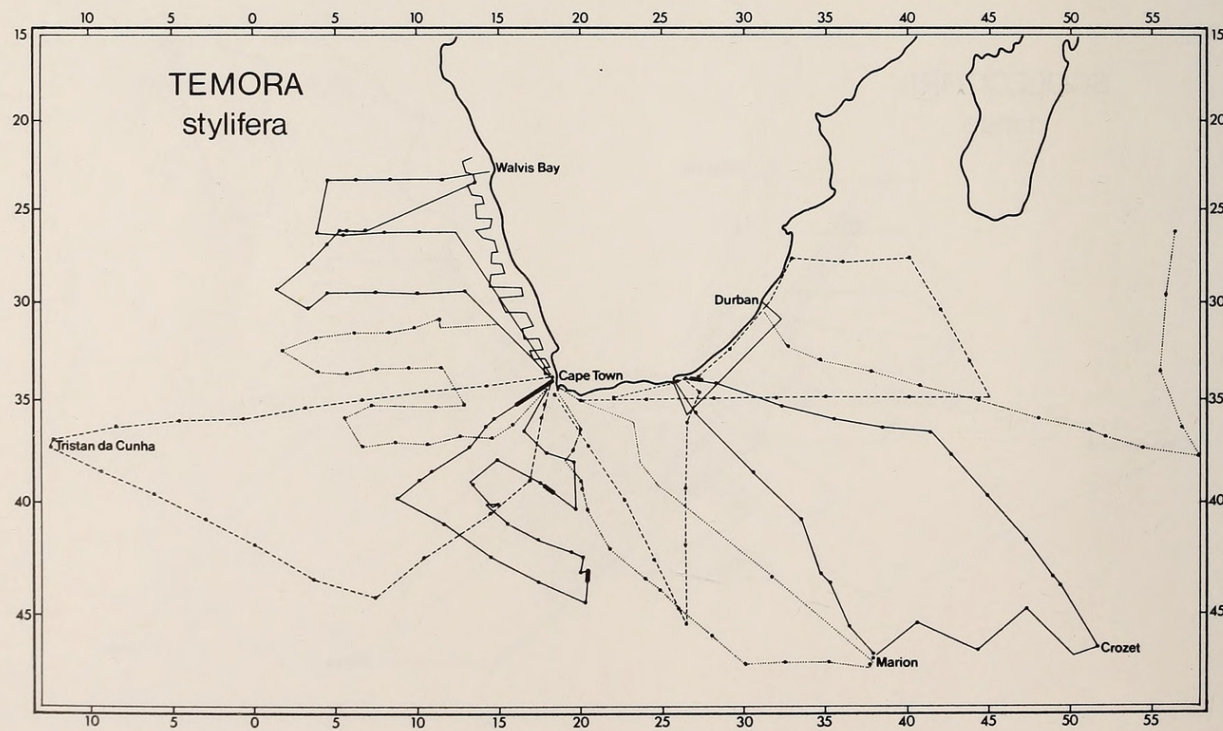
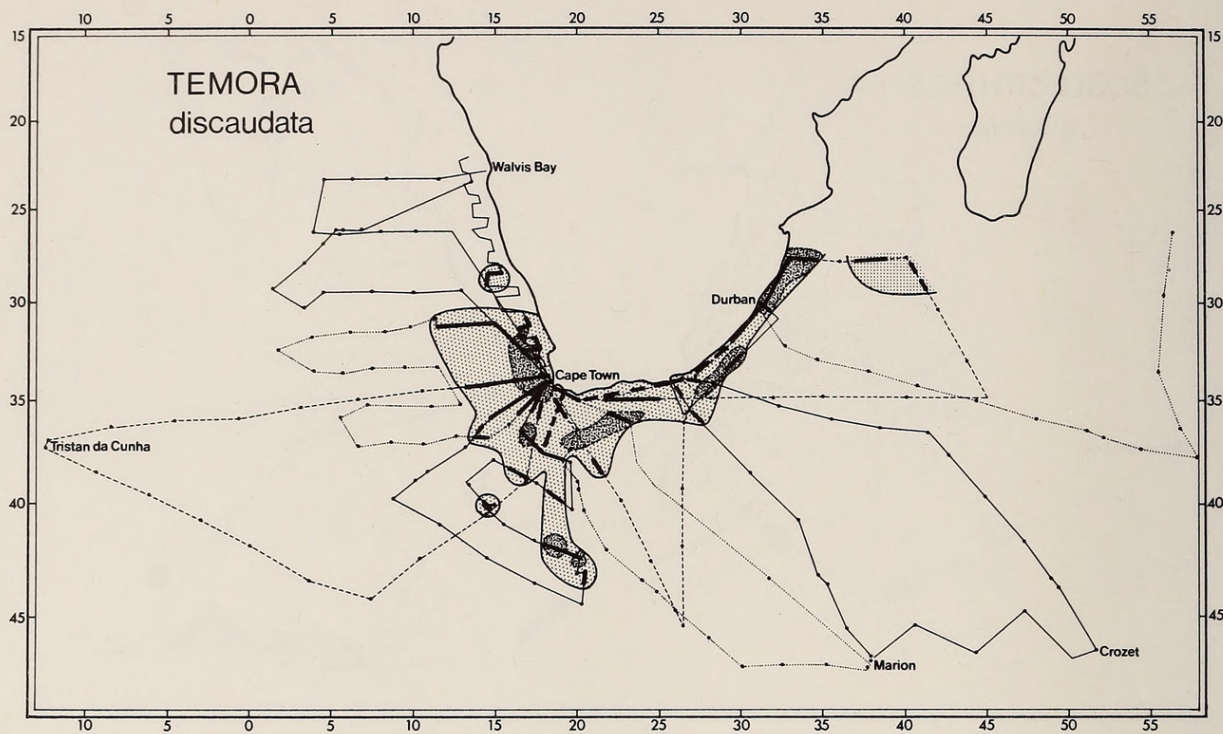




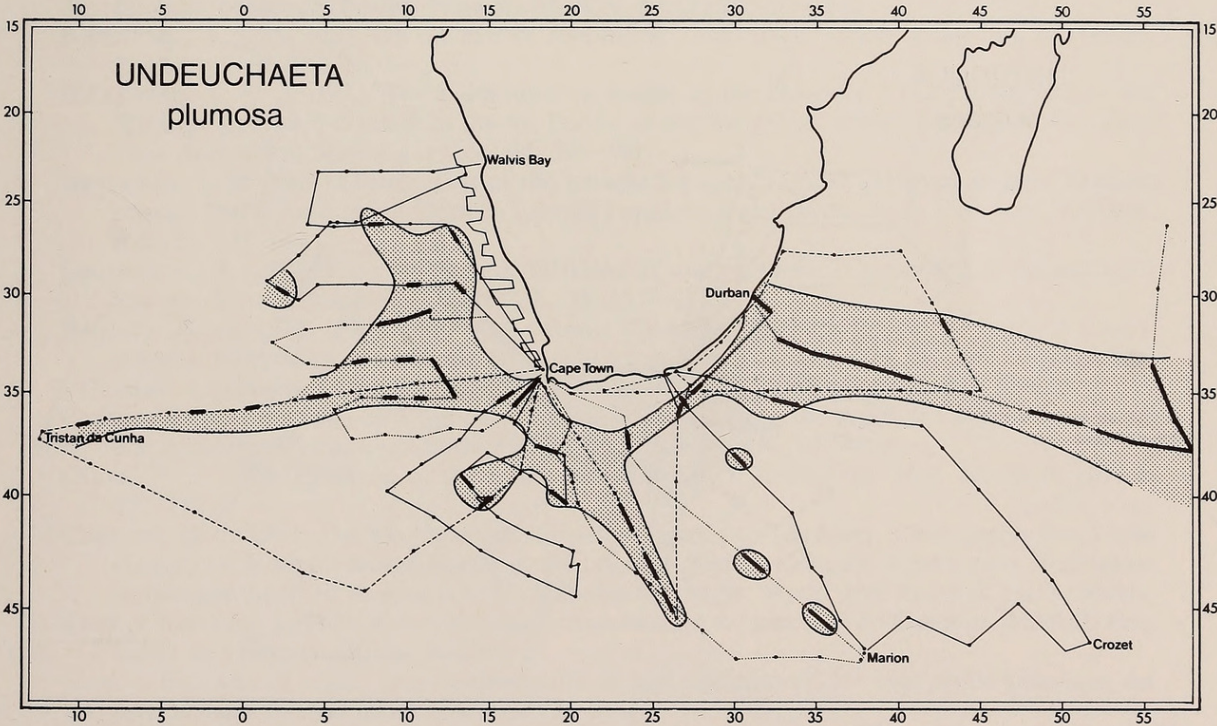
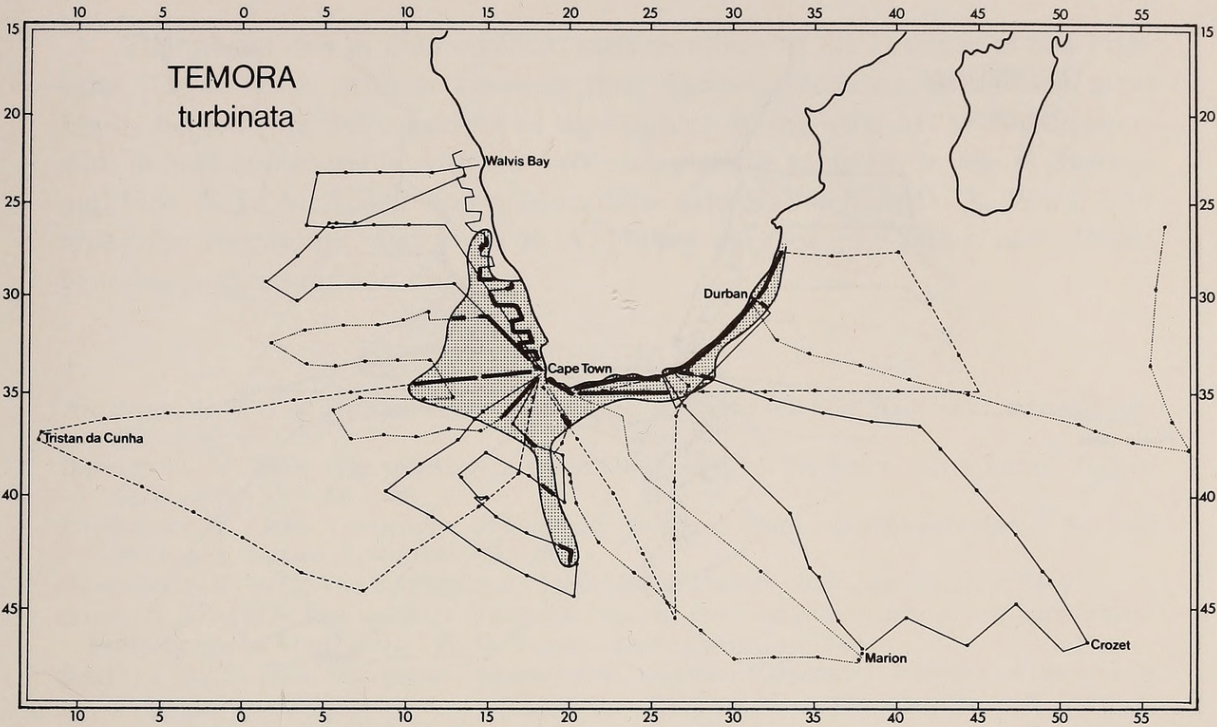




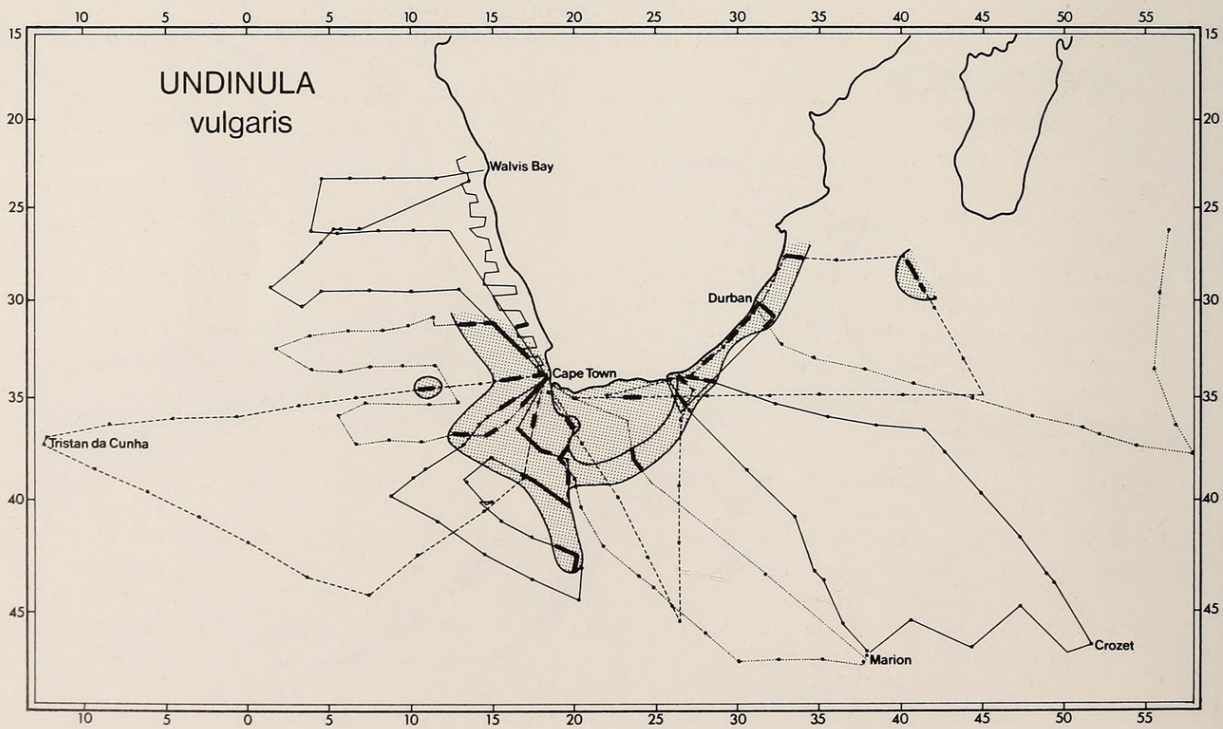
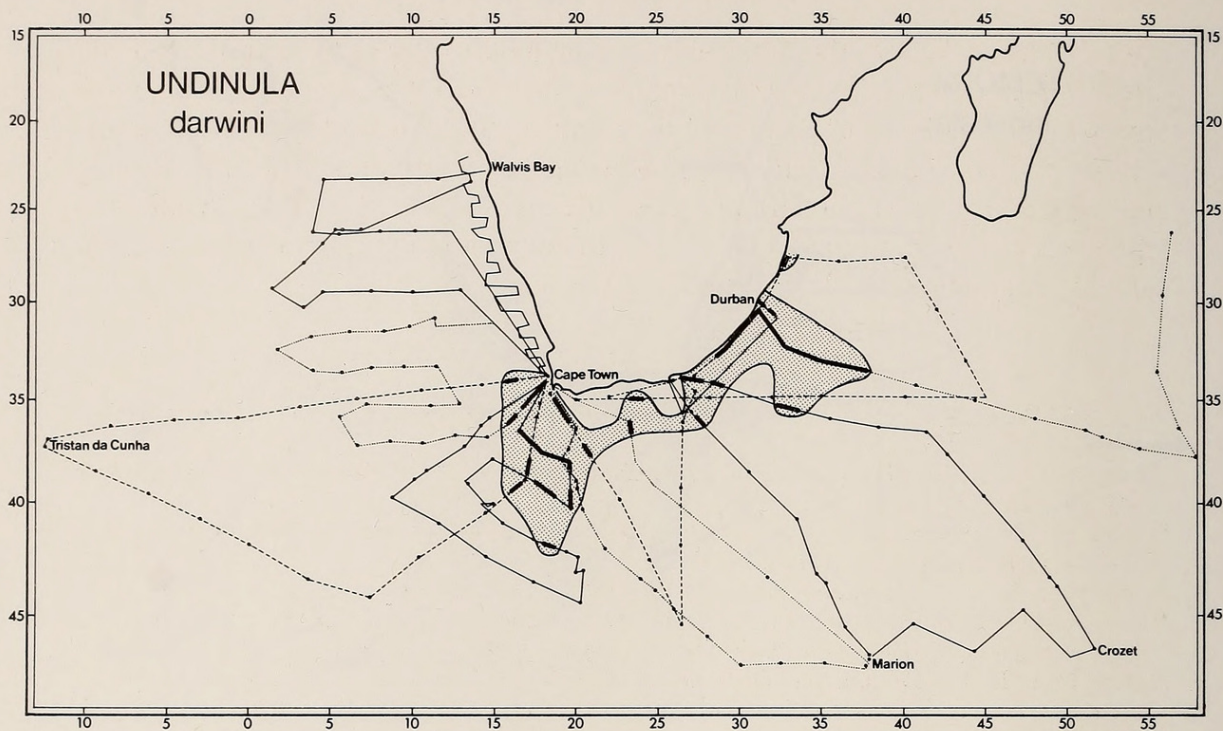














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