A review of primary production and related processes on the Agulhas Bank

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Phytoplankton biomass and productivity in different sectors of the Agulhas Bank are discussed in a broad hydrographic context centred predominantly on thermocline characteristics. The delineation of the different sectors is largely subjective, though based on some degree of physical and biological uniformity within each sub-region. The primary physical forcing mechanisms of wind-driven coastal upwelling and current-driven shelf-break upwelling stimulate phytoplankton productivity in the coastal region of the western Bank and over the eastern sector, respectively. Vertical thermal structure is advectively maintained but modified by summer insolation and wind-induced mixing. Deep mixing associated with the deep pool south of Cape Agulhas severely retards primary production. In the winter the predominantly westerly wind conditions and reduced advection of bottom water onto the Agulhas Bank result in a deepening of thermocline over much of the region. The Agulhas Bank appears to be more productive with respect to phytoplankton than other major western-boundary current systems.

Hydrographic setting

General features

The Agulhas Bank covers an extensive continental shelf area ranging from Cape Point (18°E) in the west to East London (28°E) in the east. The Bank may be divided into western, central and eastern sectors, each characterized by different hydrological conditions related primarily to forcing by the Agulhas Current and wind-driven coastal upwelling. These distinct forcing mechanisms create a region of interaction between the cool eastern-boundary current system (Southern Benguela) in the west and the warm western-boundary current system (Agulhas Current) in the east.[1] The juxtaposition of two such diverse current systems creates complex patterns of water-mass movements and characteristics with considerable overlap, particularly in the western sector. Therefore the western inner shelf forms a natural continuation of the west-coast upwelling system,[2] whereas the outer shelf is strongly influenced by oceanic flow and at times is more characteristic of a western-boundary system.[3]

The broad east–west dichotomy over the Agulhas Bank is supported by a number of hydrological and biological characteristics including: a surface-water divergence south of Cape Agulhas,[4] bottom water supply,[5] habitat and spawning grounds of commercially important pelagic species,[6-11] biomass and production of zooplankton,[12] long-term average chlorophyll concentrations,[13] and seasonal thermocline properties.[14-18] The depth and intensity of the thermocline and the closely associated nutricline is known to exert a profound effect on phytoplankton biomass/production profiles and hence primary production in the total water column.[16] The aim of the present synthesis is to establish sub-regions or provinces identified by the primary physical forcing mechanisms that vary in influence

over the Agulhas Bank, using the thermocline/upper mixed-layer characteristics as criteria. Such hydrologically defined provinces will provide a basis for interpreting the spatio-temporal variability in primary production and related processes.

A map of the Agulhas Bank showing the different sectors under consideration (based on refs 12 and 17) and approximate depth of the upper mixed layer/thermocline in the summer (from refs 1, 14, 16 and 19) is shown in Fig. 1. During the summer, Agulhas Bank waters display a typical continental shelf condition of thermal stratification dominated in this case by Agulhas Current intrusions of warm subtropical water (> 18°C) at the surface, and cold central water (< 10°C) at the bottom. Thermoclines deepen and weaken in gradient from the inner central/eastern Bank to the western Bank.[1,14,18] West of the Alphard Banks thermoclines are generally located between 40 and 60 m and to the east typically between 20 and 40 m.

The central and eastern Bank

The inshore regions of the central and eastern Agulhas Bank are characterized by intermittent coastal upwelling, particularly downwind of prominent capes.[20-22] Winds favouring upwelling, (i.e. with an easterly component) occur predominantly in the summer and autumn when the South Atlantic high-pressure system shifts south of the continent. Shelf-edge upwelling resulting from interactions with the Agulhas Current is of greater importance in this eastern sector than in the west, and to a large extent determines the thermocline topography of the region. Shelf-edge upwelling occurs through the effect of bottom stress on the Agulhas Current, which results in an onshore Ekman layer upwelling cold, predominantly Indian Ocean central water[5] from below the warm shelf-edge flow. Additional upwelling at the shelf edge is associated with border eddies of the Agulhas Current, predominantly in the region of the Agulhas Bank Bight (22–24°E) and the shelf edge downstream of Port Elizabeth.[23]

Upwelling of Indian Ocean central water occurs continually along the eastern and south-eastern shelf edge,[5] although annual variation in the temperature of the bottom water over the inner central Bank[15] and the central shelf of the eastern Bank[1] indicates that the flow may vary seasonally. It has been proposed that the increase in bottom temperature in winter is the result of slackened upwelling over the eastern shelf edge, which would cause bottom water in winter to originate from shallower depths.[1] As the Agulhas Current shows no such pronounced seasonal variation,[24] the prevalence of strong westerlies in the winter and associated deepening of the mixed layer may be the mechanism acting to reduce the advection of cold bottom water across the shelf.[18] Shelf-edge upwelling may impact on the inner shelf at the narrow eastern extreme of the Agulhas Bank. Dynamic upwelling caused by the Agulhas Current in the vicinity of Cape Padrone can result in cool water penetrating Algoa Bay. While the wind-driven upwelling further west is generally of short duration, this current-driven upwelling may persist for a number of weeks.[22,25]
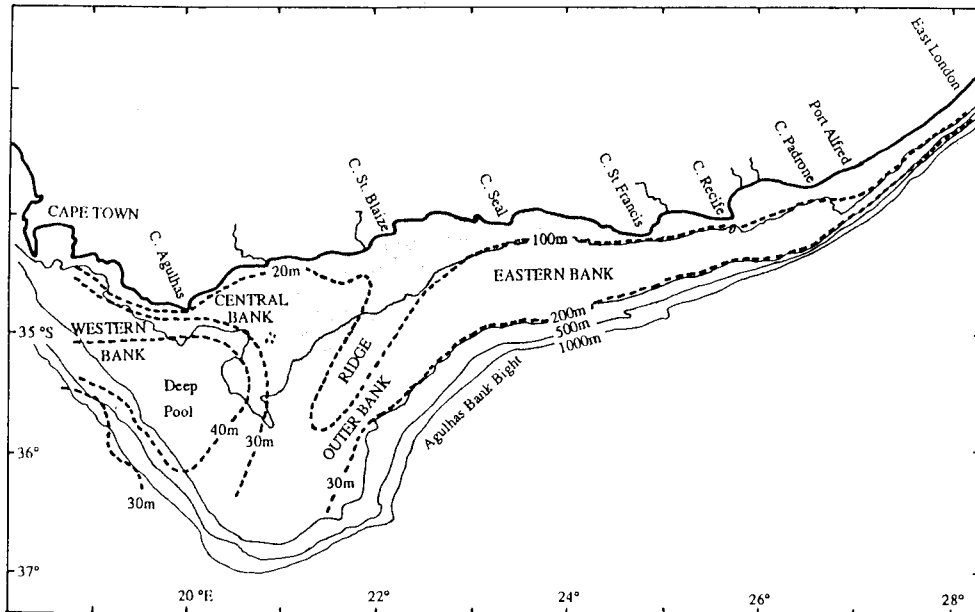
Fig 1.   Map showing the different sectors of the Agulhas Bank. Broken lines represent the approximate depth of the upper mixed layer during the summer. Shading indicates the area where the most intense thermoclines are likely to occur over the Bank.

In addition to the effect of the influx of cold bottom water on interfacial stability, thermoclines are further intensified by the continual inflow of warm subtropical surface water, predominantly over the eastern parts of the Agulhas Bank[21] and in the region of recurring plumes of frontal eddies associated with the meanders of the Agulhas Current.[1,23] Vertical thermal structure is therefore primarily established and sustained advectively, but modified by the stabilizing effect of summer insolation on the one hand and the destabilizing effect of wind-induced turbulent mixing on the other.[1]

A ridge of cool upwelled water lying west of Cape Seal and Cape St. Francis and extending roughly along the 100-m isobath appears to be a quasi-permanent component of the large-scale thermal structure on the central/eastern Bank during the spring and summer.[1,12,21] This ridge has been observed as a feature of satellite images of sea-surface temperature[21] and pigment concentration[26] in the region. The dynamics of the feature are not well understood, although a nearshore origin with waters upwelled at Cape St. Francis being advected offshore as a result of strong easterlies has been proposed.[21] However, the persistent nature of the feature, specifically during the monitoring period from October 1985 to March 1986, is regarded as indicative of oceanic forcing by the Agulhas Current.[1] Offshore of the cold ridge the whole water column moves westwards and south-westwards along isobaths under the direct influence of the Agulhas Current at the shelf edge. Inshore of the ridge, surface flow has an eastward mean direction, thus establishing a surface cyclonic flow around the feature. This conclusion about the circulation pattern is supported by acoustic doppler measurements during November 1989.[11]

Strong shelf-edge upwelling, especially at the steeply sloping shelf break, results in the doming of isotherms over the outer shelf. Cross-shelf stratification in summer and autumn therefore approximates the pattern of raised thermoclines at the shelf edge, giving way to deepening at mid-shelf with further shoaling towards the coast.[1,14,18,19,25] Doming of isotherms also appears to be a feature of the shelf break during winter and spring. In a September 1968 survey on the eastern and central Bank, the shallowest thermoclines roughly followed the 200-m isobath.[27] The potential shoaling of isotherms at the shelf break differs from the quasi-permanent ridge in intensity of thermo-

clines. Isotherms tend to splay out over the outer shelf before sloping downwards to form the shoreward edge of the Agulhas Current. Thermocline intensity is therefore roughly correlated with depth; the 3°C/10-m contour follows the 200-m isobath and the 5–7°C/10-m, the 100-m isobath. There also appears to be a high consistency of shallow, strong thermoclines (5°C/10 m) close inshore from Cape Agulhas eastwards.[18] The most intense thermoclines (9–11°C/10 m) are associated with the Alphard Banks,[19,1] extending eastwards inshore towards Cape St. Francis (Fig. 1). This region is also characterized by relatively calm wind conditions during the summer.[28] The mid-shelf upwelling ridge therefore effectively separates an inshore region of intense thermoclines from the outer Bank where thermocline development is weak. The partially mixed structure on the outer Bank suggests enhanced nutrient supply throughout the water column, however, the lack of a stable thermocline layer is not conducive to elevated rates of primary production.[17]

The western Bank

The western Bank, as in the eastern sector, is characterized by preferential upwelling on the westward side of prominent capes, though upwelling here is of a more continuous nature during the summer.[29,30] There is a persistent uptilt of isotherms towards the coast, establishing a thermocline at roughly 30 m and shallower with episodic surface upwelling. With the onset of strong south-easterly winds in September, a well-developed upwelling front is established that effectively reduces cross-shelf diffusion and contains cold, nutrient-rich water in the coastal region.[3,29] Strong winds favourable to upwelling during the summer generally persist for 2–4 days, though occasionally prolonged upwelling may occur for a 2–3-week period.[3]

Shelf-break upwelling is not as marked a feature of the western Bank as it is in the central/eastern sectors because the primary forcing factor, the Agulhas Current, retroflects south and east at the southern tip of the Agulhas Bank. The generally deeper water column and increased distance from the region of very active shelf-edge upwelling in the east further reduces the impact and influx of bottom water onto the shelf. However, evidence exists for a quasi-steady deep barotropic north-westwards flow (with reversals) along the western shelf edge, which should result in an onshore Ekman layer intruding onto

the shelf.[3,11] It has also been proposed that strong coastal upwelling will indirectly enhance bottom-water influx along the south-western edge of the Agulhas Bank,[11,18] particularly at the head of canyons.[31] The source water for bottom flow is predominantly South Atlantic central water.[5]

Warm Agulhas Current water (> 18°C) associated with frontal instabilities may, on occasion, move onto the western Agulhas Bank in the summer,[2,3,29] intensifying thermal gradients between surface and bottom water. Such intrusions, however, are not expected to be prevalent in the western sector. Therefore, although vertical temperature structure is still advectively maintained, thermoclines are generally not as intense in the west as over the central and eastern sectors, with gradients of > 10°C/10 m seldom being achieved.[32]

The general cross-shelf temperature structure on the western Bank indicates a permanent uptilt of isotherms towards the coast, with the thermocline at about 30 m and doming of isotherms over the shelf edge establishing the thermocline at 30–40 m.[3] The shelf region between the wind-driven coastal region and oceanically forced shelf-edge region is characterized by stronger and deeper stratification with a thermocline at depths of 40–60 m.[3,29] This deep thermocline topography appears to be a continuation of a trough extending eastwards to the Alphard Banks and lying between the coastal upwelling zone and ridge on the central and eastern Bank.[1] The trough deepens and broadens towards the western sector establishing a 'deep pool' south of Cape Agulhas. Long-term average thermal structure for the summer shows just such an extensive region of deep mixing off Cape Agulhas[14] with thermoclines > 50 m approximately coincident with the Agulhas Bank divergence.[4]

Winter conditions

The preceding discussion has been concerned primarily with providing a generalized review of thermal structure on the Agulhas Bank during the summer. The winter conditions are less well documented, though they appear to be characterized by more uniform conditions over much of the Agulhas Bank, especially in the context of vertical profiles of primary production. During winter, as insolation decreases and surface waters cool, deep mixing of the water column, due to predominantly westerly wind conditions[33] and reduced advection of bottom water onto the Agulhas Bank, results in a deepening of the thermocline to > 70 m.[14,15,29,34] The continuous nature of shelf-edge upwelling, however, maintains some vertical thermal structure over the western, central[17] and eastern[27] sectors.

Internal tides and wind stress

Focusing on the mean summer thermocline characteristics ignores event-scale dynamics, which may have a profound effect on biological processes. For instance, the large-amplitude internal tides (2–12 m), particularly on the narrow western Bank and outer central Bank,[17] result in a vertical displacement of the thermocline and plankton above and below the mean depths and promote turbulent mixing as they propagate across the shelf. Similarly, increased wind stress results in downwelling of the thermocline[16] and may facilitate turbulent exchange as the advective bottom layer rapidly re-establishes the thermocline at its modal depth.[1] Assuming uniform wind stress across the Bank implies that the potential impact of wind-driven inertial and Ekman motions is greatest for the shallow thermoclines of the inner central Bank.[17] In spite of these episodic events, the strong tendency for the thermocline to return to its advectively prescribed depth supports the present attempt to define hydrological provinces as a broad physical framework for discussion of phytoplankton dynamics.

Chlorophyll distribution over the Agulhas Bank

Analysis of an extensive data set for the period 1971–1989 has shown that the upper water column of the Agulhas Bank is characterized by a smaller mean chlorophyll concentration (1.48 mg m^{-3}) than the southern Benguela (2.15 mg m^{-3}).[13] The largest concentrations (> 3 mg m^{-3}) on the Agulhas Bank are found in the western sector in the upwelling-dominated coastal area. On the eastern Bank, localized patches of moderate (> 2 mg m^{-3}) chlorophyll concentration occur in Algoa Bay and in association with the upwelling west of Cape St. Francis as well as the inner reaches of the upwelling ridge. Isolated pockets of moderate concentrations may also form over the south-east shelf edge and the Agulhas Bank Bight. However, due to the sparse data coverage for these areas, it would be premature to interpret these from a physical standpoint. Interestingly, the lowest concentrations (< 1 mg m^{-3}) are found south of Cape Agulhas, roughly coincident with the deep pool discussed earlier.

A time-series analysis of the same data set revealed a marked seasonal cycle in mean chlorophyll concentrations over the Agulhas Bank.[35] Chlorophyll concentrations were shown to be at a minimum in the winter (June–August) and to increase steadily from spring (September) to reach a maximum in late summer (February–March). However, this study was considerably biased towards the western Bank and therefore not representative of the Agulhas Bank as a whole. Rather, the seasonal pattern that emerged was indicative of the similarity of the western Bank to the rest of the west-coast upwelling region. A subsequent analysis with the inshore region of the western Bank excluded revealed a quite different pattern.[36] Greatest mean chlorophyll concentrations in the upper 30 m were found in the spring (September–November) and autumn (March–May), with patches of 2–4 mg m^{-3} being fairly widespread. Summer (December–February) and winter (June–August) concentrations were moderately small (< 1–2 mg m^{-3}) but occasionally greater near the coast. The winter scenario was one of considerable uniformity over the region with little evidence of localized plumes or patches. Such a seasonal pattern may be regarded as typical for a temperate continental-shelf system.

A generalized cross-shelf pattern of chlorophyll distribution has been derived for the summer based on cruises during December 1989, November 1989[12] and January 1992 (unpublished results). The different areas discussed in terms of vertical and cross-shelf chlorophyll distributions are shown in Fig. 2. During these cruises a chlorophyll-rich zone (typically 2–5 mg m^{-3} at the chlorophyll maximum) was present throughout the inshore region of the Agulhas Bank. This enriched inshore zone is generally expressed in the vertical as a broad surface maximum at the coast, deepening in an offshore direction. The zone is narrow near Cape Agulhas and broadest on the western inner shelf coincident with strong coastal upwelling. A secondary chlorophyll maximum zone occurs in association with the mid-shelf upwelling ridge and over the outer shelf, probably associated with shelf-edge upwelling.

On the western Agulhas Bank the inshore chlorophyll maximum can extend from near surface to a depth of 20–30 m and up to 75 km offshore. The secondary offshore maximum was located at depths of 30–50 m with concentrations of about 1 mg m^{-3}. The mid-shelf region between these maxima, an extension of the trough in thermocline depth discussed earlier, supported very little phytoplankton biomass, with concentrations generally ≤ 0.5 mg m^{-3}. The zone of low chlorophyll concentration associated with this trough reached a maximum cross-shelf extension south of Cape Agulhas in the region of the warm, deep pool. Here the inshore chlorophyll maximum
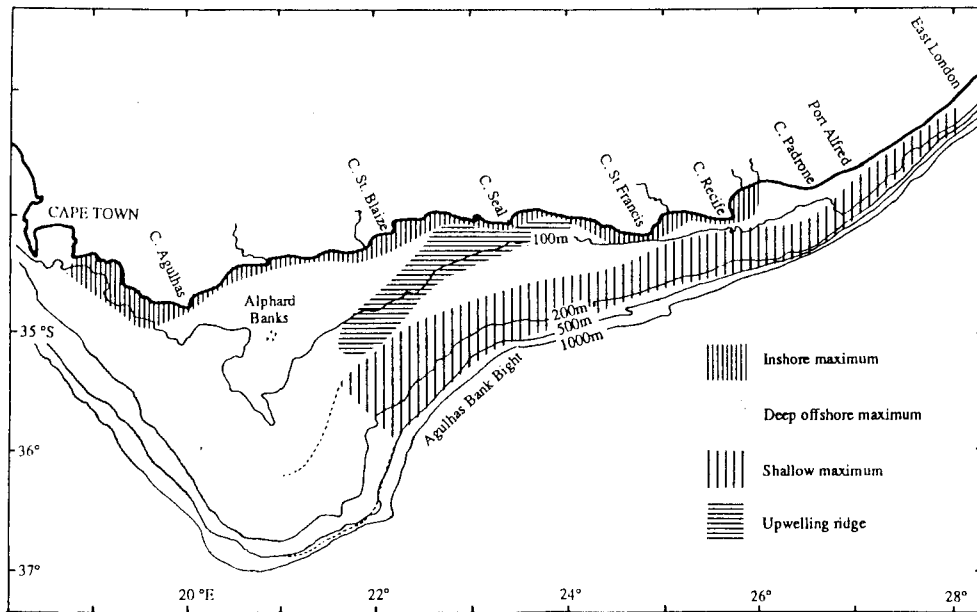
Fig 2.   Generalized distribution of different chlorophyll maximum zones as related primarily to coastal and shelf-break upwelling.

was not as well developed as further west, though the outer-shelf subsurface maximum is maintained at depths of 30–60 m and levels of about 1 mg m^{-3}. Eastwards over the outer-Bank region the outer-shelf maximum shoals and intensifies with chlorophyll concentrations of > 1 mg m^{-3}, occasionally up to 5 mg m^{-1}, generally positioned between the surface and 20 m. This offshore increase in chlorophyll concentration over the eastern sector is presumably related to more active shelf-edge upwelling than in the western sector. Similar enhancement of chlorophyll concentrations in the upper mixed layer was also noted where the upwelling ridge cuts across the central/eastern Bank. Chlorophyll maxima associated with the ridge were at depths of 10–20 m and characterized by concentrations > 2 mg m^{-3}. Where the upwelling ridge extends towards the outer shelf, in the south-east region of the Agulhas Bank Bight, it appears to interact with shelf-edge upwelling to produce a more extensive, near-surface chlorophyll maximum.

Over the eastern Bank, chlorophyll concentrations > 1 mg m^{-3} extend across the entire narrow shelf with the mid-shelf region characterized by a high degree of spatial heterogeneity in chlorophyll distribution. As elsewhere, there is both an inshore and offshore chlorophyll maximum zone, although over the eastern Bank there is a tendency for the inshore maximum to be positioned subsurface at 10–20 m as opposed to the broad surface maximum in the west. The offshore subsurface chlorophyll maximum, in agreement with the situation over the outer Bank, remains shallower and more intense (> 2 mg m^{-3}) than observed over the western and central Bank (0–30 m). There is a tendency for the offshore chlorophyll zone to penetrate further onto the shelf in the eastern sector as the shelf narrows. In the narrow eastern extreme of the Agulhas Bank this dynamic, upwelling-related zone extends close inshore.

Examples of chlorophyll profiles in the upper water column for the different sectors of the Agulhas Bank are shown in Fig. 3. The deepening of the thermocline towards the west and associated dramatic weakening of the subsurface chlorophyll maximum is demonstrated in Figs 3a and b. The broad, shallow chlorophyll maximum, characteristic of coastal upwelling zones is shown for an inshore profile of the western Bank (Fig. 3c). The weakly stratified winter condition is depicted in Fig. 3d for an inner-shelf station on the western Bank.[34] Typically, the mixed layer extends to 65–75 m with a weak

thermocline at this depth. Chlorophyll concentrations are usually low (0.5–1.5 mg m^{-3}) and evenly distributed throughout the euphotic zone. Spring profiles are similar in appearance to the winter condition, although chlorophyll concentrations are doubled, indicating the start of the spring bloom.

The limited data available at present suggest that the inner reaches of the central and eastern Bank, an area that at times is
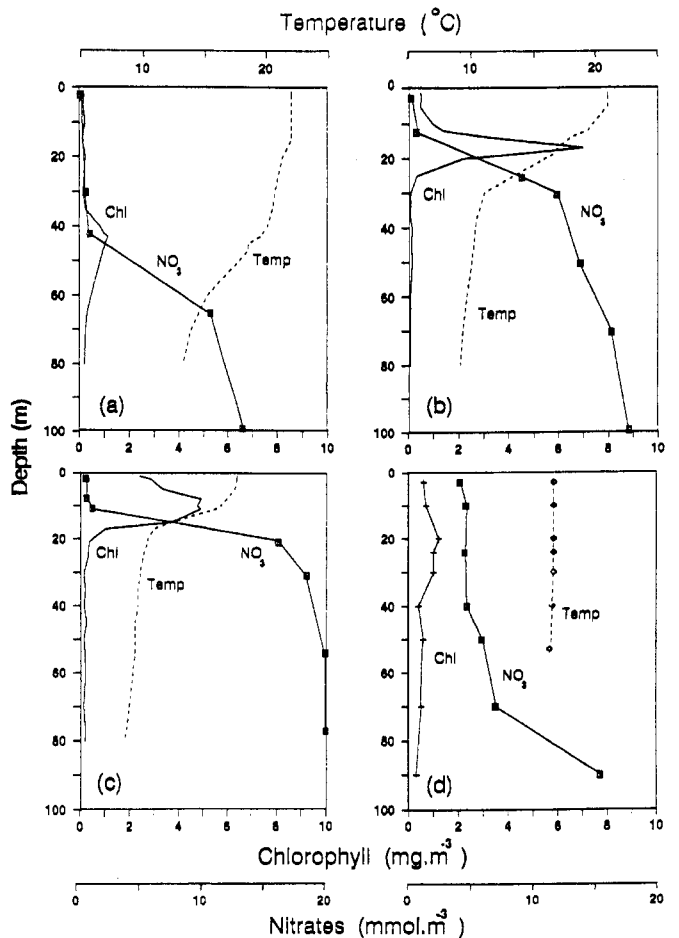

Fig 3.   Examples of NO$_3$, chlorophyll and temperature profiles for the summer (January 1992): a, western Bank mid-shelf; b, eastern Bank mid-shelf; c, western Bank inshore; and the winter (July 1988):[34] d, western Bank inshore.

characterized by intense thermal stratification,[19] is subject to extreme variability in thermocline topography and related phytoplankton dynamics. For instance, chlorophyll maximum concentrations may more than double over a 2-day period (up to 40 mg m^{-3}) in association with intensification of stratification.[16] Similarly, considerably smaller chlorophyll maximum concentrations (< 2 mg m^{-3}) have been measured at the same station during surveys conducted during January 1987 and 1988, when the thermocline was deeper and characterized by weaker thermal gradients than during the March 1986 cruises.[32] The marked variability in depth of the upper mixed layer and thermocline structure in this inner central Bank is presumably related to the dynamics of the upwelling ridge and wind stress. A similar, though not as large, increase in chlorophyll maximum with shoaling of the thermocline has also been observed on the western Bank shelf.[34] It appears that the formation of the most intense subsurface chlorophyll maxima on the Agulhas Bank occurs only when the upper mixed layer is < 30 m.

Such extreme variability emphasizes the need for a dynamic approach to defining hydrological and biogeochemical provinces on the Agulhas Bank. Clearly, remote sensing will be necessary to provide for synoptic perspectives at the broad scales under consideration. However, the subsurface chlorophyll maxima typical of the region have limited surface expression. Therefore, future research emphasis on the Agulhas Bank must in part strive for reliable direct confirmation of satellite data with the primary goal of defining as many sources of variability as possible.

Primary productivity

Aereal production

A summary of integrated primary production for the different sub-regions of the Agulhas Bank is given in Table 1. Production values have been assigned to a particular province on a subjective basis and in some cases not necessarily according to position. Specifically, in the western sector production stations may fall either in the western Bank inner shelf or mid-shelf owing to the dynamic nature of the upwelling front on the western Bank. In broad terms, the eastern Bank appears to be characterized by higher levels of primary production than elsewhere over the Agulhas Bank. Primary production is lowest over the deep pool and central Bank excluding the region characterized by intense thermal stratification. As was the case for chlorophyll concentrations, the intense thermocline region on the central Bank, including the Alphard Banks, appears to be an area of extreme variability. On the western Bank, primary production is greatest inshore, decreasing seawards to the shelf edge. Winter measurements (July 1988) on the western Bank suggest a cross-shelf uniformity in primary production. However, to date, the Agulhas Bank has been grossly undersampled with respect to winter conditions.

The variation in primary production on the Agulhas Bank roughly follows the general east-to-west trends in depth of the thermocline, with areas of shallow thermoclines exhibiting greater rates of primary production than those characterized by deeper thermoclines. This is demonstrated in Fig. 4, where integrated phytoplankton production is related to depth of the upper mixed layer. Although of limited predictive capability, the relationship does imply some coherence between hydrological and biogeochemical processes.

Primary production rates in Table 1 have been area-weighted to give a mean rate for the whole Agulhas Bank of 2 035 mg C m^{-2} day^{-1} for the stratified period in summer and an annual rate of 656 g C m^{-2} yr^{-1}. The area of the different subregions used in the weighting procedure was subjectively estimated from Figs 1 and 2. The annual estimate is similar to the 681 g C m^{-2} yr^{-1} estimated previously from a smaller subset of the present data.[13] Primary production on the Agulhas Bank appears to be greater than that measured for other western-boundary current systems such as the Brazil Current and Gulf Stream. An annual production rate of about 300 g C m^{-2} yr^{-1} has been calculated for the southern Brazilian coastline during 1972.[37] Similarly, phytoplankton production of 180–470 g C m^{-2} yr^{-1} has been reported for the Mid-Atlantic Bight[38] and 171 g C m^{-2} yr^{-1} for the Georgia Bight.[39] The considerably smaller annual production for the south-eastern US shelf (Georgia Bight) is of interest as this system is perhaps most similar in a physical sense to
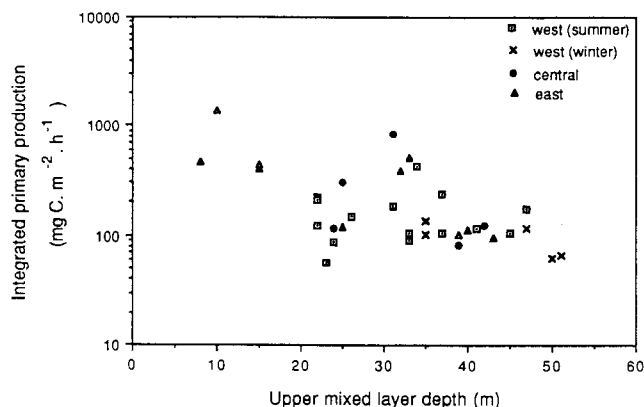
Table 1. Summary of measured rates of primary production in different sub-regions of the Agulhas Bank: Data were obtained from 1, ref. 34; 2, Brown (unpublished results); 3, Mitchell-Innes (unpublished results); 4, ref. 32; 5, Carter (unpublished results).

Sub-region	Date	Primary production mg m^{-2} h^{-1} (s.d.)	n	Source
Western Bank				
Coastal	Jul. 1988	95 (25)	2	1
	Oct 1987	244 (95)	3	1
	Nov 1981	270	1	2
	Dec 1986	289 (201)	2	1
	Jan 1988	196 (54)	5	1
Mid-shelf	Jul 1988	120	1	1
	Nov 1981	121	1	2
	Dec 1986	86	1	1
	Jan 1987	117 (35)	4	1
	Jan 1988	132	1	1
Deep Pool	Dec 1985	17	1	3
	Mar 1986	6	1	5
Shelf break	Jul 1988	108 (49)	2	1
	Nov 1981	35	1	2
	Dec 1986	81 (30)	2	1
Central Bank				
Inner shelf	Nov 1981	79 (19)	2	2
	Mar 1986	162	1	5
Alphard Banks	Jan 1987	417 (310)	3	4
	Jan 1988	107 (20)	2	4
	Mar 1986	572 (578)	3	4
Upwelling ridge	Feb, Mar 1986	104 (28)	6	5
Outer Bank	Mar 1986	34	1	5
Eastern Bank				
Coastal	Feb 1992	444 (53)	2	3
Shelf	Feb 1992	888 (485)	2	3
Shelf break	Feb 1992	231 (162)	3	3
Agulhas Current				
Eastern sector	Feb 1992	99 (3)	2	3

Fig 4. Semi-logarithmic plot of integrated hourly primary production (PP) against depth of the upper mixed layer (UML) for different sectors of the Agulhas Bank. The relationship can be described by: log PP = 621.4 – 12.0 UML (r^2 = 0.26, P < 0.002).

the eastern Bank, where the Agulhas Current is closely associated with the shelf-break. As on the Agulhas Bank, dynamical upwelling at the south-eastern US shelf break plays an important role in determining the magnitude of phytoplankton productivity.[40] During periods of very active shelf-break upwelling (spring 1979) primary production rates off the Georgia coast are considerably greater than when upwelling is absent, averaging 2 700 mg C m^{-2} day^{-1} with a maximum rate of 6 000 mg C m^{-2} day^{-1}. The low levels of phytoplankton productivity reported earlier for the Georgia Bight[39] are thus assumed to be representative of a period of diminished shelf-edge upwelling.[40] By way of comparison, the primary production rates measured for the Agulhas Bank (Table 1) indicate a system strongly influenced by dynamical upwelling.

Establishment of subsurface maxima

The formation and persistence of a subsurface chlorophyll maximum on the Agulhas Bank, as in other stratified-temperature shelf seas, is primarily the manifestation of light- and nutrient-limited growth, accumulation at the density interface and stability effects. An in-depth discussion of the possible mechanisms behind the establishment of subsurface chlorophyll maxima is provided by Cullen.[41] Shade adaptation through the increase in chlorophyll content per cell[41] will serve to intensify chlorophyll layering, but not accumulation of biomass. The increased density gradient in the thermocline can lower the sinking rate of phytoplankton cells and thus promote accumulation.[42,43] Sinking rates of phytoplankton are known to be not only a function of physical factors such as cell size and shape, but also of physiology.[44,45] The deceleration of diatom sinking rates in response to low irradiance levels[46] and increased nutrients at the nutricline[47] is perhaps of some relevance to the Agulhas Bank system. Such a mechanism has been suggested to play an important role in the development of subsurface chlorophyll maxima, especially in temperate waters having a shallow mixed layer and well-developed thermocline.[46] However, the sinking of phytoplankton cells alone is unlikely to result in accumulation if there is any grazing at all.[48] These authors suggest that growth and persistence of the chlorophyll maximum are due to in situ production, whereas sinking and accumulation results in deepening and sharpening of maxima. It is difficult at this stage to evaluate the effect of other factors such as differential zooplankton grazing[48,50] and behavioural responses of mobile phytoplankton[52,53] in the creation of a subsurface chlorophyll maximum in Agulhas Bank waters.

The thermocline provides a layer where vertical stability is maximal and hence where phytoplankton growth can potentially lead to increased biomass, provided nutrients and light are non-limiting and grazing does not decimate the standing stock.[54] Excessive vertical mixing generally associated with a homogeneous upper layer would, on the other hand, prevent any form of layering of phytoplankton biomass. During the summer stratified period, primary production maxima on the Agulhas Bank often occur at the 3–7% light penetration depth in association with, or slightly shallower than, the chlorophyll maximum,[16,34] indicating a significant contribution from in situ production in the formation of a subsurface chlorophyll maximum. Substantial production still occurs in the upper water column and the overall contribution of the subsurface production maximum to total water column production may be relatively small, especially when stratification is deep. Therefore, accumulation of upper water column production at the thermocline may indeed serve to strengthen the chlorophyll maxima, particularly those at depth. However, production in shallow chlorophyll maxima on the Agulhas Bank forms a large frac-

tion of productivity in the water column.[16] Here in situ production is presumably the predominant mechanism whereby chlorophyll maxima are generated and sustained.

During the summer on the Agulhas Bank, the euphotic zone is stratified, extending to approximately twice the depth of the upper mixed layer.[34] By contrast, the deep mixing associated with winter and spring results in a homogeneous euphotic zone. Primary production maxima under these conditions occur near the surface at the 40–85% light-penetration depths. The winter scenario is typical of a light-limited situation, whereas during the summer, nutrient limitation of primary production is regarded as being most important.[34] Such generalizations may apply where the upper mixed layer accounts for the majority of water-column primary production but ignores the classical partitioning of a stratified euphotic zone into a lower light-limited zone and an upper nutrient-limited zone.[55] Photosynthesis and growth at the base of the euphotic zone are almost surely limited by light, not nutrients, especially in intense subsurface chlorophyll maxima. In support, it has been shown that in well-developed subsurface chlorophyll maxima on the Agulhas Bank, primary production decreases dramatically with depth through the layer, indicating light limitation due to self-shading.[16] Although a light-limited chorophyll maximum generally does not contribute much to water-column production per se, it does provide an innoculum of viable cells that may bloom in the upper water column when increased turbulent mixing and internal waves erode the thermocline and transport nutrients and cells from depth to the mixed layer where light is not limiting.

A pronounced subsurface chlorophyll maximum functions as an effective nutrient trap, limiting the diffusive invasion of nutrients to the upper mixed layer.[48,55,56] Consequently, one would expect production in the upper mixed layer to be driven predominantly by the regenerated nitrogen sources of NH_4 and urea, because the primary mechanism of NO_3 renewal in a stratified water column is turbulent diffusion from deeper waters. Although no direct measurements for the Agulhas Bank are yet available, the close association of the chlorophyll and production maxima with the nitracline suggests an important contribution from NO_3 to phytoplankton growth in this layer. Measurements of NH_4 and C uptake indicate that approximately half the nitrogen requirements of the subsurface maximum in well-stratified Agulhas Bank waters may originate from this source.[57] It has been calculated, using estimated vertical fluxes of NO_3, that the renewal of NO_3 from vertical mixing and its assimilation in the subsurface chlorophyll maximum supports up to 50% of total net primary production in the well-stratified waters of the English Channel.[58] Direct evidence for the important role of NO_3 at the base of the euphotic zone is provided by ^{15}N-tracer experiments. In well-stratified temperate coastal waters the subsurface chlorophyll maximum has been shown to be fuelled largely by NO_3, whereas the shallower primary production maximum is based on regenerated nutrients.[59] Similarly, the consequence of grazer aggregation at depths shallower than the chlorophyll maximum[50,51] would be an intensification of nutrient regeneration in these upper layers, which in turn fuels the primary production maximum in an otherwise nutrient-deficient mixed layer. The subsurface chlorophyll maximum (and primary production maximum on the Agulhas Bank) therefore assumes greater importance in terms of water column new production[60] than total production. A chlorophyll maximum dependent on NO_3 is consistent with in situ growth as a mechanism of formation, given that net synthesis of phytoplankton biomass can only occur at the expense of new nutrients, whereas nutrient regeneration implies destructive processes.[60]

Summary

The depth of the thermocline appears to be a reasonable criterion for delineating hydrological provinces over the Agulhas Bank. The association between thermocline topography and the primary physical forcing mechanisms operating in the region, namely, the advection of Agulhas Current water onto the Bank and wind-driven upwelling, leads to the hypothesis that the different hydrological regimes are characterized by different biological rates. In a broad sense, this does appear to be the case with the shallow, more intense thermoclines on the eastern Bank supporting more primary production than in the western sector, where thermoclines are generally deeper and weaker. Similarly, primary production on the western Bank decreases offshore, with maximal rates being recorded in the coastal upwelling zone.

Implicit in this approach is that boundaries are dynamic, responding to the intensity, duration and spatial extent of the physical driving mechanisms. The large day-to-day variability that has been measured during time-series studies emphasizes the potential response of phytoplankton to a rapidly changing physical regime. In addition to temporal intermittency is a large degree of spatial heterogeneity, particularly over the eastern Bank where Agulhas Current intrusions are most pronounced. Such variability may realistically be addressed only by remote sensing, and in this respect the Agulhas Bank is not unique. An important component of future research in the region should therefore be the development of empirical or semi-analytical algorithms that relate satellite-detectable properties to primary production.

Tasks would include the local calibration of SeaWIFS satellite data both in terms of measured chlorophyll concentrations over the upper attenuation length and upwelling spectral irradiance. Use of light-photosynthesis models in the primary production algorithm require a detailed investigation of the physiological parameters and pigment distribution. A major challenge exists in relating chlorophyll detected by satellite to pigment content in the productive column for a region such as the Agulhas Bank which is typified by non-uniform pigment profiles. An approach similar to that of Morel and Berthon[61] should perhaps be pursued, whereby statistically constrained 'typical pigment profiles' are adopted for specific trophic categories or defined by satellite-detectable chlorophyll. Ideally, it may be expected that each of the hydrologically defined provinces will be further characterized by a typical pigment profile. Alternatively, modelled chlorophyll profiles may be computed along a trophic continuum as a function of satellite-detectable chlorophyll.[61] Furthermore, meaningful interpretation of measures or estimates of primary production require information on the new and regenerated moeties.[59] To this end, improved knowledge of nitrogen utilization in the different sub-regions of the Agulhas Bank is essential.

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Horse mackerel on the Agulhas Bank — summary of current knowledge

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Horse mackerel are ubiquitous in South African waters and even occur in river estuaries. On the south coast, average size increases offshore and eastwards. Distribution patterns reflect trends in availability produced by migrational habits. The poor quality of the long-term data series for horse mackerel hinders stock assessment for this resource. Although catch and catch rate (CPUE) data are available for each of the fleets involved in the fishery, each of the CPUE series has specific biases and none of them can be used as a reliable index of abundance. A surplus-production model was developed to allow for multiple CPUE series.[1,2] This model was used in the past with reservations because the data series were poor. Preliminary results from an acoustic survey of part of the stock indicate that the production model may have underestimated the size of the resource. Consequently, it is felt that the Sea Fisheries Research Institute is not yet in a position to supply scientifically defensible management advice for the horse mackerel resource. All South African horse mackerel south of the Orange River are considered as one stock, although otolith dimensions and maturation patterns differ between west- and south-coast specimens. Pub-lished growth constants (K) and 50%-maturation lengths vary considerably, ranging from 0.325 yr^{-1} to 0.556 yr^{-1} and from 32 to 43 cm TL, respectively. Two major spawning periods are identified, one lasting from May to August and the other from October to January. Spawning does not seem to be confined to specific areas. The diet consists mainly of planktonic crustacea, but horse mackerel are not specialist feeders. Retention lengths are available for horse mackerel but the results are largely masked by biases inherent in the methods used. Perspectives are given for future research directions.

Until the late 1960s, horse mackerel (*Trachurus trachurus capensis*) were mainly caught by the pelagic purse-seine fleet along the South African west coast (all areas west of 20°E). There, landings decreased from a maximum of 118 100 tons in 1954 to a minimum of some 1 300 tons 14 years later.[3] The decline of the horse mackerel fishery on the west coast was accompanied by an increasing contribution of the species to the landings of the demersal fishery on the south coast (all areas east of 20°E). During the 1970s some 80% of all demersal landings originated from the Agulhas Bank,[4] and in 1977 the peak landing from the Agulhas Bank was reported as about