Mar. Freshwater Res., 2002, **53**, 307–318

Spawning on the edge: spawning grounds and nursery areas around the southern African coastline

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Abstract. The southern African coastline is dominated by strong currents. Along the eastern seaboard, the warm western boundary Agulhas Current sweeps close inshore along the shelf edge before diverging from the coast on the Agulhas Bank and retroflecting back into the Indian Ocean. On the western seaboard, strong jet currents develop in the southern Benguela, associated with the strong thermal gradients induced by upwelling and Agulhas Current intrusions and eddies. There is, in general, northward drift of surface waters in the Benguela Current with strong offshore losses in the vicinity of an exceptionally active upwelling region off Lüderitz. Several potent mechanisms exist for offshore dispersal and loss from the productive shelf waters, such as eddies, filaments, retroflections and offshore Ekman drift, which pose special problems for successful retention of planktonic eggs and larvae from broadcast spawners. Most fish species in southern Africa have evolved highly selective reproductive patterns, which ensure that sufficient progeny are retained or can enter the nursery grounds along the coastline. Four important reproductive habitats, comprising spawning areas, transport mechanisms and nursery grounds, occur between Moçambique and Angola. These are used by a wide variety of pelagic, demersal and inshore-dwelling fish species.

Introduction

Despite a relatively wide shelf and high primary productivity, the fish yields of southern Africa are not particularly high (Hutchings 1992, 1994; Ware 1992; Cury *et al.* 1998). This suggests that fish productivity is restrained in some other manner, such as consumption by top, non-exploited predators such as seabirds or marine mammals, or there are oceanographic constraints on the reproductive strategies of many fish species (Parrish *et al.* 1983). This paper focuses on the latter aspect and synthesizes some of the information on the spawning and nursery areas of a variety of economically and ecologically important fish species around the southern African continental shelf and considers the currents and planktonic productivity associated with different sectors of the coast from southern Moçambique on the east coast to the Angola–Benguela front on the west coast.

The coastline of Southern Africa is one of the smoothest and least convoluted in the world, with a minimum of embayments or enclosed seas (Fig. 1). Moreover, it is swept by a strong western boundary current, the Agulhas Current, on the eastern coast and on the west coast there is strong offshore Ekman drift associated with vigorous upwelling and strong shelf-edge jet currents between the cold upwelled waters and warmer offshore waters. Instabilities in these strong currents and jets can lead to the development of offshore filaments that can transport shelf waters hundreds of kilometres offshore, resulting in the loss of shelf biota to the oligotrophic oceanic interiors. Superimposed on the overall pattern imposed by the major ocean currents is a high degree of seasonal and shorter-term variability in weather patterns as a consequence of the location of the shelf at latitudes of 30–40°S, where westerly cyclones can pass freely south of the continent. These factors are likely to place enormous constraints on the reproductive strategies employed by the wide variety of fish species that inhabit these diverse shores. Moreover, changes in sea level of ~130 m over the past 16 000 years since the last glaciation have resulted in substantial changes to the shelf topography (Hutchings 1992) and it is not surprising that much of the shelf fish biota is dominated by opportunistic species, such as hake, sardines, anchovy and horse mackerel, typically found in upwelling ecosystems (Crawford *et al.* 1987; Japp *et al.* 1994). All these species are broadcast spawners, producing large numbers of small eggs and larvae that are widely dispersed in ocean currents. Bakun (1996) has outlined the most important characteristics necessary for

 10.1071/MF01147 1323-1650/02/020307

enhanced larval survival of pelagic fish, incorporating enrichment, retention and concentration mechanisms. Clearly, the retention and concentration mechanisms are likely to be suboptimal in the southern African shelf region, except for particular areas.

The objective of this paper is to review the spawning and nursery grounds of a variety of common or dominant species and to examine the physical mechanisms that allow a sufficient number of the larvae and juveniles to be retained on the shelf to replenish the adult population. These adults migrate, often against food gradients, to spawn 'on the edge' of current systems where there is apparently an equal likelihood of being transported far offshore into the oceanic interior as of being carried into the productive inshore nursery ground.

Ichthyoplankton sampling has covered most of the west and east coasts of South Africa, except for a large gap on the south coast between Cape Infanta (21°E) and Port Elizabeth (30°E), where sampling has been limited to Calvet net tows in November only, focussing on clupeid spawning. Most spawning and nursery areas have, however, been identified, although much is inferential rather than actual data.

Three major nursery grounds can be identified, and one minor ground: *(a)* The Natal Bight; *(b)* the Agulhas Bank; *(c)* the inshore Western Cape coast and *(d)* the central Namibian shelf region (Fig. 1). Each is linked to a spawning area, a transport and/or recirculation mechanism, a potential for deleterious offshore or alongshore transport and an enriched productive area of coastal or shelf-edge upwelling.

The Natal Bight nursery ground (*Fig. 2*)

The sparid *Chrysoblephus puniceus*, or slinger, is an important linefish species on the KwaZulu-Natal shelf (Garratt 1993). The distribution of slinger extends from

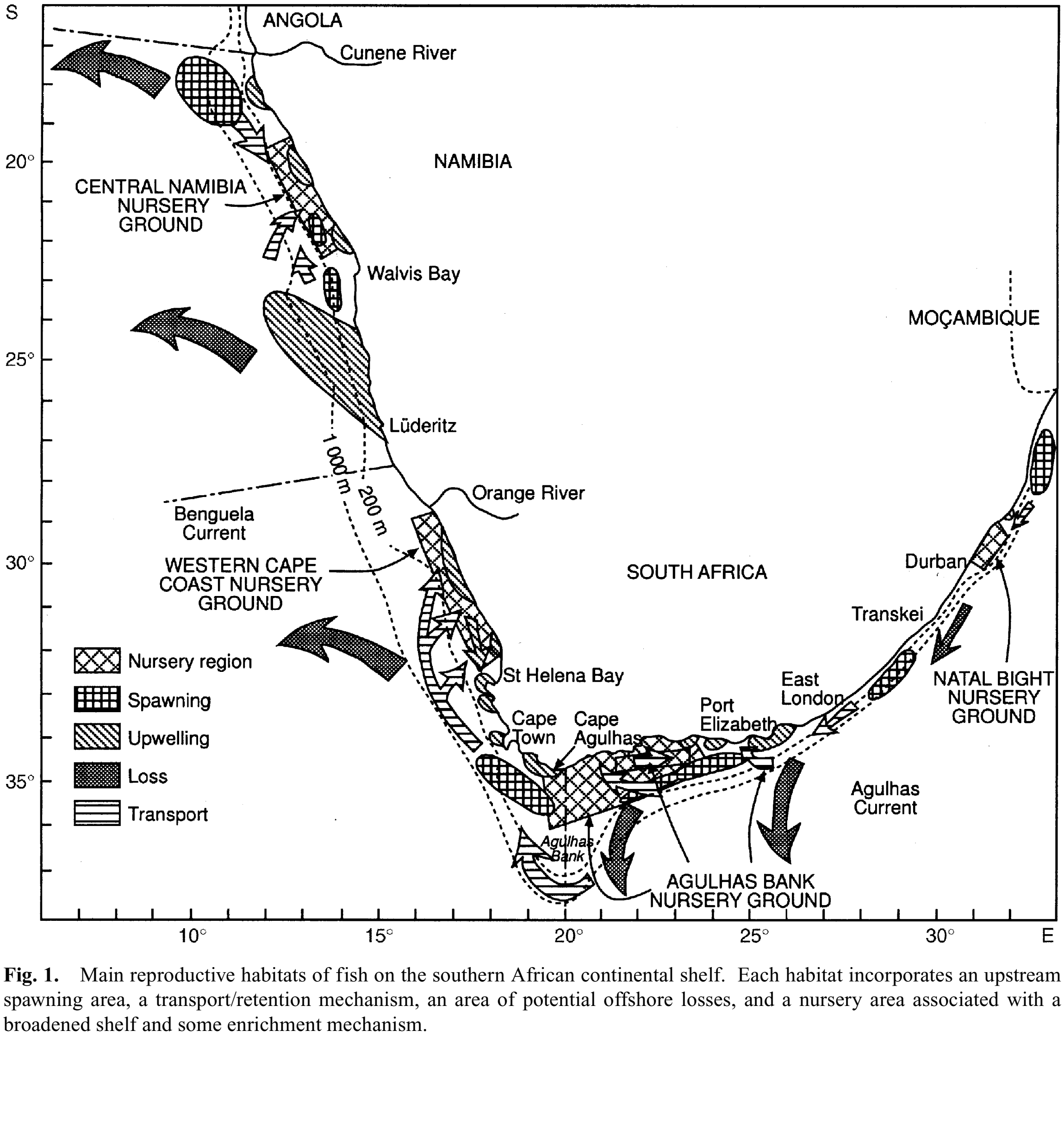

Fig. 1. Main reproductive habitats of fish on the southern African continental shelf. Each habitat incorporates an upstream spawning area, a transport/retention mechanism, an area of potential offshore losses, and a nursery area associated with a broadened shelf and some enrichment mechanism.

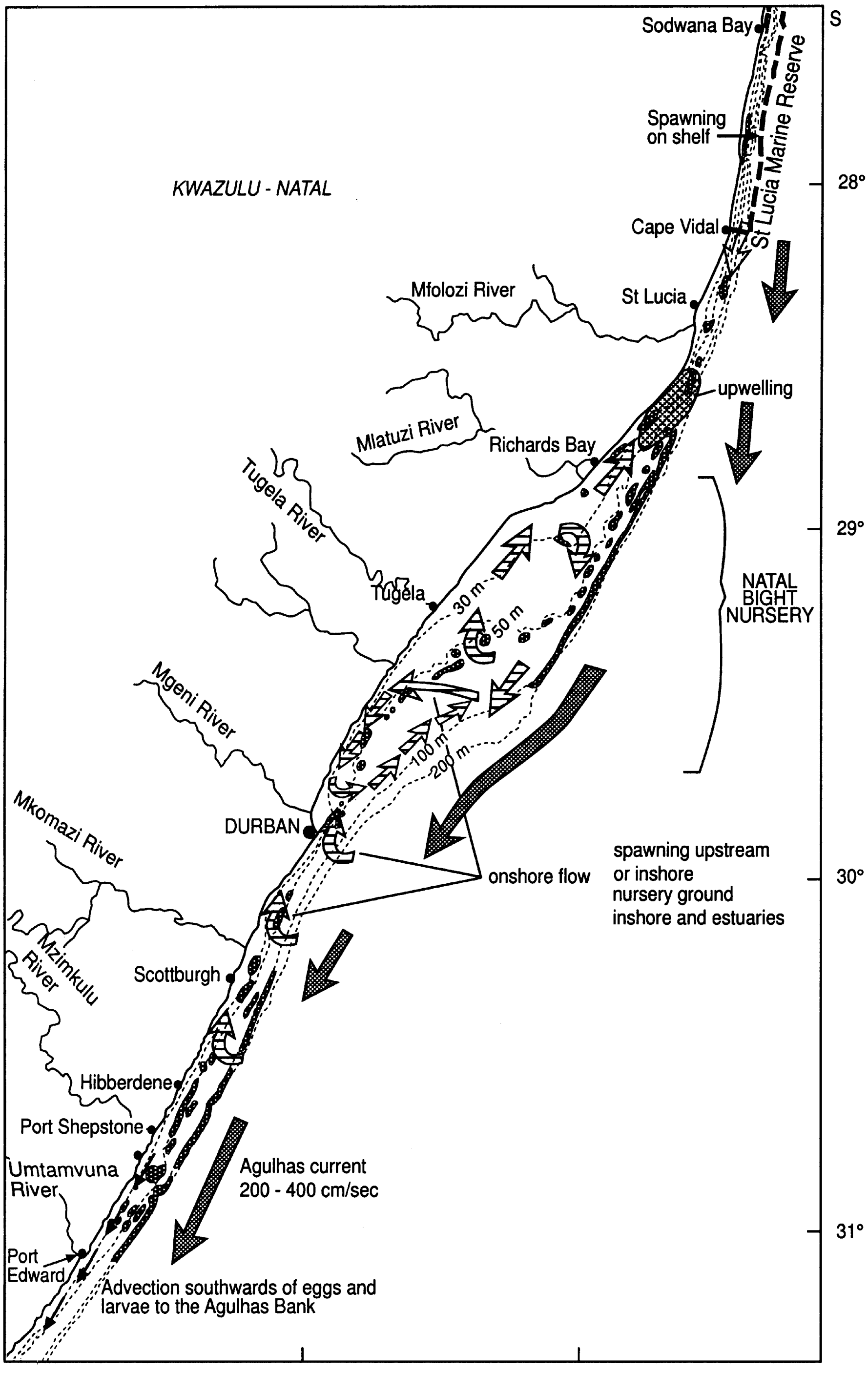

Fig. 2. Details of the Natal Bight nursery area, showing the major circulation features, the distribution of reefs and major rivers and bottom topography.

southern Moçambique to the Northern Transkei; owing to heavy fishing pressure, the mean size of fish in the catch has been declining in recent decades. As the fish is a protogynous hermaphrodite (females become males as they grow older), there is a dearth of males in KwaZulu-Natal waters. This implies that most of the recruitment of juveniles must come from the north, because most adult males are confined to the deep reefs on the shelf in the St Lucia marine reserve or to the relatively lightly exploited (until recently) Moçambique waters. If eggs and larvae are entrained in the Agulhas Current beyond the shelf, typically moving southwards at speeds of 1–2 m s^{-1}, the juveniles would be transported too far south for successful recruitment to the reef systems of Kwazulu-Natal (Fig. 2). Juveniles spawned in shelf waters would also be transported southwards, but not as fast as in the current core itself. The Natal Bight offers opportunities for successful recruitment to the shelf region.

This is the smallest of the identified nursery areas but is extremely important in a local context, because the Natal Bight is a 45 km wide shelf north of Durban, whereas the mean shelf width along the rest of the KwaZulu-Natal coastline is ~11 km (Schumann 1988). This bight is the origin of a major source of variability in the Agulhas Current, where an offshore meander, termed the Natal Pulse (Grundlingh 1983; Lutjeharms and Roberts 1988), first appears and tracks downstream at ~17 km day^{-1}, leading to major perturbations in the flow path of the Agulhas Current (Shillington 1993). A clockwise eddy occurs within the Bight area, which, together with some upwelling and enhanced phytoplankton levels in the northern extremity of the Bight (Lutjeharms *et al.* 2000), creates the necessary conditions for enhanced survivorship of early larvae and juveniles of pelagic spawners by incorporating enrichment, retention and concentration mechanisms. It also determines a southern limit to the distribution of some tropical species. In addition, the distribution of rocky outcrops (Penney *et al.* 1999) (Fig. 2), sand and mud belts (Flemming and Hay 1988) and the proximity of estuaries provide a wide variety of habitats for settlement of juveniles of benthic species, provided they can avoid adverse advection.

Beckley and van Ballegooyen (1992) have listed the mechanisms likely to aid entrainment and retention of larvae on the shelf: Agulhas intrusions, minor upwellings, cyclonic eddies and changes in wind direction or current reversals, sometimes associated with coastal lows, can all contribute to shoreward movement. The Agulhas Current off Durban is subject to short-term excursions inshore and offshore (Schumann 1982), driven in part by local weather patterns (Hunter 1988). Shoreward currents have been deduced from the nature of bottom sediments in the vicinity of the Tugela River, Durban, and between Scottburgh and Hibberdene (Flemming and Hay 1988). Near Port Edward, the current approaches close to the coast and accelerates, resulting in rapid southward movement of the shelf waters, but not at the speed of the core of the current, which often exceeds 1 m s^{-1} (Schumann 1988). If larvae being transported along these narrow-shelf regions are to be retained in subtropical waters, they would have to enter estuaries (Harris *et al.* 1995, 1999) or remain in the nearshore zone where some northward transport is generated though SW winds and swells. The onshore movements of shelf water caused by wind reversals and current meanders are also crucial to the retention of larvae and juveniles on the shelf.

To the south of the Bight, the shelf is extremely narrow and the Agulhas Current approaches close inshore, driving the inshore currents on the shelf rapidly to the south. South of the Bashee River (26°E), a strong thermal front is generally found (Beckley and van Ballegooyen 1992), constituting a temperature barrier to the southward extension of tropical and subtropical species. Any warm-water vagrants, advected southwards beyond this point, are unlikely to survive. Although the shelf currents themselves have been studied as part of research into the fate of effluents from numerous pipelines along the coast, the inner boundary of the Agulhas Current, so crucial to the survivorship of the pelagic biota, has not received the attention it deserves..

The Agulhas Bank nursery ground (*Fig. 3*)

The Agulhas Bank is both a spawning ground and a nursery area and is the centre of abundance of numerous warm temperate species, including several endemic sparids. Many of the species appear to move eastward and northwards to spawn in KwaZulu-Natal shelf waters. Species such as the elf, or shad (*Pomatomus saltatrix*) and the geelbek (*Atractoscion aequidens*) spawn in September–October on the narrow shelf off KwaZulu-Natal, and juveniles are found inshore along the Agulhas Bank. *Pomatomus* juveniles are widespread inshore across the Bank and even occur on the west coast (Govender and Radebe 2000, whereas geelbek juveniles (0–1+) occur mostly in the inshore waters of the south-eastern Cape, moving westwards as they grow older (Griffiths and Hecht 1995). There are clearly different behavioural responses amongst the different species to select suitable habitats for settlement within the Agulhas Bank nursery area.

The white steenbras *Lithognathus lithognathus* spawns in July–August off the Transkei (Eastern Cape) coastline in the vicinity of the mudbanks deposited by rivers in the region (Bennett 1993). The young stages first enter estuaries which open in late winter along much of the south coast, and juveniles must therefore be retained or swim to the nearshore zone in order to enter these estuaries.

Squid spawn in the nearshore zone on the eastern Agulhas Bank (Augustyn *et al.* 1994), but differ from the other species described here in laying benthic egg sacs. The paralarvae that hatch from the sacs are distributed close inshore. If they move too far east in surface waters, they are likely to be entrained into the complex oceanography of the Agulhas offshore divergence off Port Elizabeth. Juvenile squid are dispersed over the entire shelf region of the Agulhas Bank and it is more likely that paralarvae and early juvenile squid use the bottom currents, which generally move slowly westwards (Boyd and Shillington 1994). Dense aggregations of copepods occur close to the bottom, and these provide an adequate food source. If squid spawn too far to the west, larvae and juveniles are likely to be transported to the west coast nursery area, where their distribution is constrained by low-oxygen water inshore, derived from the sedimentation and breakdown of the plankton in this highly productive region, and cold bottom

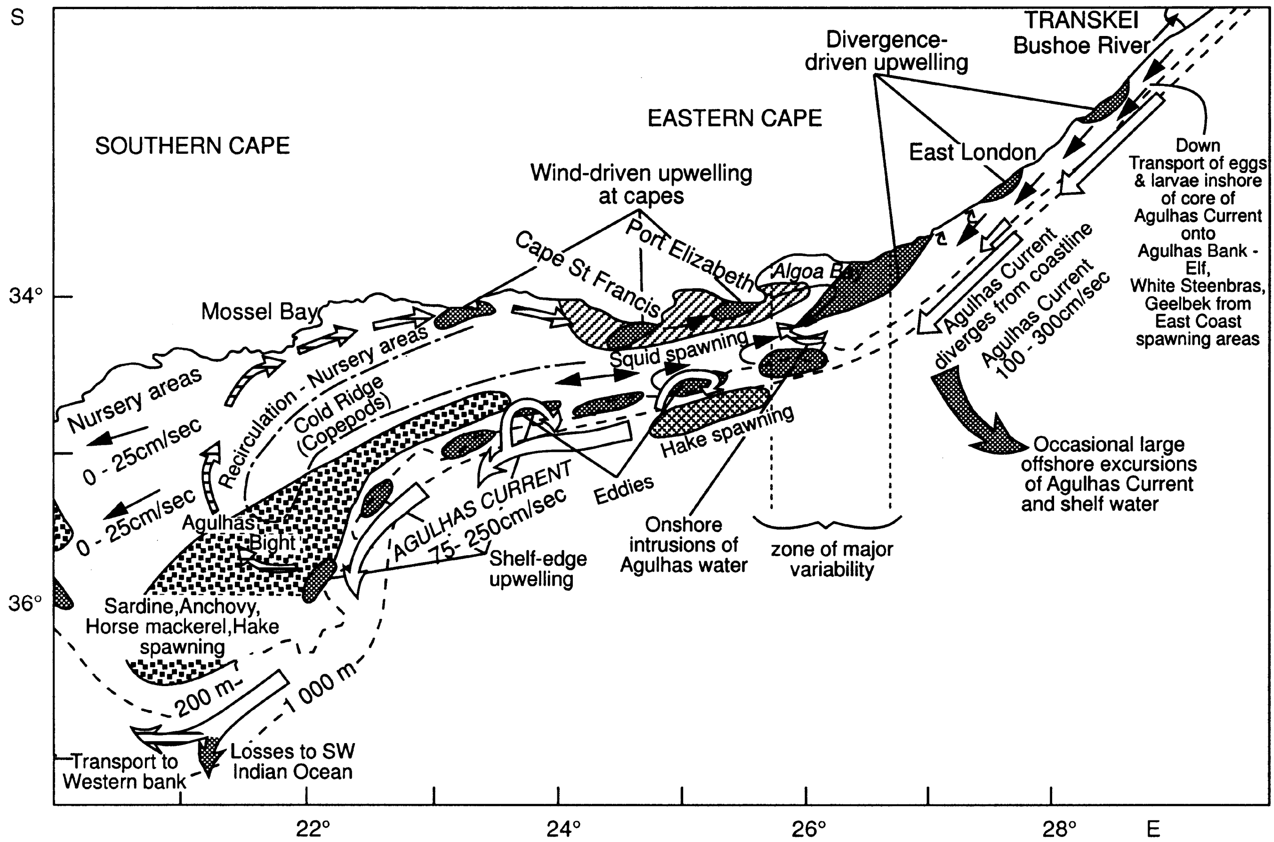

Fig. 3. Central-eastern Agulhas Bank nursery/spawning ground.

water offshore. Lower numbers of squid juveniles are found on the west coast than on the Agulhas Bank.

Beckley and van Ballegooyen (1992) and Beckley (1993) have dispelled the myth of the Agulhas Current as the main vector for the transport of shelf-zone fishes to the south along the east coast (Heydorn *et al.* 1978). Eggs and larvae of the species that spawn on the shelf in KwaZulu-Natal do not occur in the current core, but are confined to the shelf waters immediately adjacent to the Agulhas Current, where they are transported southwards along the narrow shelf before entering the Agulhas Bank nursery area (Beckley 1993).

The Agulhas Bank is a broad extension of the South African coastal plain in a roughly triangular shape, with a basal width of ~800 km and a width of 250 km at its apex, totalling ~116 000 km^2, with a mean depth of just over 100 m. Approximately 60% of the Bank consists of hard substratum, and high-profile reefs exist in a number of places, both close inshore and extending offshore south of Cape Agulhas (20°E). The waters over the Bank vary seasonally, despite the relatively low latitude. In summer, there is a mixture of subtropical surface water, separated by strong thermoclines from cool waters, which are drawn onto the shelf by dynamic processes linked to the divergence of the Agulhas Current from the coast as it follows the shelf break offshore, at longitude 25–28°E. Strong easterly winds cause cold water to well up to the surface at promontories along the southern Cape coast, and cool water is drawn off westwards to form an extensive subsurface cold-water ridge to the west (Beckley 1983; Swart and Largier 1987). The whole Bank is moderately productive, and complex circulation patterns occur, with several gyre-like patterns (Boyd and Shillington 1994). Winds blow equally frequently from the east and from the west (Jury 1994) and drive the surface waters in the general direction of the wind, with little resultant net displacement of biota. In winter, westerly winds predominate over easterlies and strong mixing occurs to depths of 80–90 m.

There are a number of critical areas where eggs and larvae spawned upstream may enter the Agulhas Bank shelf region. Probably of crucial importance is the area near Port Elizabeth, where complex circulation occurs as the Agulhas Current leaves the coast, following the shelf break (Fig. 3) (Boyd *et al.* 1992; Boyd and Shillington 1994; Goschen and Schumann 1988). Cold-water eddies, intrusions of Agulhas water onto the shelf and large offshore meanders or excursions of the Agulhas Current all occur at this location. These mechanisms may entrain eggs and larvae onto the

Agulhas Bank, or they may displace them far offshore. Further west, the surface currents close inshore run mostly eastwards, while bottom currents on the whole Bank generally flow to the west (Boyd and Shillington 1994). The cold ridge of water, which is a prominent subsurface feature during most summers on the central Bank (Swart and Largier 1987), must play an important role in fish life-history strategies on the Agulhas Bank, because currents tend to circulate clockwise around the ridge. The ridge is associated with elevated phytoplankton concentrations (Probyn *et al.* 1994) and dense concentrations of copepods (Verheye *et al.* 1994) and clupeoid fish eggs (Roel *et al.* 1994).

The Agulhas Current closely follows the shelf break at ~200 m depth, and several shear-edge eddies appear to bud off the inner edge of the current at frequent intervals, moving slowly to the south-west. Reverse currents within these eddy regions indicate some net movement of near-surface waters to the north-east, opposite to the offshore south-westerly flow of the Agulhas Current (Boyd and Shillington 1994) (Fig. 3). This counter flow would enable eggs and larvae from shelf-edge spawning to be retained on the shallow parts of the Bank. Sporadic shelf-edge upwelling is also a feature of this dynamic region, which enhances the productivity along the outer margins of the Bank.

At the apex of the Agulhas Bank, the Agulhas Current leaves the shelf entirely and retroflects into the Indian Ocean, except for occasional Agulhas rings, which break off and move into the South Atlantic. An offshoot of the current travels north-west, along the outer edge of the western Agulhas Bank. The apex of the Bank is therefore another critical area for retention of spawning products. Any eggs, larvae or juveniles of shelf species that are entrained into the Current itself have little chance of survival in the open ocean or of return to the productive shelf environment of the Bank.

The West Coast nursery ground (*Fig. 4*)

Many pelagic species that are characteristic of the major upwelling systems use the central or western Agulhas Bank as a spawning area. The western Agulhas Bank shows a general drift of surface waters to the north-west, with coastal upwelling occurring inshore in late summer. This convergent water mass develops into a coastal jet current that accelerates along the west coast past the very active upwelling centres off Cape Town and Cape Columbine and is responsible for the transport of eggs and larvae to the west coast nursery grounds. At Cape Columbine, the jet currrent appears to diverge, with offshore, alongshore and inshore components (Boyd *et al.* 1992).

Horse mackerel (*Trachurus trachurus capensis*) spawns over the east/central Agulhas Bank during winter months, with juveniles close inshore off the southern Cape coastline (20–26°E) but with a considerable overlap onto the inshore west coast nursery habitat during summer months (Barange *et al.* 1998). As they mature they become more demersal and move offshore and migrate back to the Agulhas Bank as adults.

Anchovies spawn on the whole Agulhas Bank (Figs 3 and 4), peaking during mid summer (November–December), with some shifts to the west coast in years when Agulhas Bank water intrudes strongly north of Cape Point (van der Lingen *et al.* 2001). The bulk of the recruits are found along the west coast, with <5% on the south coast inshore (Hampton 1992). Anchovy spawn on the western Agulhas Bank, but older fish appear to shift further east to the central and eastern Bank, often spawning between the cool ridge and the Agulhas Current (Roel *et al.* 1994). Since 1994 there has been a distinct eastward shift in the spawning distribution, to the east-central Bank. Anchovy are known to spawn on the shelf on the east coast (Armstrong *et al.* 1991; Beckley and Hewitson 1994) but the narrow shelf limits the population size of the spawners.

Sardines spawn over a similar area to anchovy during November, but generally have two spawning peaks, in early spring and autumn, on either side of the peak anchovy spawning period. There has been a recent shift westwards in the distribution of sardine spawning in November, so now the bulk of spawning occurs on the west coast, between latitudes 31°S and 35°S, and, with lesser spawning intensity, off the central and eastern Agulhas Bank, coincident with anchovy. There is also sardine spawning on the east coast and even off KwaZulu-Natal (Beckley and van der Lingen 1999), where sardine eggs are found during the period July–November.

Of importance is the distribution of eggs of both species far offshore on the Agulhas Bank and often extending right over the shelf break on occasions. These eastern and central Bank spawners show astonishing brinkmanship, as they spawn in a narrow zone between the cool upwelling ridge and the swiftly flowing Agulhas Current (Fig. 3). A number of possibilities for transport exist, some advantageous and some disadvantageous:

(a) Occasional shoreward meanders of the Agulhas Current can entrain whole swathes of eggs and larvae and sweep them off to the south Indian Ocean or south Atlantic Ocean interiors, which would obviously be bad for future recruitment;

(b) Some of the eggs and larvae may be transported rapidly along the shelf edge, around the tip of the Agulhas Bank and move NW to join the convergent flow that eventually forms the jet current transporting spawning products from the western Agulhas Bank to the west coast;

(c) eggs and larvae may drift westwards across through the younger spawners on the western Agulhas Bank, who have the potential to inflict considerable cannibalistic mortality on the young stages, in the absence of alternative prey;

(d) eggs and larvae may be transported shorewards, around the cool ridge and onto the western Agulhas Bank and so into the jet currents; or

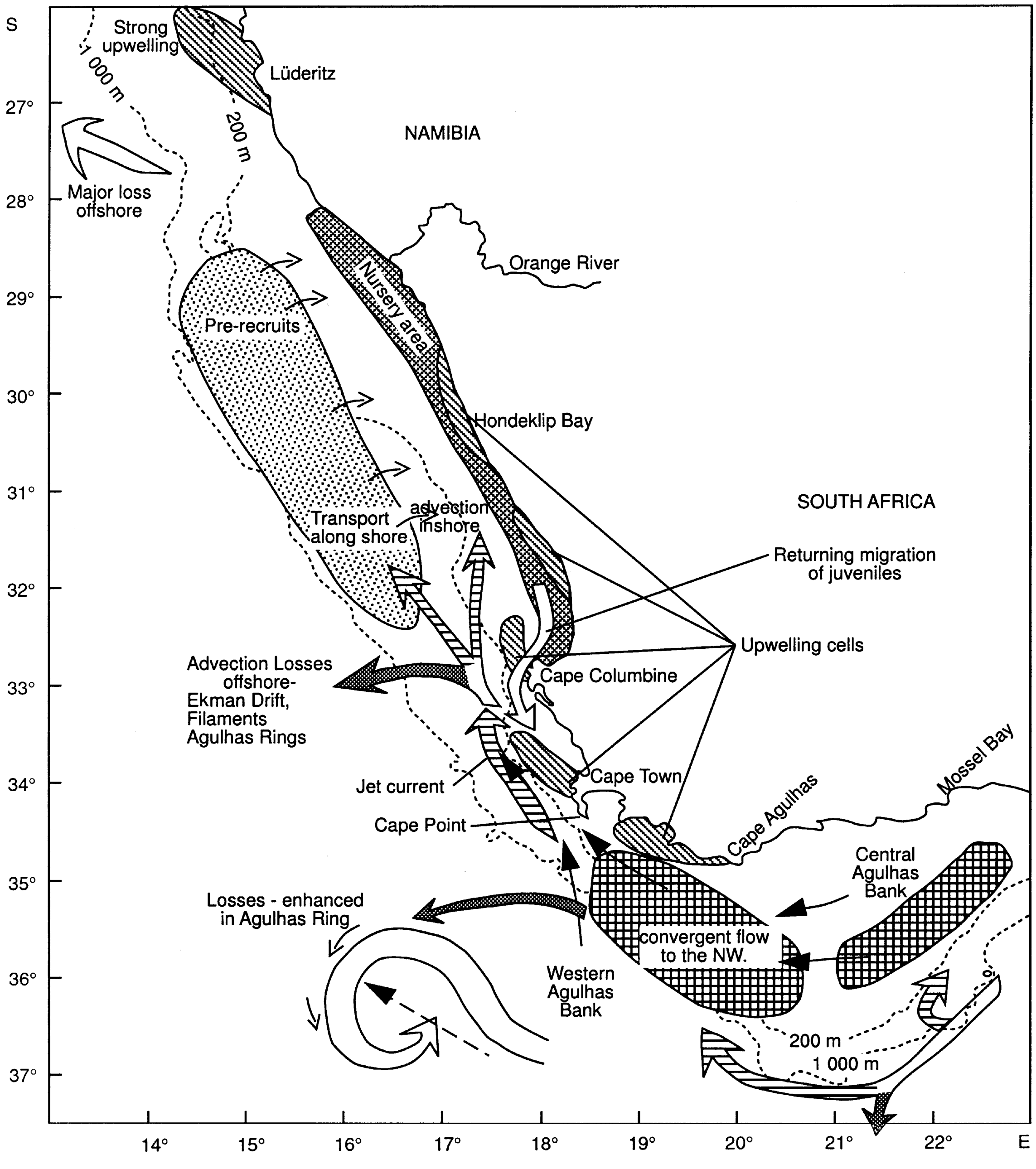

Fig. 4. West Coast nursery ground and western/central Agulhas Bank spawning ground.

(e) they may be transported to the NE, immediately inshore of the Agulhas Current, in a series of counterflows associated with eddy-like features of the Agulhas Current, and remain on the Bank.

However, anchovy and sardine recruitment of juveniles on the south coast is normally a small fraction of the recruitment on the west coast (Hampton 1992), implying that the Agulhas Bank is not as good a nursery or recruitment ground for anchovy and sardine as the inshore west coast. It is uncertain if this is a result of *(i)* high mortality of early egg and larval stages caused by the large biomass of pelagic and mesopelagic planktivorous fish present during summer, *(ii)* starvation of pre-recruit fish or *(iii)* predation of older recruits by large predatory fish on the Agulhas Bank.

On the west coast, sardine eggs, which are spawned on the outer parts of the shelf, are subject to offshore Ekman drift during periods of strong equatorward winds, and entrainment in filaments or Agulhas Rings, which can displace the eggs and larvae far offshore. Sardines have a protracted spawning season, with peaks in late winter–spring and in autumn, when southerly winds are not at their summer maximum. Most of the west coast recruits may be derived from eggs spawned before or after the summer southerly wind maximum.

Given that several of these transport pathways appear deleterious, it is strange that older fish continue to spawn in these places, as if they were the optimal areas for spawning. Models of egg and larval transport, be they empirically derived from acoustic Doppler current profiles (Shannon *et al.*1996) or driven by average winds and geostrophy (Skogen 1999), do indicate that most of the pelagic eggs spawned on the central and eastern Bank may reach the west coast within a period of 1–3 weeks, whereas eggs spawned offshore on the west coast in midsummer are displaced far offshore, away from the nursery grounds. The widespread offshore distribution of pre-recruit anchovy on the west coast and the gradual increase in mean size as the fish are detected closer inshore (van der Lingen and Merkle 1999), suggest an easterly (shoreward) movement of successful recruits. Whether this is an active or passive process is unclear, because preliminary studies of vertical distribution suggest that the pre-recruits are close to the surface, where they are subject to considerable offshore Ekman drift during the summer period. Relaxation of upwelling events, intrusions of Agulhas Bank water containing eggs and larvae close inshore and shoreward meanders in the frontal jet currents past Cape Columbine are mechanisms being evaluated as a means for recruits to move inshore.

The gadoids *Merluccius capensis and M. paradoxus* (hake), the gempylid *Thyrsites atun* (snoek) and the clupeid *Etremeus whiteheadii* (round herring) also move to the western Agulhas Bank and southern west coast to spawn, generally in late winter and early spring (Crawford *et al.* 1987; Griffiths *in prep*.), when offshore Ekman losses are at a minimum and the eggs and larvae drift northwards and inshore to the west coast nursery grounds.

Hake represent a different solution to the problem of offshore advective losses in upwelling systems, in that they spawn at depth, and the eggs are small and relatively heavy. The eggs rise slowly through the water column until just before hatching, and so are entrained in the upwelling circulation and are drawn shorewards at depth, rather than offshore at the surface in the Ekman drift, during development (Sundby *et al.* 2001). Nevertheless, the strong jet currents on the west coast oblige the adult hake to shift southwards to spawn, to ensure that juveniles enter the west coast nursery grounds downstream.

Further up the west coast, there is a dearth of spawning either inshore or offshore between Hondeklip Bay (31°S) and Lüderitz (27°S) (Olivar and Fortuno 1990), as strong offshore trajectories of flow occur at the most active upwelling centre in the world at Lüderitz (Bakun 1996), as indicated by models (Skogen 1999) and by satellite-tracked drogues (Nelson and Hutchings 1983; Largier and Boyd 2001).

The Central Namibian nursery ground (*Fig. 5*)

Hake spawning commences again north of the powerful Lüderitz upwelling centre (27°S) and continues up to the Angola–Benguela Front (16–19°S). Sardines and horse mackerel also spawn in the region between Lüderitz and the Angola–Benguela front. Circulation patterns at depth reveal complex eddying and considerable southward and onshore transport beneath the general surface drift to the north-west (Sundby *et al.* 2001). Sardine spawning peaks 30–80 km offshore during September–October off the central Namibian shelf, with larvae occurring slightly further offshore and recruits appearing close inshore, so there appears to be a simple inshore–offshore movement over the wide Namibian shelf. Spawning also occurs in mid summer in the vicinity of the Angola–Benguela Front (Crawford *et al.* 1987). During late summer (December–March) warm water from the Angolan Current pushes southwards into central Namibian waters, allowing pelagic spawning products to be brought into the nursery grounds off central Namibia. There is also a high likelihood of substantial offshore transport associated with this convergent frontal region (Shannon 1985).

Discussion

Broadcast spawning is the dominant mode of spawning of marine fishes, allowing continual exploration of potential habitats. Populations can reach high biomass levels only when the triad of factors favouring enrichment, retention and concentration achieve some optimal compromise (Bakun 1996). In southern African shelf waters, the strong currents and high short-term variability in driving forces such as winds place severe constraints on the reproductive success of fishes. The four areas where the shelf broadens provide the best opportunities for nursery grounds for the dominant fish biota. Parrish *et al.* (1983) have demonstrated that pelagic fish in most upwelling areas use different behaviour to optimize reproductive success. Most pelagic species spawn downstream from the upwelling centres, where wind mixing and offshore advection are minimized and eggs and larvae disperse a moderate distance offshore in a productive habitat and then return as juveniles to the near-coastal zone. Because of strong currents and a smooth coastline, southern Africa does not generally follow this pattern, except in Namibia.

Many of the dominant fish species in southern Africa, be they clupeids, sciaenids, sparids, merluccids, carangids or gempylids, and even squid, move upstream to spawn. Their nursery grounds lie on broad extensions of the shelf at variable distances downstream from the spawning areas. There are other spawning and recruitment strategies in this area. At one extreme, rock lobster larvae on the eastern,

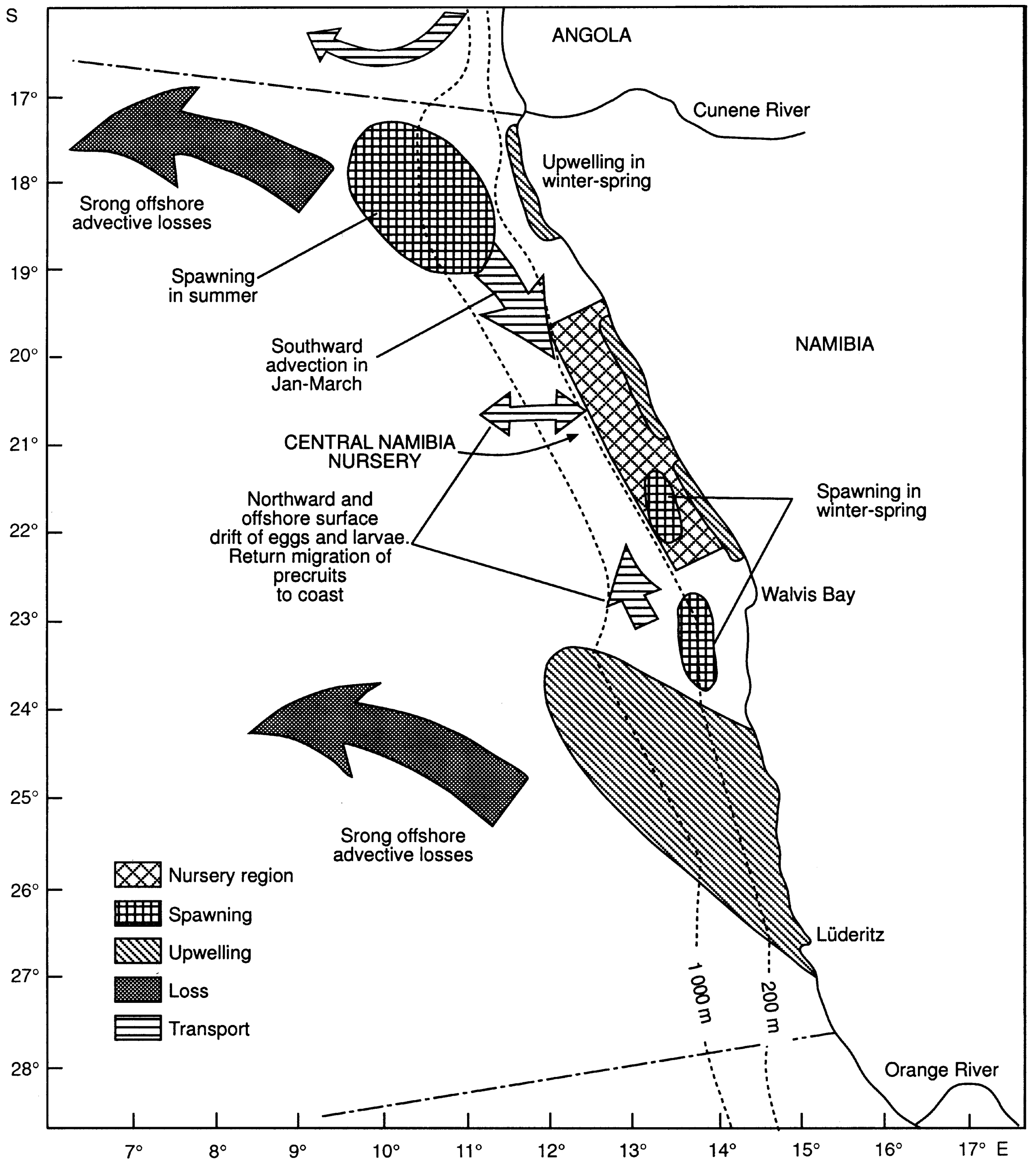

Fig. 5. Central Namibian spawning/nursery ground, between the Lüderitz upwelling cell and the Angola–Benguela Front.

southern and western coasts have a prolonged early life history of months to years in the ocean gyres of both the Atlantic and Indian Oceans before resettlement to their coastal habitats. At the other extreme, many species spawn close inshore and probably rely on recirculation within embayments or limited alongshore displacement to maintain discrete stocks. Few species appear to have adopted a demersal or nesting strategy, two examples being the sparid *Spondyliosoma emarginatum* (Aiken and Mann 2000) and the pelagic goby *Sufflogobius bibartus* off central Namibia (Crawford *et al.* 1987).

Sardine are of interest because they appear to spawn throughout their range, from north of Durban to the Angola–Benguela front, although they too, do not spawn on the west coast from 31°S to 25°S (Lüderitz). However, they do not appear to significantly expand or contract the range of their habitat as the population level fluctuates, but occur more frequently within the whole habitat range. In Japan, sardines spawn in near-coastal waters at low population levels, and expand their spawning and foraging range radically into the Kuroshio–Oyashio oceanic mixing area at high population levels. Similarly, in the Humboldt and California Current systems, sardines expand their habitat range significantly during periods of high biomass (Bakun 1996)). The inshore west coast, with its broad shelf, sluggish currents, moderate stratification and high productivity, appears to be an ideal place for pelagic fish to spawn. Selection has obviously favoured spawning in warmer, more stable but more oligotrophic waters further south, where offshore losses are apparently far greater yet the strategy is more successful, since it places the juveniles in the productive nursery ground.

The high short-term environmental variability that is characteristic of southern Africa has implied that serial broadcast spawning of pelagic eggs upstream of the major nursery grounds is the most successful strategy in this dynamic environment, despite the likelihood of considerable loss of spawning products to the surrounding deep ocean. Fecundity has to be high and batch spawning is necessary to overcome the short-term variability and substantial losses likely in this marginal spawning environment. This upstream migration, often against the food gradient, has several implications:

(i) it is likely to be energetically costly, at the expense of investment in growth or reproduction;
(ii) several species are likely to delay the onset of maturity so that fish can grow to a large size more suitable for the stresses of migration;
(iii) marine protected areas have limited applicability for protecting migratory species by reducing fishing mortality, unless they are strategically placed and enforced at particular times and places, e.g. during spawning or within feeding aggregations.

As a result of the spatial separation of spawning and nursery areas, critical areas or multiple ‘gateways’ are situated in the transport pathway, where eggs and larvae may be retained or lost from the productive coastal habitat. These sites include:

(1) the northern boundary of the Natal Bight (29°S,32°E);
(2) off Port Elizabeth (34°S,26°E), where the Agulhas Current diverges from the coast;
(3) off the tip of the Agulhas Bank (35°S,21°E), where the current diverges from the continental shelf and retroflects;
(4) off Cape Columbine (31°S,18°E) on the west coast, where the jet current appears to bifurcate;
(5) off Lüderitz (25–27°S,15°E) at the very active upwelling area;
(6) off the Angola–Benguela Front at 16–19°S,13°E), where the Angola and Benguela currents converge and flow westwards into the South Atlantic.

Monitoring of currents in these areas and the development of suitable eddy-resolving models of the circulation should improve the understanding of these mechanisms; high-frequency, spatially intensive satellite monitoring and the development of indices of successful or failed retention and plankton productivity would provide valuable insights into future recruitment trends.

Monitoring of productivity in the nursery areas and proper surveying of the number of juveniles and pre-recruits entering the area each year would greatly contribute to our understanding of mechanisms influencing recruitment strength and would provide invaluable information for management of long-lived species, in which infrequent good year-classes are often interspersed with a series of poor year-classes. Eggs and larvae of oceanic species, entrained in the Agulhas or Benguela Current systems (Olivar and Beckley 1994), are likely to benefit from the enrichment provided by shear-edge features or mixing with productive shelf water before they are returned into the ocean interiors; however, the opposite is true for coastal species, whose young are unlikely to survive if they are advected too far offshore. Spawning on the edge of the southern African continental shelf is therefore a high-risk but apparently successful strategy for a wide variety of species.

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Manuscript received 21 May 2001; revised and accepted 29 November 2001