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STOCK STRUCTURE OF SNOEK *THYRSITES ATUN* IN THE BENGUELA: A NEW HYPOTHESIS

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It has long been accepted that snoek *Thyrsites atun* in the Benguela system constitute a single stock that undergoes seasonal longshore migration in waters between southern Angola and the west coast of South Africa. Based on a review of past literature and evaluation of new data, it is contended that Benguela snoek exist rather as two separate sub-populations – divided by the upwelling cell in southern Namibia – with limited, medium-term exchange (c. 5 years), driven mainly by temperature and food availability.

Key words: migration, nursery areas, spawning grounds, sub-populations, *Thyrsites atun*

The snoek *Thyrsites atun* is a medium-sized, pelagic predator (max. size 9 kg, Nepgen 1979a) that inhabits the coastal waters of the temperate southern hemisphere (Kailola *et al.* 1993). Southern African snoek have been recorded from northern Angola to Algoa Bay on the South African east coast, but are found mostly between the Kunene River and Cape Agulhas, i.e. in the Benguela ecosystem. *T. atun* has been an important commercial species in the system since the early 1800s, caught initially with handlines but also by trawlers after 1960 (Crawford 1995). The total reported catch peaked at about 81 000 tons in 1978, but it then dropped considerably following the exclusion of foreign trawlers from Namibian fishing grounds in 1991 (FAO 1978, 1981, 1990, 1997). Between 1991 and 1994 the annual catch ranged between 14 437 and 22 920 tons, of which 93% was taken in South African waters (FAO 1995). *T. atun* is by far the most important species caught by the South African commercial linefishery (constituting 39% of catches between 1986 and 1997). It is also targeted by recreational anglers, but catch statistics are not available for this fishing sector. Around 40% of the reported South African catch between 1990 and 1996 was made by commercial handline fishers and 60% by trawlers. *T. atun* is one of the major predators of anchovy *Engraulis capensis* and sardine *Sardinops sagax* in the southern Benguela (Wickens *et al.* 1992), and it has been implicated in top-down effects on both prey and consequently zooplankton populations (Verheye *et al.* 1998).

Despite its circumglobal distribution, *T. atun* is confined to coastal waters where it often consists of discrete stocks. For example, three stocks are recognized off New Zealand (Hurst and Bagley 1989) and there are between three and five stocks off Australia (Blackburn and Gartner 1954, Grant *et al.* 1978). Understanding the stock structure of snoek in the Benguela system is essential to successful and realistic ecosystem modelling as well as wise management of the resource.

Prompted by large interannual fluctuations in *T. atun* availability, and the profound effects these had on the linefishery, the first investigation into their migratory patterns and stock structure in the Benguela was conducted in 1934, involving the tagging of 3 755 fish off Namibia (22–23°S). Of these 17 were recaptured, and all had moved southwards, 13 (74%) into South African waters (De Jager 1955). Some of these 13 fish moved as far south as Cape Point off the Cape Peninsula, a distance of about 1 300 km. Based on these results, on anecdotal reports on the seasonal nature of line catches at different localities (Van Wyk 1944, Davies 1954, De Jager 1955), and on temporal patterns in trawl catches, Crawford and De Villiers (1985) postulated that snoek in the Benguela constituted a single stock. The population was believed to undergo a seasonal longshore migration, moving south into South African waters to spawn in winter, then returning north, to as far as southern Angola, in spring/summer. This theory became widely accepted (Crawford *et al.* 1987, Crawford 1995), but a recent study by Griffiths (2002) showed that adult snoek are available to South African linefishers throughout the year, and that the seasonal availability of adults on the trawl grounds results from an offshore spawning migration rather than southward movement from Namibian waters. Griffiths (2002) also demonstrated that higher handline catch rates north of Cape Columbine (Fig. 1) in autumn were caused by juvenile snoek following clupeoid recruits inshore (i.e. within range of linefish vessels) rather than the southward displacement of adults en route to the Agulhas Bank. The results of a South African tagging study conducted during the mid 1970s (3 139 tagged

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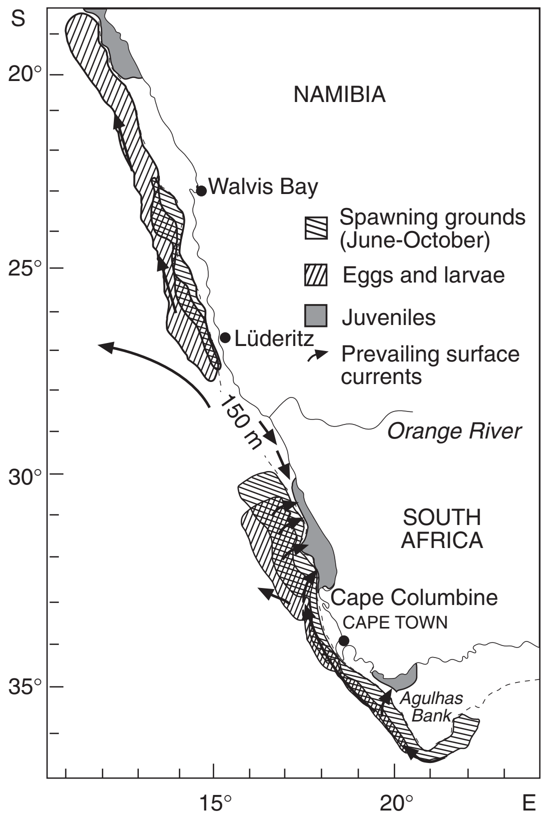

Fig. 1: Conceptual model summarizing available knowledge of the life history of Benguela snoek and prevailing current patterns. South African life history information after Griffiths (2002); Namibian life history information inferred from spatial patterns in size composition presented by Vendiktova (1987) egg and larval distributions after Olivar and Fortuño and Olivar and Shelton; and physical oceanography after Boyd *et al.* (1992) and Gründlingh (1999)

and 18 recaptured) are also not consistent with the concept of seasonal longshore movement of adult snoek; despite liberty periods of 22–377 days (seven for >200 days), only local and random movement was recorded (Nepgen 1979a).

Ichthyoplankton surveys conducted between 1977 and 1986 reveal that snoek eggs and larvae are present throughout the Benguela system in winter/spring, distributed as two disjunct bands (Fig. 1) that are separated by the intense Lüderitz upwelling cell (25–27°S) off southern Namibia (Olivar and Fortuño 1991, Olivar and Shelton 1993). The results indicate that spawning occurs simultaneously in both northern and southern Benguela, which negates the spawning migration hypothesis, and furthermore implies that the southern African snoek stock may exist as two separate sub-populations. The Lüderitz upwelling cell represents a major environmental barrier to many fish species, including anchovy and sardine (Boyd and Hewitson 1983, Cruickshank and Boyd 1985), principal prey items of *T. atun* (Nepgen 1979b, 1982, Griffiths 2002). The concept of two separate sub-populations is further supported by:

(i) low snoek catches in the vicinity of the environmental barrier (Crawford and De Villiers 1985);
(ii) the existence of spawning grounds and nursery areas in both South African (Griffiths 2002) and Namibian (Venidiktova 1987) waters (Fig. 1); and
(iii) the local and random movement of adult snoek tagged off South Africa.

An inverse relationship between annual handline catch trends off Namibia and South Africa (Crawford *et al.* 1990, 1995) suggests migration between sub-populations in the medium term (approximately 5 years), but that not all fish migrate from the waters of one country to those of the other. Given that snoek biomass off each of these countries has been correlated with the abundance of principal prey species (Crawford 1995), it may be that limited medium-term migration occurs in response to prey availability.

A model of separate sub-populations, with medium-term migration, also accommodates the "contradictory" results of the two tagging studies. The tagging experiment conducted by Nepgen (1979a) between 1973 and 1975 took place when handline catches off South Africa were high and off Namibia were low (Crawford *et al.* 1995). This was apparently the result of reduced prey availability in Namibia, caused by the southward intrusion of warm equatorial water, following a Benguela *Niño* (Shannon *et al.* 1988), and a coincident increase of anchovy off South Africa (Shelton *et al.* 1985). Therefore, it is not surprising that no migration to the northern sub-population was recorded. On the other hand, the 1934 tagging experiment off Namibia was conducted during a major Benguela *El Niño* event (Shannon *et al.* 1986), which resulted in the southward movement of all recaptured fish. Although it may be contended that migratory patterns could switch from extensive seasonal movement to stock displacement (Crawford *et al.* 1990), the facts that large fluctuations in South African handline catch have taken place in accordance with prey availability since the late 1800s (Gilchrist 1914, Crawford *et al.* 1987), and that catches off South Africa and Namibia have been negatively correlated since as early as 1965 (the earliest date for which catch data are available for both countries), together tend to render this argument unlikely.

It is possible that three genetically distinct populations exist: two resident and one migratory (*sensu* Fréon and Misund 1999). Even though catch statisics reveal that not all snoek migrate, genetic (satellite DNA) and/or extensive tagging studies would be necessary to test this hypothesis. However, regardless of whether there are two sub-populations or three distinct stocks, interannual (v. seasonal) movement patterns are not common in pelagic fish. Moreover, examples of "interannual variation of habitat selection" (Fréon and Misund 1999) involve changes to migratory routes rather than the same route with a multi-year cycle.

The stock structure and movement patterns of *T. atun* in other parts of the southern hemisphere are complex. For example, Australian populations appear to overlap spatially but not temporally (Blackburn and Gartner 1954). In addition, some stocks undertake extensive seasonal migrations of several hundred kilometres, e.g. Australia and the east coast of New Zealand, whereas others undergo only local movement, e.g. Chatham Islands (New Zealand) and Tristan da Cunha (Blackburn and Gartner 1954, Hurst and Bagley 1989, Andrew *et al*. 1995). The existence of sub-populations off southern Africa, which mix in the medium term through extensive migration, provides additional variation to an already diverse theme.

Although snoek found off Namibia and South Africa appear to be separate sub-populations, the fact that there may be extensive interaction in the medium term means that Benguela snoek are ultimately a shared resource. The implications of the sub-population model for international management are, however, extremely complex. For example, the impact of fishing activity off one country on the catches of the other will vary according to the temporal proximity of the catch date to a migratory event. Given that movement between sub-populations may be driven by fluctuations in prey availability, and that biomass predictions for small pelagic fish (i.e. snoek prey) are unreliable, long-range predictions of snoek migration are not possible at this stage. Assuming that dynamic properties would vary between sub-populations (in accordance with environmental conditions), future stock assessments should, while treating the resource as a single stock, incorporate information from both sub-populations. Attempts should also be made to standardize management objectives, biological reference points and regulations (e.g. minimum size) through a bi-national management plan.

Although southward movement of snoek from Namibian to South African waters has been confirmed by tag recaptures, northward movement between the two countries has not been established. It is recommended that tagging programmes be implemented simultaneously in both countries to provide a better understanding of rates of exchange between sub-populations.

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