

The population biology of the living coelacanth studied over 21 years

Hans Fricke · Karen Hissmann · Rainer Froese ·
Jürgen Schauer · Raphael Plante · Sebastian Fricke

Received: 28 April 2010 / Accepted: 2 March 2011
© Springer-Verlag 2011

Abstract Between 1986 and 2009 nine submersible and remote-operated vehicle expeditions were carried out to study the population biology of the coelacanth *Latimeria chalumnae* in the Comoro Islands, located in the western Indian Ocean. *Latimeria* live in large overlapping home ranges that can be occupied for as long as 21 years. Most individuals are confined to relatively small home ranges, resting in the same caves during the day. One hundred and forty five coelacanths are individually known, and we estimate the total population size of Grande Comore as approximately 300–400 adult individuals. The local population inhabiting a census area along an 8-km section of coastline remained stable for at least 18 years. Using LASER-assisted observations, we recorded length frequencies between 100 and 200 cm total length and did not encounter smaller-bodied individuals (<100 cm total

length). It appears that coelacanth recruitment in the observation areas occur mainly by immigrating adults. We estimate that the mean numbers of deaths and newcomers are 3–4 individuals per year, suggesting that longevity may exceed 100 years. The domestic fishery represents a threat to the long-term survival of coelacanths in the study area. Recent changes in the local fishery include a decrease in the abundance of the un-motorized canoes associated with exploitation of coelacanths and an increase in motorized canoes. Exploitation rates have fallen in recent years, and by 2000, had fallen to lowest ever reported. Finally, future fishery developments are discussed.

Introduction

During the last 30 years, our knowledge of the biology of coelacanths has dramatically increased (Lockett 1980; Balon et al. 1988; Forey 1988, 1990, 1991, 1998; Fricke 1993, 2007; Hissmann et al. 2000). While early studies concentrated on populations around the Comoro Islands, other locations have now been discovered in the Indian Ocean, where coelacanths have been either seen underwater or have been caught by local fishermen, including South Africa (Venter et al. 2000; Hissmann et al. 2006), Mozambique (Bruton et al. 1992), Kenya (DeVos and Oyugi 2002; Boy 2001), Tanzania (Nyandwi 2006), Madagascar (Heemstra et al. 1996) and Indonesia (Erdmann et al. 1998; Fricke et al. 2000).

Today, coelacanths are thought to be more common than earlier predicted (Bruton and Coutouvidis 1991). There is even the suggestion that a panmictic population once existed in the western Indian Ocean (Springer 1999). Often the discovery of a few coelacanths in one location is taken as evidence of a viable population (Venter et al. 2000).

Communicated by C. Harrod.

Dedicated on the occasion of the 80th birthday of Prof. Dr. Wolfgang Wickler.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-011-1667-x) contains supplementary material, which is available to authorized users.

H. Fricke · S. Fricke
Max-Planck-Institut für Marine Mikrobiologie, Bremen,
Germany

H. Fricke · K. Hissmann · R. Froese · J. Schauer
Leibniz-Institut für Meereswissenschaften, Kiel, Germany

R. Plante
Centre d'Océanologie de Marseille, Marseille, France

H. Fricke (✉)
Traubingerstr 47, 82327 Tutzing, Germany
e-mail: hfricke@jago-sub.de

However, coelacanths must still be considered as rare, while the existence of viable subpopulations in the western Indian Ocean remains controversial (Schartl et al. 2005; Fricke 2007; Sasaki et al. 2007).

Bruton and Armstrong (1991) summarized a number of key aspects of coelacanth biology (e.g. abundance, age, population structure) to provide insight into their population dynamics. Froese and Palomares (2000) estimated key life history characteristics for *Latimeria chalumnae* from a series of published accounts. The period of embryogenesis (as determined by scale rings of juveniles) extends for ca. 3 years, the longest among vertebrates. Initial studies on metabolic demands and daily food intake revealed that coelacanths have the lowest metabolic rates among vertebrates (Hughes and Itazawa 1972; Hughes 1976; Fricke and Hissmann 2000).

We have previously reported our field studies on the biology of the living coelacanth using research submersibles at Grande Comore in the western Indian Ocean (e.g. Fricke et al. 1987; Fricke et al. 1991a, b; Hissmann et al. 2000; Fricke 2007), where coelacanths inhabit habitats located at depths below 160 m. We tried to characterize coelacanth habitat (Fricke and Plante 1988; Fricke et al. 1991b) and showed that a high structural complexity is a prerequisite for coelacanth settlement. Examining the habitat use and behaviour of acoustically tagged coelacanths, we were able to provide an insight into long-term changes in utilization of space and time and to determine some dynamics in the developments of the local population (Hissmann et al. 2000). Our initial estimates based on the identification of individual fish inhabiting volcanic caves (during surface daylight hours) indicated a population of 230–650 adult individuals at Grande Comore (Fricke et al. 1991a). These caves were subsequently frequently surveyed in order to study inter-cave movements, site fidelity, occupation rates, cave preferences and home range sizes. A summary of observations can be seen in Fricke and Hissmann (1994), Hissmann et al. (1998), Hissmann et al. (2000) and Fricke (2007).

In this study, we summarize the results of more than two decades of research into the ecology of the Grande Comore coelacanth population. Over this period, our research was driven by the following questions: how many coelacanths exist at Grande Comore? Is there a viable population? Here, we provide preliminary answers to these questions.

Methods and materials

Observation area, census area and schedule

A series of submersible dives took place over a series of expeditions: Expedition 1, December 1986 to January 1987 (42 dives, area I, Anjouan, Moheli); Expedition 2, April–

May 1987 (11 dives, area I); Expedition 3, October–December 1989 (72 dives, area I); Expedition 4, October–November 1991 (89 dives, area I); Expedition 5, November–December 1994 (45 dives, area I); Expedition 6, November 1995 (44 dives, area II); Expedition 7, November 2000 (47 dives, area I); Expedition 8, October–November 2008 (35 dives, area I and Tanzania); and Expedition 9, October 2009 (3 ROV dives, area I).

Figure 1 shows the observation areas along the west coast of Grande Comore. A literature search revealed that all but one coelacanth have been captured within an area that encompasses ca. 97 km of coastline (boundaries shown in Fig. 1), which we consider as the coelacanth habitat of Grande Comore.

After an initial survey during Expedition 1 and 2, we selected an observation area (Area I) of 18-km coastline for regular investigation from 1989 onwards. In 1995, we selected a second observation area (Area II) of 19-km coastline, located approximately centrally on the west coast of Grande Comore (Fig. 1).

We investigated an 8-km stretch of coastline within observation area I by visual inspections conducted from a submersible. We also followed acoustically tagged coelacanths in order to find all coelacanth caves. Tagging techniques and telemetry results are detailed in Schauer et al. (1997) and Hissmann et al. (2000). These 8 km of coastline were taken as the census area. The number of coelacanths within this area was defined as the local

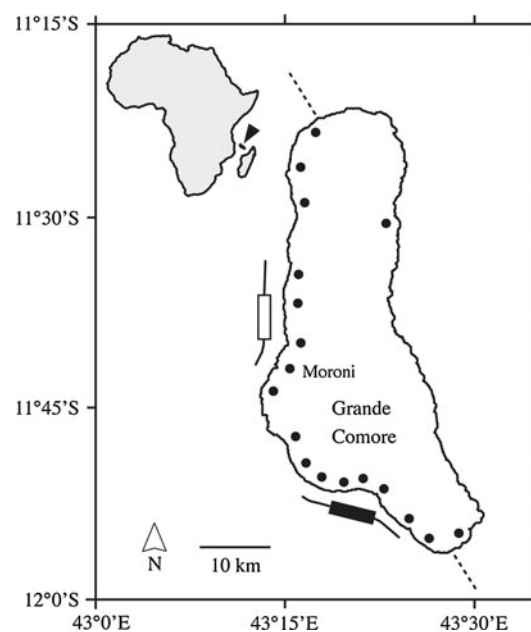


Fig. 1 Locations of recorded coelacanth catches at Grande Comore (black spots). Dotted lines in the North and South denote boundaries of the coelacanth habitat. The bars in the observation areas (Area I (black) and Area II (open)) show where coelacanths were monitored. The black bar is the census area

population density. We took only resident coelacanths into account and defined a resident coelacanth as an individual identified and encountered on different days at least twice within the census area. Although we did search intermittently for other coelacanths outside the census area, these individuals were not included in population estimates. Details of the techniques and definitions were published in an earlier article (Fricke and Hissmann 1994). Coelacanths show unique patterns of white markings and were identified individually from photographs, film and videotapes. We tried to document coelacanths using patterns recorded from both sides of the body, but this was not always possible.

Laser measurements of body length and body depth

In order to estimate coelacanth total length (TL, cm) and body depth, we projected three LASER beams (two green, one red) arranged in an equidistant triangle from the submersible onto the flank of individual coelacanths (Fig. 2). However, the red LASER was often difficult to detect on videotape. Measurements were taken when the individual was almost parallel to the submersible window. Measurement error (<5%) was calculated by estimating the size of an object of known size across a range of distances similar to those where coelacanths were encountered.

Analysis of re-encounters of individual coelacanths

We documented re-encounters of individual coelacanths made across the entire study period of 21 years. We used these data to estimate the rate of natural mortality and the intrinsic rate of population increase with the following considerations and assumptions. Firstly, we assumed that from 1991 onwards, we obtained reasonably complete counts and individual identifications in the census area. In the count of individuals for a given year, we included



Fig. 2 Lateral view of a coelacanth of about 170–179 cm length showing projected LASER beams used for size estimation. NB: the red beam is not visible

individuals that were not seen in this, but in previous and subsequent years, assuming that they were part of the living population but were missed in that year's observation exercise. For the observation years 1989–2008, we treated newly encountered coelacanths in a given year as a cohort and followed their decline in numbers over the observation events. We standardized numbers of 'survivors' as fraction of the initial cohort size, so that all data could be used in one analysis. A linear regression was fitted, with intercept removed, to the natural logarithm of survivor numbers over the number of years since the first encounter of the cohort. We used a robust regression analysis that gives less weight to outliers in an iterative process (Hintze 2001). The absolute slope of the regression curve provides an estimate of the total instantaneous rate of mortality. The standard error of the estimate was used to calculate the 95% confidence limits. In this procedure, we assumed that individuals emigrating from the census area (instead of dying) were balanced by individuals immigrating to the census area (instead of being recruits, in the sense that their parents lived in the census area).

Fishing activities

During the study period, coelacanths were only caught by fishermen in traditional, un-motorized outrigger canoes known as *galawas*. The number of operational seagoing *galawas* can be taken as a first estimate of fishing pressure exerted on the coelacanth (Plante et al. 1998). In October/November 2008, all *galawas* and motorized boats, called *vedettes*, were counted in 53 fishing villages and off the capital Moroni. Counts were conducted between 11:00 and 16:00 h, when most of the canoes and boats were on the beach. We only included *vedettes* with engines in our counts. In collaboration with local investigators, standardized interviews were conducted with fishermen in every village. Questions oriented towards recent coelacanth catches, but also fishing techniques and unusual events during fishing were recorded.

Results

Individually recognized coelacanths

From 1987 onwards, we recorded 115 individually known coelacanths in the observation area located off the southwest coast of Grande Comore (Fig. 1). The results of all coelacanth sightings are available as electronic supplementary material (Table S1). Our initial observations in 1987 included a total of 6 coelacanths. Three of them were re-sighted in 1989, 5 in 1991, 2 in 1994, 2 in 2000 and 1 in 2008 (Table 1). The re-sighting of individual 38 in 2008

Table 1 Number of coelacanths re-sighted in different years after first encounter and proportion of newcomers and individuals sighted only once

Year	Total	Re-sightings of					New-comers	Individuals sighted only once
		1987	1989	1991	1994	2000		
1987	6						6	1
1989	37	3					34	3
1991	62	5	29				28	3
1994	55	2	20	20			13	3
2000	68	2	23	20	7		16	4
2008	59	1	17	13	5	5	18	10

confirms that coelacanths are at least 21 years old. This is the first real evidence of the coelacanth's minimum age. The differences in re-sightings in subsequent years confirm that sometimes the animals temporarily leave the census area. The duration of such absence was at least 3 weeks, which was the usual duration of the observation periods.

In 1989, we discovered that during daylight hours, coelacanths reside in marine caves of volcanic origin (Fricke et al. 1991b) (Fig. 3). In 1991 and 1994, coelacanths fitted with acoustic tags guided us to new caves within our observation area. We found a total of 15 caves of which 11 were inside the census area. A cave at 253 m depth (No. 5) was inhabited only once. We visited this cave at irregular intervals 11 times over a period of 5 years, but never recorded its subsequent use by a coelacanth. These observations confirm that coelacanths sometimes utilize caves different to their regular 'home' caves. Within the census area, we found eight suitable deep caves between 138 and 259 m depth, which were according to our irregular cave checks not occupied by coelacanths.

Re-sightings of individuals, newcomers and individuals sighted only once are summarized by year of observation in Table 1. Of 37 coelacanths encountered in 1989, 17 were still present in 2008 and one individual observed in 1987 was still present in 2008. This confirms that coelacanths



Fig. 3 The entrance of the cave 9 in observation area I at 199 m depth under natural light conditions

occupy the same area over many years and display remarkable site fidelity, covering at least 21 years. We suggest that individuals only encountered once may be vagrants, indicating that coelacanths occasionally visit areas outside of their home range.

Size frequency and sex ratio

We earlier underestimated the size of small individuals (as between 60 and 80 cm, e.g. Fig. 12 in Fricke et al. 1991a) due to optical distortion from the window of the submersible. Following correction, these coelacanths were included in the 100–120 cm size class. The size distribution (TL) of a sample of 52 individual coelacanths encountered during underwater surveys (88% of the total local population) is shown in Fig. 4. Coelacanths were sized between 100 and 200 cm TL. No individuals smaller than 100 cm (i.e. juveniles or subadults) were encountered in the census area. In October 2009, we encountered a single subadult of ca. 50–60 cm in cave 9, located outside of the main census area (Fig. 3). This is by far the smallest coelacanth ever encountered at the Comores.

As we never encountered juvenile coelacanths in the census area during all dives conducted between 1987 and 2008, it is apparent that recruitment to the local population results from immigration of adults and subadults, rather than from juveniles originating from the observation area.

Coelacanths exhibit a distinct sexual dimorphism in body size. The distribution of the length classes reveals two distinct peaks: one at 120–129 cm, the other at 160–179 cm TL. The first peak comprises mature males and young mature females, the second mature females only. This is reinforced by literature data of sexed coelacanths (Bruton and Armstrong 1991): males 128 cm TL, SD = 7 cm ($n = 28$), females 148 cm TL, SD 18 cm ($n = 32$). The difference in TL is highly significant (t -test, $p < 0.001$).

Males typically have a more slender body shape and display a smaller body depth than females. Adult females are 40–50 cm deep, males 20–30. The thickness ratio (TR = body height/total length) allows the separation of

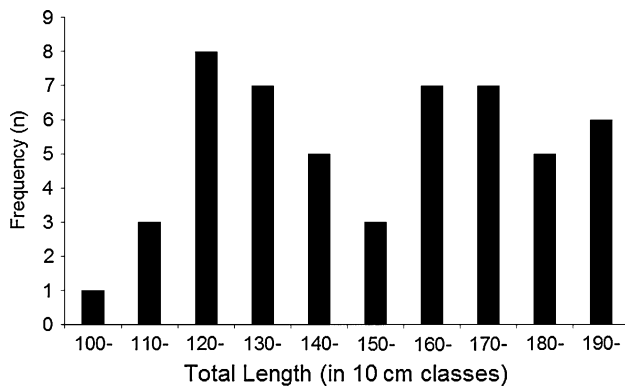


Fig. 4 Size distribution (TL) of 52 coelacanths in the census area

the sexes. Mean (\pm SD) TR was 0.21 (0.02) in males and 0.26 (0.03) in females (Fig. 5). The difference between the sexes was highly significant (t -test, $p < 0.001$). The thickness ratio of males confirms that their body is almost a perfect laminar spindle (Hertel 1963).

The local population size

Due to its large size, we were not able to survey the entire observation area on a daily basis. However, we recorded daily the number of coelacanths inside each cave located within the census area, and recorded the cumulative number of newly sighted individuals (Fig. 6).

The data indicate that ca. 53–55 coelacanths seem to be the carrying capacity of that area. The local population size of the census area remained stable over a period of 18 years. In 1994, a marked decline occurred, with a drop of 32% compared with data of other years (Hissmann et al. 1998). In 1994, we recorded the highest temperature at cave depths between 178 and 199 m (25.1°C compared with 22.1°C in 1991). In 1994, the highest temperature measured in deep water at 224 m depth was 24.3°C. These increased temperatures probably explain why the occupation rate of the caves dropped during this period. For

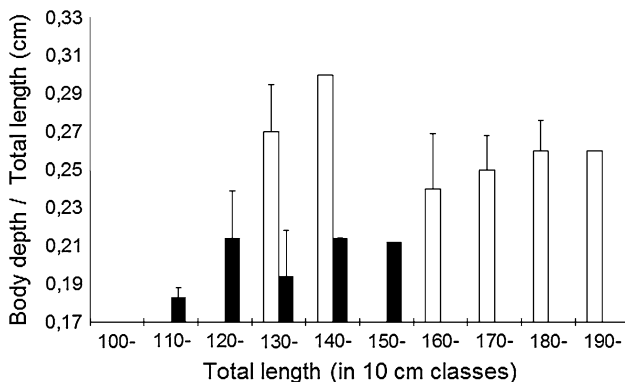


Fig. 5 The thickness ratios (means and standard deviations) of females ($n = 31$) (open bars) and males ($n = 20$) (black bars)

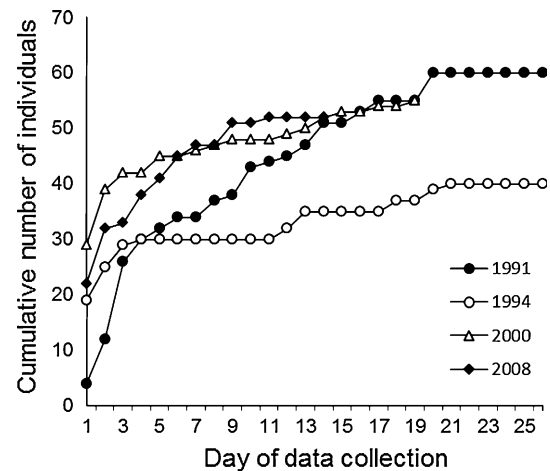


Fig. 6 Cumulative numbers of recorded coelacanths in the census area in relation to the day of data collection in various years

example, cave 3 (depth 178 m) was occupied between 38 and 79% of observations in 1991, 2000 and 2008, but was only occupied in 4% of observations in 1994. Cave 6 (depth 180 m) was occupied between 86 and 100% cases in 1991, 2000 and 2008, but was only occupied for 38% of observations in 1994 (Table 2). Several individuals (numbers 10, 16, 20, 25, 33, 36, 37, 53, 61 and 62) were not sighted in 1994, but were recorded again in subsequent years (Table S1), suggesting that they left the census area temporarily in 1994, probably to inhabit deeper, colder waters.

The utilization of caves by coelacanths

Between 1989 and 2008, we recorded the occupation of caves by coelacanths during a total of 115 survey days. Table 2 shows the occupation frequency, the minimum and the maximum number as well as the average number of coelacanths found in each cave of the census area between 1991 and 2008. Larger group formations of more than ten individuals were rare events.

Certain individuals were encountered each year after their first sighting (individuals 1, 2, 4, 5, 8, 13, 17, 18, 22, 24 and 31, see Table S1). The utilization of the caves by these individuals between 1989 and 2008 during the 115 recording days is shown in Table 3. No coelacanths were recorded on all 115 survey days: The most frequently encountered coelacanth was recorded on 59 days; at the other extreme, another individual was only recorded on six occasions across the 115 days. Our data suggest that coelacanths utilize as yet un-surveyed caves located either within or outside of the census area.

Coelacanths 2 and 8 visited all caves within the census area. Individuals 4, 5, 17 and 31 never visited cave 1, individuals 1, 13, 18, 22 and 24 were never seen in cave 4.

Table 2 Cave checks in census area of observation area I and details of occupation by cave inhabitants during survey years 1991, 1994, 2000 and 2008

Cave	Depth (m)	Number of cave checks	Occupation-rate %	Min–max occupation	Average occupation	Average group size
1991						
1	192	14	57	1–5	1.5	2.6
2	199	17	59	1–7	1.9	3.3
3	178	19	79	2–12	4.8	6.1
4	182	17	82	1–5	2.2	2.7
6	180	21	100	3–14	8.2	8.2
7	184	18	78	1–7	1.9	2.4
1994						
1	192	23	74	1–11	2.8	3.8
2	199	23	39	1–5	0.7	1.9
3	178	24	4	2	0.1	2
4	182	22	23	1–2	0.4	1.6
6	180	24	38	1–6	1	2.6
6a	236	7	100	1–7	3.7	3.7
6b	206	7	14	3	0.4	3
7	184	22	45	1–7	0.9	1.9
2000						
1	192	11	27	1	0.3	1
2	199	11	64	1–13	3.5	5.4
3	178	12	50	1–3	1	2
4	182	11	36	1–4	1	2.8
6	180	19	100	2–11	6.2	6.2
6a	236	16	63	3–13	4.5	7.2
6b	206	19	53	1–12	1.4	2.7
7	184	11	64	1–6	1.9	3
2008						
1	192	7	86	1–6	2.7	3.2
1a	200	5	60	1–3	1	1.3
2	199	10	100	1–9	4.2	4.2
3	178	13	38	1–8	1.2	3.2
4	182	11	64	1–8	1.5	2.4
6	180	14	86	1–6	3.1	3.6
6a	236	12	92	1–9	4.3	3.7
6b	206	14	79	1–7	2.4	3
7	184	11	45	1–5	1.5	3.4

In 1994, two new caves (6a, 6b) were discovered

Some caves (cave 2, 6, 6a and 6b) were visited by all coelacanths that we recognized in the population. Our data indicate that cave 6 was preferred by coelacanths, as in 1991 and 2000 this cave was occupied on all survey days.

Figure 7 shows an overview of individual coelacanths ($n = 98$) observed over the years in the census area and the use of the caves we sampled. The highest occupation rate was found in caves 2, 6a and b and 6. Most coelacanths were recorded from caves 6a and b ($n = 81$), with only 30 individuals recorded from the smallest cave (cave 4).

During the study (i.e. between 1987 and 2008), a total of 16 coelacanths were only encountered once in the census

area. Assuming that these individuals were occasional vagrants, we might expect them to utilize caves located on the periphery of the census area (e.g. caves 1 and 4). However, the sightings of these individuals were distributed across the entire census area, with most sightings occurring in caves 2, 6a and b and 6 ($n = 10$).

The impact of the fishery on coelacanths

During the study, we did not witness any predation on coelacanths by larger predatory fishes, although we sometimes encountered the large sand tiger shark *Odontaspis*

Table 3 Occupation of different caves in census area and their preferential use by 11 coelacanths

Individual	Cave 1	Cave 2	Cave 6a + b	Cave 6	Cave 3	Cave 7	Cave 4	<i>n</i>
1	8	7	4	5	7	5		36
2	4	2	5	30	11	1	6	59
4		4	11	15	4	4	3	41
5		2	1	2			1	6
8	2	3	1	6	7	5	2	26
13	2	7	13	17	1			40
17		3	4	14	13	5	8	47
18	4	5	2	10	1	2		24
22	7	6	6	9	1	2		31
24	6	10	8	16	3	3		46
31		5	2	1		4	2	14
Total	33	54	57	125	48	31	22	370
	8.9%	14.6%	15.4%	33.8%	13.0%	8.4%	5.9%	

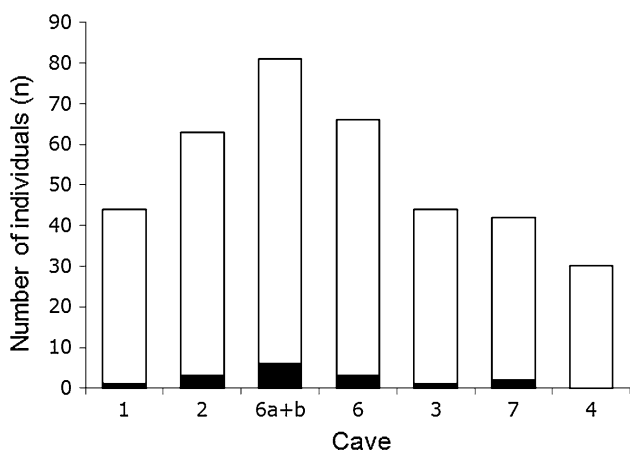


Fig. 7 Number of different individuals observed in caves 1–7. *Open bars* indicate individuals which were seen more than once (residents), *black bars* individuals which were seen only once. The order of caves corresponds to their spatial sequence. Caves 6a and b were summarized because they are located side by side

taurus. The only known cause of mortality to coelacanths was the local fishermen, who accidentally catch coelacanths with hook and longline during their nocturnal fishing for the oilfish *Ruvettus pretiosus* (i.e. Stobbs and Bruton 1991).

The number of un-motorized fishing boats on Grand Comore has declined since 1995, while the number of motorized boats has increased slightly (Fig. 8). The only threat to coelacanths arises from fishermen utilizing the unpowered *galawas*. Presently, the inshore waters are almost fished out and fishery has shifted offshore using motorized *vedettes*. Motorized fishing usually takes place outside known coelacanth habitat, and as such is unlikely to reflect a threat for coelacanths.

Two to four coelacanths have been taken annually by Grand Comore fishermen between 1954 and 1995 (Fig. 9).

After 2000, the annual catch rate decreased to 0.3 coelacanths per year. For comparison, the annual catch rate of coelacanths in Tanzania from 2003 onwards was 13 coelacanths per year following the development of deep-water netting in 2003.

Estimates of natural mortality and intrinsic rate of population growth

For this analysis, we only used individuals that had been observed at least once in the census area. Some of these individuals were also found in neighbouring caves outside the census area, and we treated such encounters as if they had occurred within the census area. For the years 1991, 1994, 2000 and 2008, we measured the total coelacanth population in the census area as 59, 38, 55 and 52 individuals, respectively. Treating the groups of newly observed individuals in a given year as cohorts and following their decline in numbers over time, we derived the

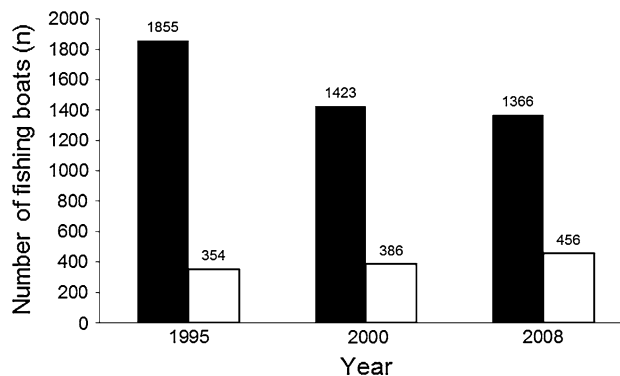


Fig. 8 The development of motorized (*vedettes* open bars) and unmotorized (*galawas* black bars) fishery at Grande Comore from 1995 to 2008

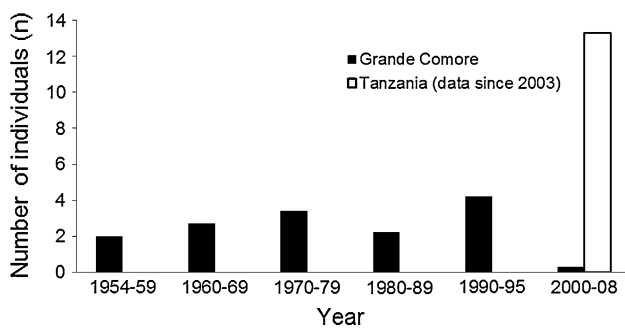


Fig. 9 The annual catch rate of coelacanths at Grande Comore since their first discovery in 1954 (black bars), in comparison with the annual catch rate of Tanzania (open bar)

mean rate of decrease in adult coelacanths as $M = 0.044$ (95% CL = 0.039–0.048, $n = 18$, $r^2 = 0.963$, SE of estimate = 0.0731) (Fig. 10).

For a population to persist and stabilize at an equilibrium size N_{∞} , the rate of decrease due to death and emigration M has to match the rate of recruitment and immigration P .

$$\frac{dN}{dt} = P_{\infty}N_{\infty} - MN_{\infty} = 0$$

We used the observed decay rate $M = 0.044$ and the mean population size of $N_{\infty} = 53$ individuals of coelacanths. The predicted mean number of annual deaths $D_{N_{\infty}}$ and corresponding number of recruits $R_{N_{\infty}}$ was then obtained from

$$D_{N_{\infty}} = N_{\infty} - N_{\infty}e^{-M} = 2.28 = R_{N_{\infty}}$$

The average number of 2.28 deaths and newcomers per year falls well within the observed range of 1.8–2.2 newcomers and 1–3.3 deaths per year, i.e. we conclude that

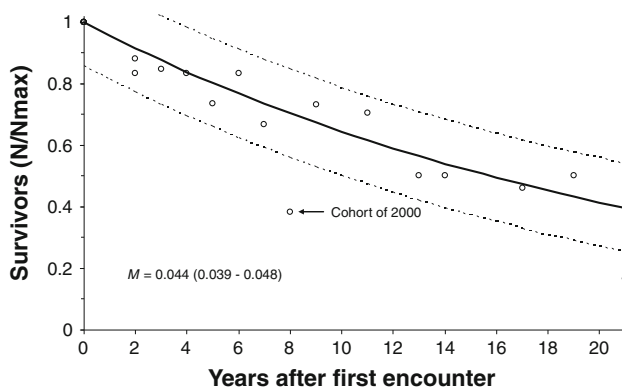


Fig. 10 Decline in numbers over time in observed groups of individuals of coelacanths, with indication of mortality rate M , predicted number of survivors, and 95% confidence limits of the prediction. The survival of the cohort of 2000 is probably an underestimate, because individuals overlooked in 2008 had no chance of been encountered and corrected in subsequent years

the population is near equilibrium and limited by recruitment.

Discussion

Our surveys revealed that the coelacanths of Grande Comore occupy several kilometres of steep volcanic landscapes at depths between 170 and 240 m. During the night, they are piscivorous drift hunters and perform vertical movements down to 500 m (Fricke and Hissmann 1994; Hissmann et al. 2000). In the early morning, they relocate to their familiar daytime resting caves.

Home range system, site fidelity and recruitment

Our field data reveal that all coelacanths encountered during our survey also utilized areas outside of the census area. For instance, even the most frequently observed coelacanth (individual 2, see Table S1) was only encountered on 59 days of 115 survey days between 1989 and 2008, meaning that it must have occupied also other caves. The census area is part of a large home range system of individually overlapping home ranges, and some exchange of individuals between neighbouring home ranges can be expected. Coelacanths occupy several caves within their home range (Fricke and Hissmann 1994; Hissmann et al. 2000). Although there are other caves and crevices available, our information indicates that they preferentially use certain caves.

The utilization of the caves by coelacanths was independent of the distances between the caves. It is questionable whether, for example, an occasional immigrant finds a cave by trial and error. Although there may be several suitable caves available within the census area, only certain caves are selected. This indicates knowledge of the location of the preferred caves. We assume that coelacanths have a fairly good knowledge also of areas outside of their own occupied home range. The orientation of coelacanths would be a fascinating topic for future research.

Our study revealed that some newcomers appeared suddenly and were recorded thereafter in the following years. These adults were considered as recruits to the local population. However, the total absence of juveniles or subadults in our census area over a time span of 21 years is indeed enigmatic.

Over 18 years, we recorded the number of coelacanths in the census area; we witnessed nine occasions of groups consisting of 11–14 individuals. The largest ever observed group consisted of 16 individuals observed in a spacious cave outside the census area but within the boundaries of observation area I. We never witnessed any agonistic

behaviour and the group behaviour was extremely peaceful. There was no indication that coelacanths aggregations arose in a sexual context.

The question of the juvenile depth distribution

The coelacanth size structure in the study area confirms our earlier observations that the local population consists of adult individuals only. Subadults and juveniles were not encountered by us either in the Comoros or in any of our other diving sites off Indonesia, South Africa or Tanzania. These size classes were also absent from shallower waters, and therefore, we conclude that they live in deep water below the depth range inhabited by adults. Juveniles are born with TL of about 35 cm (Fricke and Frahm 1992). The apparent habitat segregation may reflect a risk of cannibalism, as at this size they are potentially susceptible to piscivorous adults. The catch inventory of Bruton and Coutouvidis (1991) lists only eight specimens between 42.5 and 85 cm among a total of 158 coelacanths. This may reflect a different juvenile diet that reduces vulnerability to hook and line fishing, but may also reflect a deeper depth distribution where fishing activity is reduced. In 2009, a coelacanth of birth size was filmed off Indonesia at a depth of ca. 160 m, in about the same depth range as the adults (personal communication Masa Iwata, Fukushima Aquarium Japan; Holden 2009). Despite this single record, the depth distribution of juveniles and their depth of birth remain enigmatic and need further investigations.

Mortality, longevity and population growth

Previously, coelacanth growth and longevity were determined from scales. Hureau and Ozouf (1977) counted 2–23 scale rings starting from a 31-cm full-term embryo to a 180 cm adult, and assumed that two rings were laid down each year. This indicates that an adult coelacanth would then be 11 years old, with an annual growth increment of 13 cm. Balon et al. (1988) disputed these numbers and suggested one ring per year, thus doubling the age. Suyehiro (1983) suggested a life span of 10 years, Uyeno (1984) suggested 7–8 years for a total length of 170 cm. Bruton and Armstrong (1991) estimated an age of 20 years and possibly 40–50 years, but did not reveal the basis for their assumptions. Using growth data, Froese and Palomares (2000) proposed an age of 48 years. Our field observations serve as positive proof that coelacanths are at least 19–21 years old. Of the 34 newcomers identified in 1989, 17 were also recorded in 2008. As these individuals were adults, and body growth was so slow to be undetectable during the observation period, the real age of the coelacanths we encountered must be much higher.

Given the low rate of known captures of coelacanths from the census area, we assumed that fishing mortality was negligible. If we assume that none of the individuals was overlooked, that exchange of individuals with neighbouring habitats balanced each other, and that catches by fishers were negligible, then our estimate of natural mortality for coelacanths is 0.044 (0.039–0.048), which is clearly at the lower end of observed mortality rates, similar to that known for long-lived deep-water rockfishes of the Genus *Sebastes* (Archibald et al. 1981). With this mortality rate, Hoening's (1983) empirical relationship based on a variety of marine organisms suggests coelacanth longevity of 103 (95–117) years.

$$\ln Z = 1.44 - 0.984 \ln t_{\max}$$

Or in another approximation, of a cohort with 100 individuals and with a mortality rate of 0.044, only one individual would be alive after 103 years. This estimate of longevity exceeds previous estimates; however, maximum ages of around 100 years have been commonly found in deep-water fishes (Stevens et al. 2004).

If the adult mortality rate is more or less constant, then the mean adult life expectancy E and thus the mean duration of the reproductive phase are given by $E = 1/M = 22.7$ (20.8–25.6) years (Charnov 1993). This is confirmed to a degree by the observation of those individuals first encountered in 1989. This cohort decreased by 50% (from 34 to 17 individuals) in 19 years. Assuming a duration of pregnancy of 3 years (Froese and Palomares 2000) and immediate fertilization thereafter, this would suggest that the average coelacanth female gives birth seven times during her productive life. Known fecundities are 5, 19, 23, 23 and 26 pups (Smith et al. 1975; Fricke and Frahm 1992). Assuming a mean fecundity of 20 pups, a female would produce about 140 offspring during her expected lifespan, of which at least two have to survive to replace their parents and thus stabilize the population.

Total population size at Grande Comore

Coelacanths are rare fish, raising the question of the minimal viable population size. Our first estimation of the total population size located off the west coast of Grande Comore (assuming that our census area is representative of the coelacanth habitat, which comprises 97 km of coastline) from 1991 indicated a total of 550 adult individuals, taking the number of observed residents as a base for calculations. A total of 650 individuals were estimated considering all identified coelacanths, compared with 230 individuals estimated from average cave occupation (Hissmann et al. 1998). However, calculations using the average cave occupations are unrealistic, as our cave utilization data

show that other (unknown) caves are utilized, which would increase the total population size.

The cumulative number of new individuals recorded in subsequent days obtains saturation after several days of cave checking (Fig. 6). This value is similar to the total of observed residents and would account for a total population of 550 coelacanths. In 2008, we obtained saturation at a level of 52 individuals or approximately 580 coelacanths for the total area. This population size is only valid if the census area is representative for the entire coastline. However, this is not the case. Plante et al. (1998) compared the fishing effort of *galawas* in five arbitrarily selected sectors along the west coast and presented evidence of varying coelacanth densities in those sectors with highest value in our observation area I. To demonstrate unequal coelacanth densities, we started observations in a new area (Area II, see Fig. 1) in sector 2 of Plante et al. (1998) in 1995. Although this sector is one of the largest with high fishing activity, we only recorded 26 coelacanths. As such, observation area I is not representative for the entire coelacanth habitat. Therefore, we applied a correction factor for each sector which is bonded to fishing activity and coelacanth landings. Use of this correction factor provides a total population of 410 individuals, which seems to be a more realistic number (Table 4). Hissmann et al. (1998) gave evidence that the total suitable coelacanth habitat of Grande Comore is one-third less than previously thought and that means that the entire population consists of approximately 300 individuals. About 300–400 individuals seem to be the total population size of coelacanths at Grande Comore. In 1991, 2000 and 2008, the population counts of the census area were between 52 and 59 individuals, indicating a very stable population.

The decline of observed population size in 1994

The cumulative recording of coelacanths newly arriving in the census area revealed the number of residents and occasional vagrants. It gave a fairly good insight into the local population size and can be taken as a sensitive measure for changing environmental conditions. The marked decline (32%) of the estimated population in 1994 was unexpected. Hissmann et al. (1998) pointed out that the environment of the coelacanth is relatively stable and unaffected by human pollution. 'It is therefore unlikely that the observed decline in a relatively short period is due to natural fluctuations of the population'. The decline was probably linked to the increase in water temperature and the temperature-dependent saturation of the coelacanth blood with best saturations between 15 and 19°C (Hughes and Itazawa 1972). Coelacanths have to avoid warm water because of respiratory and metabolic demands. The influence of warmer waters was particularly visible on the

Table 4 Observed and predicted population numbers, counts of coelacanth catches and counts of outrigger canoes (*galawas*) in four coastal sectors defined in Plante et al. (1998) along the west coast of Grande Comore

Sector	1	2	3	4
Sector length (km)	18	27	13	39
<i>Galawas</i> no.	302	402	92	390
Catch/100 <i>galawas</i>	0.3	1.7	2.4	3.1
A: catch/100 <i>galawas</i> /km	0.0167	0.0630	0.1846	0.0795
Population density (no.)		26		253
B: population/km		0.96		6.49
Ratio B/A		15.24		81.64
Mean B/A ratio	48.44			
Predicted B = 48,44 × A	0.8089		8.9420	
Pred. + obs. population no.	15	26	116	253
Total				410

The mean catch rate of coelacanths performed from *galawas* was used to estimate the missing population numbers of sector 1 and 3

occupation rate of the caves in 'shallower' waters (178–180 m). After 1994, the local population size increased again. Ten known coelacanths were not recorded during the 1994 events, but reappeared in subsequent years.

Due to their temperature-dependent oxygen saturation of their haemoglobin (Hughes and Itazawa 1972), coelacanths are potentially vulnerable to climate changes. If the 18°C thermocline of the subarctic waters retreats into deeper zones, coelacanths could react to global warming. The structural complexity of the slopes at the Comoros gets less with depth and would then force coelacanths into less favourable environments. For example, three ROV dives below 400 m that ranged to a maximum depth of 1,071 m adjacent to the study area revealed eroded sand-covered slopes without prominent geological features, and cave structures like those utilized by adult coelacanths were not encountered.

The impact of human exploitation

Coelacanths are considered as highly endangered species and are listed on CITES list Appendix I in IUCN (2009). Figure 8 showed that Grande Comore coelacanths are presently reasonably protected because of shifts of fishing technique towards motorized offshore fishing, which does not inflict harm on the coastal coelacanth population.

The traditional nocturnal maze fishing with hook and longline from outrigger *galawas* is a less favoured fishing technique, which is mainly performed by older experienced fishermen (Plante et al. 1998). The number of maze-fishing canoes fell during the last decade. Because the coastal waters are almost devoid of a sustainable fish population, other fishing techniques are employed. Although we

witnessed first instances of dynamite fishing in shallow water, this probably does not influence the population of coelacanths. If one compares the fishing developments of the Comoros with those of Tanzania, an intensified dynamite fishing in the shallow water of the Comoros would wipe out the edible small fish population. As in Tanzania, deep-water gill nets will then probably be employed. Deep-water nets came into operation for the first time in 2003 in Tanzania. Since then, more than 80 coelacanths had been caught, with the number increasing annually. Given the low rate of recruitment established in this study, it is highly likely that coelacanths are highly endangered in the Tanga region of Tanzania where most coelacanths were caught.

Earlier Bruton et al. (1989), Bruton and Stobbs (1991) and Plante et al. (1998) proposed the south-west coast of Grande Comore as a protected area, and we support that suggestion. The protocol of our population measures and our population counts will be valuable in building a case for such decision.

Acknowledgments This study was supported by grants of the German Research Council DFG to H. Fricke, the last expedition in 2008 by grant No. FR 369/22-1. We thank the Max Planck Institute for Marine Microbiology in Bremen, Germany for financial and administrative assistances. The Max Planck Society in Munich, Germany, and the Frankfurt Zoological Society-Help for Threatened Wildlife supported our research over many years. The Leibniz Institute of Marine Sciences IFM-GEOMAR in Kiel, Germany supplied technical support. We thank all captains and crews of the vessels METOKA, SEA EAGLE, DEEP SALVAGE, INDIAN OCEAN EXPLORER and SOLAND for successful operations during the many years of our submersible operations. We are especially thankful to Paul Allen from Vulcan Co. who placed his MY OCTOPUS with diving equipment at our disposal. The government of the Islamic Republic of the Comoros allowed our diving operations within their territorial waters. The German Embassy in Antananarivo helped with all governmental matters, the CNDRS in Moroni with official internal affairs. Many thanks to Rik Nulens who supplied us with coelacanth literature and to Peter Forey for valuable comments on the text and for smoothing our English. We are especially grateful to Anja Fricke for her valuable help to improve the manuscript. Special thanks also to Mrs. Andree Koechlin and our friend Dr. Heinrich Vischer, both from Basle, Switzerland, for their generous support.

References

- Archibald CP, Shaw W, Leaman BM (1981) Growth and mortality estimates of rockfishes (Scorpaenidae) from British Columbia Waters, 1977–1979. *Can Tech Rep Fish Aquat Sci* 1048:57
- Balon EK, Bruton MN, Fricke H (1988) A fiftieth anniversary reflection on the living coelacanth, *Latimeria chalumnae*. *Environ Biol Fish* 23:241–280
- Boy G (2001) Kenya's first coelacanth. *Swara* 24:24–26
- Bruton MN, Armstrong MJ (1991) The demography of the coelacanth *Latimeria chalumnae*. *Environ Biol Fish* 32:301–311
- Bruton MN, Coutouvidis SE (1991) An inventory of all known specimens of coelacanth *Latimeria chalumnae*, with comments on trends in the catches. *Environ Biol Fish* 32:371–390
- Bruton MN, Stobbs RE (1991) The ecology and conservation of the coelacanth. *Environ Biol Fish* 32:313–339
- Bruton MN, Hughes GR, Buxton CD et al (1989) Recommendations on marine conservation in the Federal Islamic Republic of the Comoros. *Invest Rep JLB Smith Inst Ichthyol* 34:1–103
- Bruton MN, Cabral AJP, Fricke H (1992) First capture of a coelacanth, *Latimeria chalumnae* (Pisces, Latimeriidae), off Mozambique. *S Afr J Sci* 88:225–227
- Charnov EL (1993) Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford
- DeVos L, Oyugi D (2002) First capture of a coelacanth, *Latimeria chalumnae* Smith, 1939 (Pisces, Latimeriidae), off Kenya. *S Afr J Sci* 98:345–347
- Erdmann MV, Caldwell RL, Moosa MK (1998) Indonesian 'king of the sea' discovered. *Nature* 395:335
- Forey PL (1988) Golden jubilee for the coelacanth *Latimeria chalumnae*. *Nature* 336:727–732
- Forey PL (1990) The coelacanth fish: progress and prospects. *Sci Prog* 74:53–67
- Forey PL (1991) *Latimeria chalumnae* and its pedigree. *Environ Biol Fish* 32:75–97
- Forey PL (1998) History of the coelacanth fishes, 1st edn. Chapman & Hall, London
- Fricke H (1993) Der Quastenflosser—Biologie eines legendären Fisches. *Biologie in unserer Zeit* 23:229–237
- Fricke H (2007) Die Jagd nach dem Quastenflosser. C.H. Beck, München
- Fricke H, Frahm J (1992) Evidence for lecithotrophic viviparity in the living coelacanth. *Naturwissenschaften* 79:476–479
- Fricke H, Hissmann K (1994) Home-range and migrations of the living coelacanth *Latimeria chalumnae*. *Mar Biol* 120:171–180
- Fricke H, Hissmann K (2000) Feeding ecology and evolutionary survival of the living coelacanth *Latimeria chalumnae*. *Mar Biol* 136:379–386
- Fricke H, Plante R (1988) Habitat requirements of the living coelacanth *Latimeria chalumnae* at Grande Comore, Indian Ocean. *Naturwissenschaften* 75:149–151
- Fricke H, Reinicke O, Hofer H, Nachtigall W (1987) Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. *Nature* 329:331–333
- Fricke H, Hissmann K, Schauer J, Reinicke O, Kasang L, Plante R (1991a) Habitat and population size of the coelacanth *Latimeria chalumnae* at Grande Comore. *Environ Biol Fish* 32:287–300
- Fricke H, Schauer J, Hissmann K, Kasang L, Plante R (1991b) Coelacanth *Latimeria chalumnae* aggregates in caves: first observations on their resting habitat and social behaviour. *Environ Biol Fish* 30:281–285
- Fricke H, Hissmann K, Schauer J, Erdmann M, Moosa MK, Plante R (2000) Biogeography of the Indonesian coelacanth. *Nature* 403:38
- Froese R, Palomares MLD (2000) Growth, natural mortality, length-weight relationship, maximum length and length-at-first-maturity of the coelacanth *Latimeria*. *Environ Biol Fish* 58:45–52
- Heemstra PC, Freeman ALJ, Wong HY, Hensley DA, Rabesandratna HD (1996) First authentic capture of a coelacanth, *Latimeria chalumnae* (Pisces:Latimeriidae), off Madagascar. *S Afr J Sci* 92:150–151
- Hertel H (1963) Struktur, Form und Bewegung. Krauskopf-Verlag, Mainz
- Hintze J (2001) NCSS 2001. NCSS, LLC, Kaysville
- Hissmann K, Fricke H, Schauer J (1998) Population monitoring of the coelacanth (*Latimeria chalumnae*). *Conserv Biol* 12:165–758
- Hissmann K, Fricke H, Schauer J (2000) Pattern of time and space utilisation in coelacanths (*Latimeria chalumnae*), determined by ultrasonic telemetry. *Mar Biol* 136:943–952

- Hissmann K, Fricke H, Schauer J, Ribbink AJ, Roberts M, Sink K, Heemstra P (2006) The South African coelacanths—an account of what is known after tree submersible expeditions. *S Afr J Sci* 102:1–10
- Hoenig JM (1983) Empirical use of longevity data to estimate mortality rates. *Fish Bull US* 81:898–903
- Holden C (2009) Infant fossil. *Science* 326:132
- Hughes GM (1976) On the respiration of *Latimeria chalumnae*. *Zool J Linn Soc* 59:195–208
- Hughes GM, Itazawa Y (1972) The effect of temperature on the respiratory function of coelacanth blood. *Experientia* 28:1247
- Hureau JC, Ozouf C (1977) Détermination de l'âge et croissance du coelacanthé *Latimeria* Smith, 1939 (poisson, crossoptérygien, coelacanthidé). *Cybium Ser 3* 2:129–137
- IUCN (2009) IUCN red list of threatened species. Version 2009.1
- Locket NA (1980) Some advances in coelacanth biology. *Proc R Soc Lond Ser B* 208:265–307
- Nyandwi N (2006) Coastal Tanzania, a new home to the living coelacanth: an oceanographic analysis. *Tanz J Sci* 32:33–38
- Plante R, Fricke H, Hissmann K (1998) Coelacanth population, conservation and fishery activity at Grande Comore, West Indian Ocean. *Mar Ecol Prog Ser* 166:231–236
- Sasaki T, Sato T, Miura S, Bwanthoudi POJ, Ngatunga BP, Okada N (2007) Mitogenomic analysis for coelacanths (*Latimeria chalumnae*) caught in Tanzania. *Gene* 389:73–79
- Schartl M, Hissmann K, Schauer J, Fricke H (2005) Relatedness among east African coelacanths. *Nature* 435:901
- Schauer J, Hissmann K, Fricke H (1997) A method for deployment of externally attached sonic fish tags from a manned submersible and their effects on coelacanths. *Mar Biol* 128:359–362
- Smith CL, Rand CS, Schaeffer B, Atz JW (1975) *Latimeria*, the living coelacanth, is ovoviviparous. *Science* 190:1105–1106
- Springer VG (1999) Are the Indonesian and western Indian Ocean coelacanths conspecific: a prediction. *Environ Biol Fish* 54:453–456
- Stevens MM, Andrews AH, Cailliet GM, Coale KH (2004) Radiometric validation of age, growth, and longevity for the blackgill rockfish (*Sebastes melanostomus*). *Fish Bull* 102:711–722
- Stobbs RE, Bruton MN (1991) The fishery of the Comoros, with comments on its possible impact on coelacanth survival. *Environ Biol Fish* 32:341–359
- Suyehiro Y (1983) Some views on the dissected specimens of coelacanth. *Bienn Rep Keikyu Aburat Mar Park Aquar* 12:12
- Uyeno T (1984) Age estimation of coelacanth by scale and otolith. In: Proceedings of first symposium on coelacanth studies, pp 28–29
- Venter P, Timm P, Gunn G, le Roux E, Serfontein C, Smith P, Smith E, Bensch M, Harding D, Heemstra P (2000) Discovery of a viable population of coelacanths (*Latimeria chalumnae* Smith, 1939) at Sodwana Bay, South Africa. *S Afr J Sci* 96:567–568