

Nidamental glands in males of the oceanic squid *Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae) – sex change or intersexuality?

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Abstract

This is the first record of intersexuality to have been found within the Cephalopoda. Seven out of 16 sexually mature *Ancistrocheirus lesueurii* males from southern African waters had nidamental glands in the mantle cavity in addition to a normally developed male reproductive system (spermatophoric complex, testis and hectocotylus). The frequency of occurrence suggests that feminization in male *A. lesueurii* is not a rare phenomenon in the south-eastern Atlantic. Normal *A. lesueurii* shows sexual size dimorphism, with females growing larger than males. The intersexual males formed a distinct size group intermediate between normal males and females, and their testis mass and spermatophore length were significantly larger than in normal males. The absence of oocytes and oviducts in intersexual males indicates that feminization represents pseudohermaphroditism. Intersexuality does not seem to affect male functionality and is apparently advantageous in that larger body size is accompanied by larger testis and spermatophores.

Introduction

Oceanic squid are an important component in the diet of a large variety of oceanic predators such as fish, birds and marine mammals (Clarke, 1996) and form a trophic link between the surface waters and the deep ocean. In spite of their ecological importance, basic biological knowledge of life strategies (age, growth and reproduction) is lacking for the majority of these squid, except for the commercially important Ommastrephidae.

Squid are generally short lived (life span usually 1 year or less), with a reproductive strategy that, whether involving synchronous terminal spawning, multiple spawning or intermittent terminal spawning, is characterized by maturation and spawning towards the end of the life cycle (Rocha, Guerra & González, 2001).

However, recent observations, such as an estimated longevity of 2–3 years for the octopoteuthid squid *Taningia danae* (González, Guerra & Rocha, 2003) and the phenomenon of post-spawning egg care in the gonatid squid *Gonatus onyx* (Seibel, Hochberg & Carlini, 2000), indicate that the life-history strategies of oceanic squid are more complex.

One aspect of reproduction that all cephalopods seem to have in common is that they are gonochoristic, that is that sex is predetermined genetically, individuals develop as

males or females and remain the same sex throughout their life span (Nesis, 1987). Until now, intersexuality, hermaphroditism or sex change has not been reported for cephalopods.

The family Ancistrocheiridae is currently considered (Young *et al.*, 1998) to have a single species, *Ancistrocheirus lesueurii* (d'Orbigny, 1842). The species has a worldwide distribution in tropical and temperate oceanic waters (Roper, Sweeney & Nauen, 1984) and is preyed upon by a large variety of marine predators (Clarke, 1966; Bello, 1991; Dunning, Clarke & Lu, 1993; Imber, Jolly & Brooke, 1995; Goodman-Lowe, 1998; Smale & Cliff, 1998; Santos & Haimovici, 2001; Xavier *et al.*, 2003).

Nesis (1993) classed *A. lesueurii* as a nerito-oceanic species, in which paralarvae, juveniles and subadults are epipelagic and/or mesopelagic and adults spawn on or near the bottom. The growth zones in the statoliths of *A. lesueurii* confirm a life-history shift from the epipelagic and upper mesopelagic to a bathyal habitat (Arkhipkin, 1997).

The morphology of mature female *A. lesueurii* has been well documented (Okutani, 1976; Bello, Potoschi & Berdar, 1994; D'Onghia, Maiorano & Tursi, 1997). However, mature males are poorly known, and have been recorded only by Arkhipkin (1997), who found that *A. lesueurii* from the eastern central Atlantic showed extreme sexual size

dimorphism, with adult females attaining a mantle length up to 3.5 times and a body mass of as much as 10 times that of adult males. In addition, age and growth rates are also sexually dimorphic. Males live for *c.* 1 year, whereas females only start maturing at this age and probably live for up to 2 years. The biological meaning of this difference in age is unclear (Arkhipkin, 1997). *Ancistrocheirus lesueurii* probably spawns several egg batches because their oviducts cannot accommodate all the large eggs at once (Rocha *et al.*, 2001). Their potential fecundity is estimated to be 200 000–800 000, with ova measuring 1.75–1.85 mm (Laptikhovsky, 1999).

The primary and secondary sexual characteristics of mature *A. lesueurii* in the Iziko cephalopod collection (Iziko Museums of Cape Town, South Africa) were investigated as part of a larger study of reproduction in oceanic squid. Secondary female characteristics were discovered in seven males. The nature, functional implications and possible causes of the existence of these intersexual males will be discussed.

Materials and methods

Eighteen specimens were collected off southern Africa at depths of 432–863 m by the *F. R. S. Africana*, *R. V. Dr. Fridtjof Nansen* and *Mary Kate* (Fig. 1, Table 1); one mature female was collected from the stomach of a sperm whale (locality unknown).

Standard measurements to the nearest mm and mg were taken after fixation in 10% formalin as described and abbreviated by Roper & Voss (1983). Samples of *c.* 1 mL were taken from the anterior, middle and posterior parts of the testis of two intersexual males [dorsal mantle length (DML) 320 and 212 mm] and of two normal males (DML 202 and 155 mm). The samples were dehydrated in a graded ethanol series, cleared with toluene and embedded in paraffin wax. Sections of 3 μ m were stained with haematoxylin and eosin. Longitudinal sections of the proximal part of the nidamental glands of two females (DML 265 and 435 mm) and two intersexual males (DML 320 and 212 mm) were

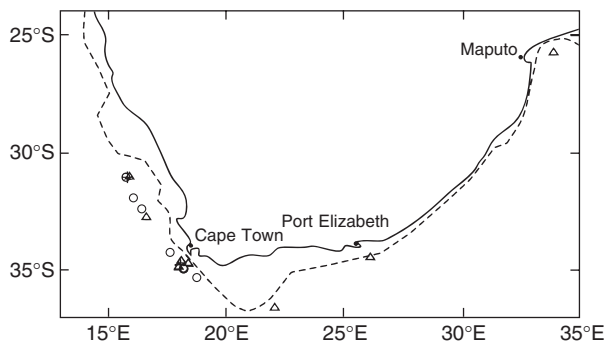


Figure 1 Localities of southern African *Ancistrocheirus lesueurii* females (+), males (Δ) and intersexual males (\diamond). Broken line indicates 200 m depth contour.

prepared as above, and were stained with toluidine blue as well as with haematoxylin and eosin.

Results

The specimens described here include the largest male and female *A. lesueurii* recorded to date. The gross morphology of southern African *A. lesueurii* is in accordance with the data provided by previous authors (Okutani, 1976; Bello *et al.*, 1994; D'Onghia *et al.*, 1997; Vecchione & Young, 1999). Photophores in mature males are arranged as in females. In addition, males have a large elongated photophore (maximum length \pm 3.0 mm) on the tips of both ventral arms.

Apart from the presence of nidamental glands, there were no other abnormalities in the gross reproductive anatomy of the intersexual males examined. The animals had a testis, spermatophoric organ and terminal organ with large, functional spermatophores and the right ventral arm was hectocotylized.

Relative dimensions of the specimens are given in Table 1. Normal mature males had a DML of 122–265 mm and a body mass of 101–737 g; mature females had a DML of 265–435 mm and a mass of 1604–3707 g and mature intersexual males had a DML of 185–320 mm and a mass of 586–1163 g (Fig. 2). Both mantle length and body mass of sexually mature normal male and female *A. lesueurii* showed sexual dimorphism. Females were significantly larger and heavier than normal males. Intersexual males formed a group intermediate between normal males and females but overlapping with both. Overall, their DML and body mass were significantly smaller than in females but larger than in normal males (Student's *t*-test, unpaired, $P < 0.05$; Fig. 2).

The mantle cavities of a normal male (DML 178 mm) and female (DML 265 mm) are illustrated (Fig. 3a and b). Intersexual males had what appeared to be nidamental glands in the mantle cavity (Fig. 3c). Five of these males had paired glands and another two had only a single, right nidamental gland (Table 1). The gross morphology and developmental stages of the glands differed between the intersexual males and may be divided into three groups:

1. A very small nidamental gland (NGL 14 mm; NGW 4 mm) was found in one specimen (DML 220) with only the right gland present.
2. Larger nidamental glands, consisting of two morphological parts, were found in two males (DML 212 and 255). The posterior part of the gland was attached to the visceral sac and measured 16–19 mm in length and 12–15 mm in width. The anterior part measured 11–16 mm in length and 3.0–5.5 mm in width and was joined to the posterior part by a narrow neck (Fig. 4a).
3. In four males, nidamental glands resembled those of females most closely, each gland being a morphological unit (NGL 50–80 mm; NGW 18–24 mm).

These nidamental glands were generally fragile, resembling glands in an advanced state of maturation. The width gradually decreased distally. The anterior parts of the glands were divided into two lobes, as is usual in fully developed

Table 1 Locality data and morphometrics of southern African *Ancistrocheirus lesueurii*

Catalogue number	SAM- S2677	SAM- S2175	SAM- S654	SAM- S3535	SAM- S3534	SAM- S2174	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	
Latitude	34°26.4'S 34°46.6'S	18°02.5'E 15°48'E	31°02'S 25°11'S	36°35'S 31°0'S	34°44'S 34°39.0'S	32°43'S 34°14'S	34°53.1'S 31°03'S	32°25'S 32°24'S	31°55'S 35°19'S	16°35'E 17°37'E	18°10,0'E 18°43'E	16°02'E 16°25'E	16°23'E 16°25'E	16°02'E 16°25'E	18°43'E 18°43'E	15°43'E 18°02.5'E	31°02'S	
Longitude	26°04.3'E 18°02.5'E	15°48'E 33°30'E	22°02'E 15°43'E	18°17'E 18°4.0'E	16°35'E 17°37'E	18°10,0'E 18°43'E	16°02'E 16°25'E	16°23'E 16°25'E	16°02'E 16°25'E	18°43'E 18°43'E	15°43'E 18°02.5'E	16°02'E 16°25'E	16°23'E 16°25'E	16°02'E 16°25'E	18°43'E 18°43'E	15°43'E 18°02.5'E	31°02'S	
Depth (m)	490	692-697	560	432	512-590	661	478	500	753	467	857-863	652	552	676	561	661	692-697	560
Date	12-X-1988	14-III-1988	22-I-2003	XI-1973	25-X-1991	22-I-2003	08-III-2005	11-II-1992	26-II-2005	15-IX-2004	11-III-1988	06-II-2003	06-II-2003	22-II-2005	07-III-2005	22-I-2003	14-III-1988	22-I-2003
Collected by	<i>Africana</i>	<i>Africana</i>	<i>Nansen</i>	<i>Mary Kate Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Nansen Africana</i>	<i>Sperm whale</i>
Sex, maturity	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	M III	F III	F III
Intersexual male																		
DML (mm)	122	136	155	162	178	202	236	245	265	185	212	220	255	267	275	320	265	305
BM (g)	119	101	198	246	453	498	535	648	737	907	586	844	779	606	998	1163	1604	1805
VMLI	91	89.7	85.8	88.3	91	95	97.5	89.8	92.5	93.5	87.3	90.9	94.1	91.8	94.5	92.2	86.8	91.1
MWI	36.9	41.2	32.3	34.6	32	42.6	25.4	24.5	30.2	45.9	32.1	38.6	29.4	-	29.1	26.9	62.3	41
FLI	80.3	74.3	78.7	92	76.4	82.2	72	-	73.6	-	74.5	72.7	68.6	67.4	72.7	71.9	89.1	82.6
FWI	90.2	82.4	86.5	118.5	-	90.1	76.3	104.5	71.7	97.3	88.7	95.5	76.5	-	72.7	68.8	112.1	-
HWI	24.6	22.8	-	22.2	25.3	26.2	-	-	-	-	27.4	-	-	-	-	20.6	30.9	23
NGLI	-	-	-	-	-	-	-	-	-	32.4	16.5	6.4 ^a	10.6	18.7 ^b	>14.5 ^a	25	40.4	26.2
NGWI	-	-	-	-	-	-	-	-	-	11.4	5.7	1.8	5.9	7.1	8.7	5.6	12.5	9.8
STN	14	±20	19	7	-	18	9	29	54	-	12	24	77	2	11	19	-	-
SMN	4	-	18	3	9	18	3	9	41	-	5	12	52	2	4	5	-	-
SPL (mm)	37-56	±65	62-72	39-52	-	54-78	85-86	63-108	62-96	-	76-87	66-98	61-96	80-82	105-112	97-102	-	-

^aOnly right nidamental gland present.

^bOnly left nidamental gland measured.

BM, body mass; DML, dorsal mantle length; FLI, fin length index; FWI, fin width index; HWI, head width index; MWI, mantle width index; NGLI, nidamental gland length index; NGWI, nidamental gland width index (across one gland); SMN, number of spermatophores measured; SPL, spermatophore length; STN, total number of spermatophores; VMLI, ventral mantle length index. Maturity scale: stage I, immature; stage II, maturing; stage III, mature (spermatophores present in terminal organ or ova in oviducts).

female squid (Fig. 4b). In one male (DML 275 mm), only the right gland of the pair was present.

All nidamental glands (in both intersexual males and females) were longitudinally divided posteriorly (Fig. 4a) and tightly packed lamellae could be seen perpendicular to the medial division. These lamellae continued into the anterior part of the gland, although there they were less tightly packed.

Longitudinal sections of the posterior part of the nidamental gland showed lamellae and interlamellar spaces (Fig. 5a and b). The thickness of the lamellae measured 200–300 µm in both females and intersexual males. The interlamellar spaces measured 60–100 µm in females, but were much smaller in intersexual males.

In both normal and intersexual males, the mass of the testis of mature male *A. lesueurii* generally increased with

mantle length (Fig. 6). Small mature males (<162 mm DML) had low testis masses (0.4–3.4 g). The male with the smallest testis (0.4 g at DML 162 mm) had large, fully developed spermatophores in the terminal organ. In normal males (DML 202–265 mm) the testis mass was 8.8–16.2 g. The largest testes were found in intersexual males and were 15.3–30.2 g. The testis mass in feminized males was significantly higher than in normal males (Student's *t*-test, unpaired, $P < 0.05$).

Histologically the testis of intersexual males showed normal male gametes, that is spermatozoa were present in the lumen of the seminiferous tubules. Earlier

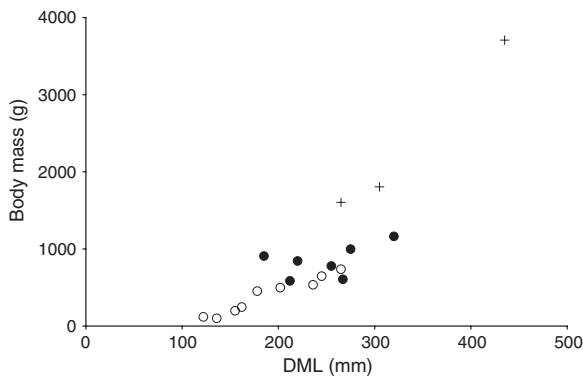


Figure 2 Length–mass relationship of *Ancistrocheirus lesueurii* females (+), males (○) and intersexual males (●). DML, dorsal mantle length.

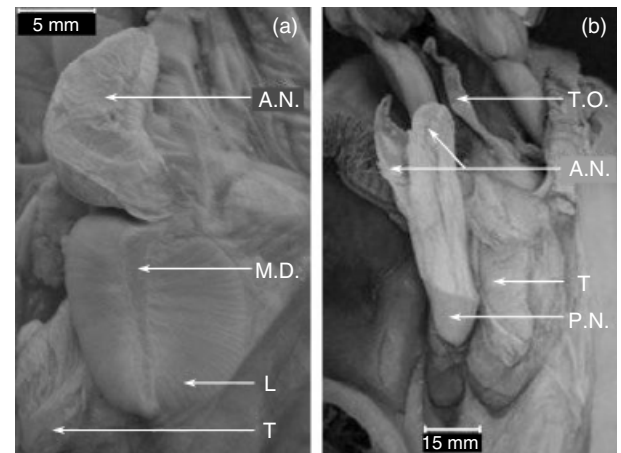


Figure 4 Morphology of intersexual nidamental glands of (a) type two and (b) type three. A.N., anterior nidamental gland; L, lamellae; M.D., medial division; P.N., posterior nidamental gland; T, testis; T.O., terminal organ.

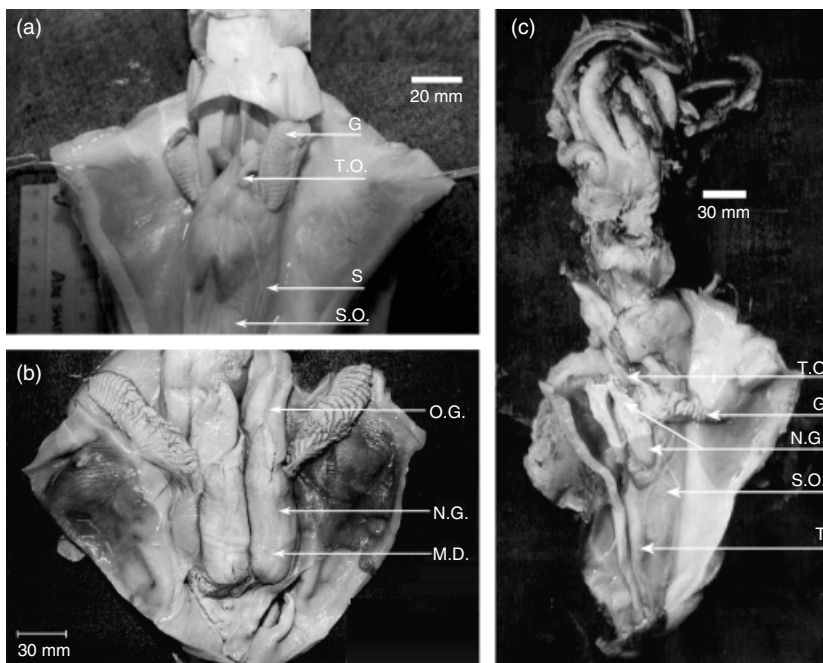


Figure 3 (a) Anterior mantle cavity of a normal male (DML 178 mm); (b) mantle cavity of a female (DML 265 mm); (c) mantle of a feminized male (DML 320 mm) with type three nidamental glands. G, gill; M.D., medial division; N.G., nidamental gland; O.G., oviducal gland; S, spermatophores; S.O., spermatophoric organ; T, testis; T.O., terminal organ.

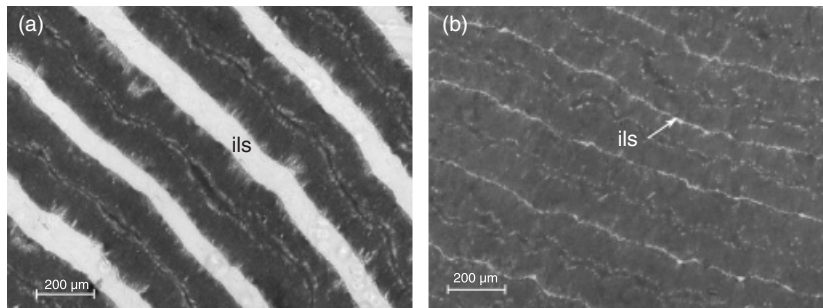


Figure 5 Histological section of the posterior part of the nidamental gland of (a) mature female (DML 435 mm) and (b) intersexual male (DML 320 mm); ils, interlamellar spaces.

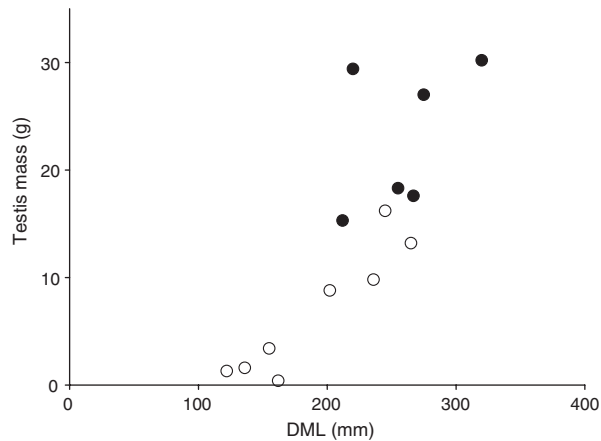


Figure 6 Testis mass and mantle length of normal male (○) and intersexual male (●) *Ancistrocheirus lesueurii*. DML, dorsal mantle length.

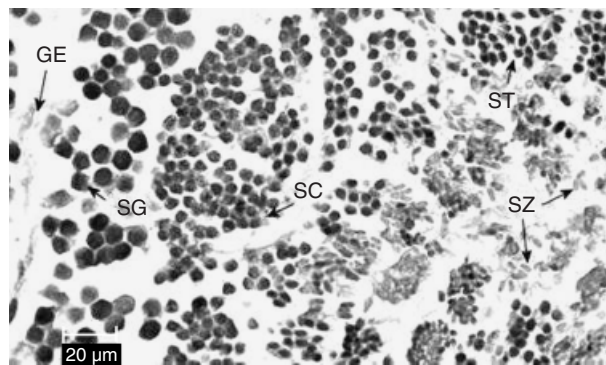


Figure 7 Histological section of the testis of an intersexual male (DML 320 mm). GE, germinal epithelium; SC, spermatocytes; SG, spermatogonia; ST, spermatids; SZ, spermatozoa.

developmental stages of male gametes (spermatogonia, spermatocytes and spermatids) could be distinguished between the lumen and the germinal epithelium (Fig. 7).

In both normal and intersexual males, spermatophore length increased with mantle length (Fig. 8), with the longest spermatophores found in the largest feminized male.

Normal males had significantly smaller spermatophores than intersexual males (Student's *t*-test, unpaired, $P < 0.05$).

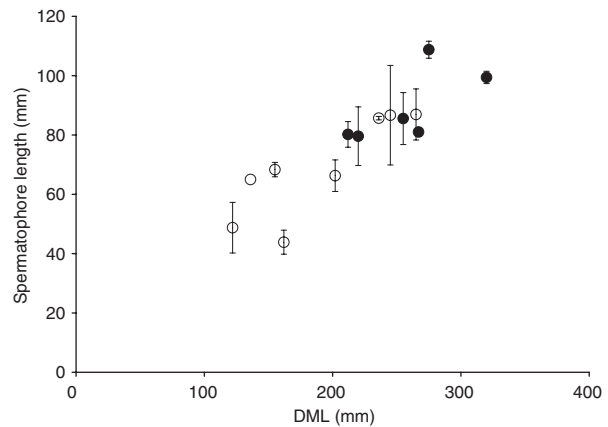


Figure 8 Average spermatophore length (± 1 sd) versus mantle length of (○) normal males and (●) intersexual males. DML, dorsal mantle length

The smallest average spermatophore length (TSL 43.9 ± 4.1) was found in a male with DML 162 mm and the largest (86.9 ± 8.6) in a male with DML 265 mm. In intersexual males the smallest average spermatophore length was 79.6 ± 9.9 mm at DML 220 mm and the largest (108.8 ± 2.9 mm) at DML 275 mm.

Discussion

The occurrence of animals with sexual characteristics intermediate between normal males and females has important implications for the reproductive biology and population structure of *A. lesueurii*. This phenomenon is also known as intersexuality (Zou & Fingerma, 2000). Intersexual animals in general may represent a transitional stage within true sex change, also known as sequential hermaphroditism. Sequential hermaphrodites are protandrous when they first mature as males, or protogynous when they first mature as females (Policansky, 1982). However, intersexuality may also be a developmental abnormality.

Nature of intersexuality

The histology of the nidamental glands in both intersexual male and female *A. lesueurii* is very similar to that of *Loligo*

forbesi (Lum-Kong, 1992), in which the lamellae lie at an angle to the longitudinal axis of the gland and are stacked on top of each other like the leaves of a book. The histology and paired nature of the glands in the intersexual males show that these are true nidamental glands.

In intersexual males the nidamental glands were shorter (6.4–32.4% DML) than in southern African females (26.3–40.4% DML) and in females from the Ionian Sea (31.4–39.6% DML; D'Onghia *et al.*, 1997). Some intersexual males had very immature nidamental glands but in others they were very well developed. The nidamental glands of the largest intersexual male most closely resemble those of females. The presence of only one gland in two of the intersexual males suggests physiological disruption.

Normal males and females show striking sexual dimorphism in size. However, the intermediate size of intersexual males suggests that their relatively large body size is related to intersexuality. Because males mature at 1 year and females only start maturing at that age (Arkhipkin, 1997), it would be interesting to determine whether the age of intersexual males is also intermediate between normal mature males and females.

If true sex change (protandry) occurs in *A. lesueurii*, the change would occur at a size intermediate between males and females, as is indeed shown in these specimens. Sequential hermaphrodites in other animals (fish, echinoderms, polychaetes, crustaceans and molluscs) change sex at the same relative body size, that is 72% of their final body length (Allsop & West, 2003). If the intersexual *A. lesueurii* indeed represent a stage in protandry, sex change would presumably occur at a specific relative size. We do not know what the final DML of the intersexual *A. lesueurii* would have been but, in these *A. lesueurii*, the mantle length of intersexual males was 43–74% of the maximum DML attained by mature females.

Real sex change would involve the presence of primary sexual characters of both sexes, for example an ovotestis, in intersexual individuals. However, histological examination of two intersexual *A. lesueurii* showed normal development of the testis but no developing oocytes, in contrast to protandrous teleosts (Devlin & Nagahama, 2002). Therefore, the intersexual males described here have only secondary sexual female characters, that is nidamental glands and large body size.

Functional implications of intersexuality

Hermaphroditism would be of evolutionary advantage for species with low population density or low motility, because sex change increases the likelihood of finding a mate (Calvo & Templado, 2005). Such a strategy would fit in the life history of *A. lesueurii*, a species that probably lives in low population densities in the eastern south Atlantic (M. R. Lipinski, pers. obs.), but low catches of this species could also be due to sampling bias.

Partial feminization does not seem to be disadvantageous in *A. lesueurii*; in fact it seems to be the reverse. Intersexual males are true males because they have a normally devel-

oped testis, functional spermatophores and a hectocotylus. In addition, the larger body size may increase fitness in comparison with normal males because it is accompanied by significantly larger testes and spermatophores (Figs 6 and 8). On the other hand, an increase in age may be detrimental to fitness (R. E. Young, pers. comm.). The viability of the spermatozoa could not be investigated in these preserved specimens.

Possible causes of intersexuality

Neither intersexuality nor sequential hermaphroditism was known for cephalopods previously. However, non-functional intersexuality and reproductive abnormalities have been recorded in a large variety of other animal groups and for some of these groups the cause has been established.

Various factors are known to cause non-functional reproductive abnormalities and partial sex reversal. Examples of these factors are genetic abnormalities in mysid shrimp (Hough, Bannister & Naylor, 1992), temperature fluctuations during development in fish species that are subject to environmental sex determination (Devlin & Nagahama, 2002), endocrine disrupting chemicals in 150 species of gastropods (Oberdörster & Cheek, 2000), infection by the bacterium *Wolbachia* in isopods (Rousset *et al.*, 1992), and intersexuality caused by viruses, parasites or natural variation in hormone production and/or reception in crustaceans (Pinn, Atkinson & Rogerson, 2001).

Pollution of the environment has recently been identified as the most important cause of endocrine disruption, which can lead to intersexuality. Endocrine disruption may occur when an organism is exposed to certain anthropogenic or natural chemicals, which have the ability to mimic endogenous hormones, antagonize their effects, alter the pattern of their synthesis and metabolism, or modify hormone receptor levels (Soto, Sonnenschein & Chung, 1995, cited by Depledge & Billingham, 1999). Exposure to these substances may affect sexual differentiation and induce sex reversal and/or intersexuality. Endocrine disruption caused by environmental pollution has been documented or hypothesized for fish (Devlin & Nagahama, 2002), molluscs (Depledge & Billingham, 1999), piscivorous birds (Fry & Toone, 1981), alligators (Guillette *et al.*, 1994), amphibians (Dalton, 2002), whales (De Guise, Lagacée & Bédard, 1994) and polar bears (Wiig *et al.*, 1998).

Although cephalopods are known to be suitable hosts for a large variety of parasites (e.g. nematodes; Abollo *et al.*, 1998; González *et al.*, 2003), none were found in the *A. lesueurii* examined and at present it is not possible to evaluate environmental, genetic or viral causes. We could not analyse body tissues for endocrine disruptors because the specimens had been fixed in formalin. However, the oceanic lifestyle of *A. lesueurii* does not make it invulnerable to endocrine disruptors. Several studies have reported the accumulation of pollutants in deep-sea organisms (Takahashi, Tanabe & Kubodera, 1997; Froescheis *et al.*, 2000; Looser *et al.*, 2000; Borghiani & Porte, 2002). Pollutants measured in surface-foraging fish (snoek *Thyrstites atun* and

hake *Merluccius capensis*) and deepwater fish (kingklip *Genypterus capensis*) from the eastern south Atlantic showed that kingklip had much higher concentrations of polychlorinated biphenyls and organochlorine pesticides than snoek and hake (Froescheis *et al.*, 2000; Looser *et al.*, 2000). This suggests that deep-sea animals may be particularly vulnerable to accumulation of these pollutants, which are known to act as endocrine disrupters. In some polluted marine areas, not only individuals but whole populations have been reported to show reproductive abnormalities as a result of endocrine-disrupting chemicals. The fact that intersexual males of *A. lesueurii* were present in significant numbers (44% of males examined were intersexual) suggests that intersexuality in this species may be caused by endocrine disruption (assuming that our sample is representative of the natural population).

As available evidence discounts neither sequential hermaphroditism nor pseudo-hermaphroditism, additional research would be necessary to determine the cause of feminization in intersexual *A. lesueurii*. At present, the absence of true intermediate stages in sex change, that is males with primary female sexual characteristics such as an ovary or oviducts, suggests that the intersexual males described here represent pseudo-hermaphrodites and not a transitional stage within true sex change.

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