Rev Fish Biol Fisheries (2007) 17:455–476
DOI 10.1007/s11160-007-9056-8

RESEARCH PAPER

Ethical and welfare considerations when using cephalopods as experimental animals

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Received: 3 January 2007 / Accepted: 26 February 2007 / Published online: 7 April 2007

Abstract When using cephalopods as experimental animals, a number of factors, including morality, quality of information derived from experiments, and public perception, drives the motivation to consider welfare issues. Refinement of methods and techniques is a major step in ensuring protection of cephalopod welfare in both laboratory and field studies. To this end, existing literature that provides details of methods used in the collection, handling, maintenance, and culture of a range of cephalopods is a useful starting point when refining and justifying decisions about animal welfare. This review collates recent literature in which authors have used cephalopods as experimental animals, revealing the extent of use and diversity of cephalopod species and techniques. It also highlights several major

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issues when considering cephalopod welfare; how little is known about disease in cephalopods and its relationship to senescence and also how to define objective endpoints when animals are stressed or dying as a result of the experiment.

Keywords Animal welfare · Animal ethics · Capture · Cephalopods · Cuttlefish · Handling · Housing · *Nautilus* · Octopus · Squid

Introduction

There is a long tradition of using cephalopods as experimental animals, particularly squid and octopus, in the field of neurophysiology (e.g. Young 1971; Wells 1978). However, more recently, the use of a range of cephalopod species for field and laboratory experiments has increased, largely due to their importance in fisheries and their potential in aquaculture. Experiments using cephalopods range from use of neural and optic material (e.g. Eyman et al. 2003), to tank experiments that manipulate biotic and abiotic growth conditions (e.g. Sykes et al. 2003), to tagging individuals and releasing them into the wild to obtain information about their ecology, biology, and behaviour (e.g. Nagasawa et al. 1993; Gilly et al. 2006). These experiments all seek to obtain information that will contribute to an accurate and informative picture of biology and/or ecology of the animal.

When considering the welfare of vertebrate animals in experiments it is recommended that the three R's (reduction, replacement, and refinement) be considered. This involves ensuring that the number of animals used in the experiments is valid (reduction), considering alternatives to live animals in experiments (replacement), and adoption of experimental methods that minimize distress to the animals (refinement). We recommend that the three R's should be a major consideration when using cephalopods in experiments. When addressing the question of whole animal biology there are limited opportunities to replace animals with alternatives, such as computer simulations and cell cultures. However, replacement is worth considering for species groups which have juveniles that are currently impossible to rear (e.g. ommastrephids and Idiosepiidae). Given the 100% mortality rates of these juveniles in culture conditions, it may be worth considering using alternative cephalopod species, for which we have developed culture techniques, as ''model species''.

Reduction and refinement are important areas to address when planning and designing experiments. Given the need to provide good water quality and live food when maintaining many cephalopods (Table 1), it is typically difficult to hold large numbers of adult cephalopods. As a result logistics will restrict the numbers of animals, however, smaller individuals (small adults and juveniles) can be potentially held in larger numbers. Therefore, reduction in the number of animals can be addressed a number of ways including, ensuring that animals in research facilities are held to answer direct biological results and not only to see if they can be held. For many commercially important species details of maintenance and culture are readily available (Tables 2–8). The number of animals needed in an experiment to determine differences among treatments is a function the variability among replicate animals. Such information is often difficult to obtain, however, an increasing number of publications (Tables 2–8) are presenting results of rigorous experiments. These studies provide estimates of inter-animal variability that is readily usable as a guide for future experimental designs. Refining the methods associated with all aspects of using cephalopods as experimental animals is one of the three R's that experimenters can readily address and should be given full consideration. Refinement based on past experience (as reported in the literature) is the major consideration of this paper.

We have identified existing expertise and literature that outlines techniques for handling and holding cephalopods in different life stages, from embryo to adults (e.g. Teuthoids and Sepioids in Boletzky and Hanlon 1983; Hanlon 1990). This depth of knowledge provides an informed basis upon which cephalopod biologists can justify decisions about the welfare of animals used in scientific endeavours. However, this realization needs to be tempered with an understanding and recognition that cephalopods have unique biological characteristics that need consideration (Table 1). In particular the very short lifespan of most species means that death in captivity

Table 1 General biological characteristics of cephalopod of particular relevance when handling and holding

Biological characteristics	Special consideration
External protection	No protection (except for Nautilus) and the delicate skin is readily damaged by physical contact e.g. handling and contact with the side of tanks. All species are marine and most have limited capacity to tolerate changes to salinity changes.
Mobility	Active species e.g. pelagic species will need to swim constantly, may jet out of tank, and repeatedly hit side of tank. Some benthic species need shelter or hides.
Response to stress e.g. attack, toxic substances, disease	Cephalopods will display a startle and escape response. The copious volumes of black ink should be removed. Self damage can occur through eating of arms and repeated contacting with the side of tanks. Lesions will be evident where damage to the skin has occurred, these lesions may be an early sign of senescence.
Food	All species are carnivores and most require live prey, especially during early life history. Artificial food suitable for cephalopod is not yet available. Cannibalism can occur when insufficient food provided. Prey size is limited by body size rather than mouth size. Prey items up to 150% larger than the juvenile can be captured and eaten.
Life span	Many inshore cephalopod species live for 12 months or less, so adults brought into the laboratory are likely to die in captivity due to natural senescence. Some species will die shortly after egg production or after hatching of juveniles.
Reproductive biology	Range of reproductive traits, with some species producing a single batch of eggs at end of life while others will produce numerous batches. Most cephalopod species produce external eggs that are sheathed and well protected by a mucilaginous coat. A suitable substrate or the presence of an egg mass often needs to be provided to encourage egg deposition. Egg size varies with species, with large egg species being easier to culture in captivity. Larger eggs have longer development times, but can be vulnerable to fungal infections the longer they are held. Removal of the parents is not necessary and in the case of *Octopus* species the females must be left in the tank to care for eggs. Eggs with no maternal care will need to be oxygenated using a gentle flow of water across the eggs.
Respiration	Oxygen is taken up via the gills and skin.
Social behaviour	Some species naturally school, particularly squid, and space and water quality needs to be carefully monitored. Some species are non-aggregative and keeping high densities of mixed genders can cause problems with constant interactions resulting in death.
Early life history	Cephalopods have a short (ca. 5 days) endogenous feeding period during which they must learn to capture prey. Many species suffer extremely high juvenile mortality in a laboratory setting, possibly due to starvation when predation behaviour fails to develop. There is variation in the size and life style of cephalopod hatchlings; small-egged species usually produce planktonic young while large-egged species produce benthic young. The latter have been easier to rear, because the juveniles look and behave as miniature adults capable of jetting, inking and prey capture.
Behaviour	Complex and diverse (Hanlon and Messenger 1996). There will need to an awareness of ''typical'' behaviours for the species being held in captivity. In particular the need for objects to hide under or in, and the interaction among individuals held in the same tanks.

(not initiated by the experimenter) is the norm not the exception, particularly following spawning (e.g. octopus species).

In most countries ethical guidelines for the use of animals in experiments are restricted to vertebrate species. As invertebrates, ethical guidelines for the use and handling of animals in science do not include cephalopods. However, cephalopods have a well developed nervous system (Young 1971; Wells 1962; Budelmann 1995) and display advanced behaviours (Hanlon and Messenger 1996), suggesting that welfare guidelines for these animals are needed. The presence of free nerve endings in the skin suggests that perception of pain is possible and behavioural responses suggest that many cephalopods do respond to pain (Mather and Anderson in press). The concept of pain can be extended to include psychological suffering, and the appropriateness of culture conditions, including behavioural enrichment should be considered (Mather 1986, 2001). Currently, there is no universal standard or legislation concerning the welfare of cephalopods, and the adoption of

Table 2 Examples of recent literature that has used Nautilidae as experimental animals

Species	Collection, Handling, Transport	Housing	Food and Feeding	Eggs, embryos and juveniles	Anaesthetics and Euthanasia	Behaviour	Treatment of Diseases	Tagging and Tracking
N. macromphalus	1, 2, 3	2, 4	2, 5, 6, 7	2, 6, 7		1, 2		3, 4
N. belauensis	2	2	2	2, 8, 9		1, 10, 11		
N. pompilius	1, 2, 12, 13, 14	2, 4, 12, 15, 16, 17, 18	2	2, 17, 19		1, 12, 15, 17		4, 12, 20
Unnamed N. species	12, 16	12, 16, 21		22		12, 22, 23, 24		12, 22, 24

(1) Ward (1987); (2) Hamada et al. (1980); (3) Saunders (1983); (4) Hamada (1987); (5) Ward and Wicksten (1980); (6) Ward (1983); (7) Mikami and Okutani (1977); (8) Okubo et al. (1995); (9) Arnold et al. (1990); (10) Carlson et al. (1984); (11) Saunders (1984); (12) Saunders and Landman (1987); (13) Saunders and Spinosa (1978); (14) Wells and Wells (1985); (15) Zann (1984); (16) Carlson (1987); (17) Fields (2006); (18) Westermann et al. (2004); (19) Arnold et al. (1993); (20) O'Dor et al. (1990a); (21) Spinosa (1987); 22. Boyle and Rodhouse (2005); (23) O'Dor et al. (1993); (24) Ward et al. (1984)

Table 3 Examples of recent literature that has used Sepiida as experimental animals

Life Stage	Collection, handling, and transport	Housing	Feeding	Reproduction	Behaviour	Anaesthetics	Health, disease, and treatment	Tagging and tracking
Eggs	1, 2, 3, 4, 5	6, 7, 4, 8					2, 3	
Juveniles		4, 9, 10, 11, 12, 13, 14	14, 15, 16	17, 18, 19, 20, 21	22			
Adults	23	9, 10, 22, 24, 25, 26, 27	28, 29	5, 9, 19, 30, 31, 32, 33	19, 34, 35, 36, 37, 38	39	21, 24, 40, 41, 42, 43,	44, 45, 46

(1) Blanc and Daguzan (1998); (2) Boletzky (1998); (3) D'Aniello et al. (1990); (4) Minton et al. (2001); (5) Oka (1993); (6) Bouchaud and Daguzan (1989); (7) Cronin and Seymour (2000); (8) Paulij et al. (1991); (9) Correia et al. (2005); (10) Forsythe et al. (2002); (11) Hanley et al. (1998); (12) Koueta and Boucaud-Camou (1999); (13) Sykes et al. (2003); (14) Domingues et al. (2003); (15) Blanc et al. (1998); (16) Moltschaniwskyj and Martínez (1998); (17) Boal and Ni (1996); (18) Boletzky and Roeleveld (2000); (19) Crook et al. (2002); (20) Hanlon and Messenger (1996); (21) Warnke (1994); (22) Sherrill et al. (2000); (23). Forsythe et al. (1991); (24) Hanley et al. (1999); (25) Loi and Tublitz (1999); (26) Sykes et al. (2006); (27) Domingues et al. (2002); (28) Castro and Lee (1994); (29) Domingues et al. (2005); (30) Boletzky (1987); (31) Corner and Moore (1980); (32) Hall and Hanlon (2002); (33) Nabhitabhata and Nilaphat (1999); (34) Adamo et al. (2000); (35) Boal et al. (1999); (36) Castro and Guerra (1989); (37) Lipiński et al. (1991); (38) Quintela and Andrade (2002); (39) Aitken et al. (2005); (40) Castro et al. (1992); (41) Halm et al. (2000)l; (42) Sangster and Smolowitz (2003); (43) Reimschuessel et al. (1990); (44) Ezzedine-Najai et al. (1995); (45) Jackson et al. (2005); (46) Watanuki and Iwashita (1993)

Table 4 Examples of recent literature that has used Sepiolida as experimental animals

Species	Collection, handling, and transport	Housing	Feeding	Eggs, embryos and juveniles	Behaviour
Sepietta spp, *Rossia* spp, *Sepiola* spp, *Euprymna scolopes*	1, 2, 3	1, 2, 3, 4	2, 3, 4, 5	1, 2, 6, 7, 8, 9, 10	2, 5, 11, 12

(1) Summers (1985); (2) Summers and Colvin (1989); (3) Hanlon et al. (1997); (4) Claes and Dunlap (2000); (5) Bergström (1985); (6) Salman (1998); (7) Anderson and Shimek (1994); (8) Boletzky (1975); (9) Yau and Boyle (1996); (10) Arnold et al. (1972); (11) Moynihan (1982); (12) Shears (1988)

Table 5 Examples of recent literature that has used Idiosepiidae as experimental animals

Species	Capture, Handling, Transport	Housing	Feeding	Eggs, embryos and juveniles	Behaviour
Idiosepius biserialis			1		
I. notoides	2, 3	3	2, 3, 4		
I. macrocheir					
I. paradoxus			5	6, 7, 8, 9	
I. picteti					
I. pygmaeus	5, 10, 11		12, 13	6, 8, 14, 15	17, 18
I. thailandicus	19, 20	19, 20	19, 20	20	

(1) Hylleberg and Nateewathana (1991); (2) English (1981); (3) Tracey et al. (2003); (4) Eyster and Van Camp (2003); (5) Kasugai (2001); (6) Kasugai (2000); (7) Kasugai and Ikeda (2003); (8) Natsukari (1970); (9) Yamamoto (1988); (10) Jackson (1992); (11) Moynihan (1983); (12) Jackson (1989); (13) Semmens (1993); (14) Jackson (1993); (15) Lewis and Choat (1993); (16) Van Camp (1997); (17) Roberts (1997); (18) Sasaki (1923); (19) Nabhitabhata (1994); (20) Nabhitabhata (1998)

legislation by scientists is patchy. For example, in the UK *Octopus vulgaris* is included in the legislation, Canada includes all cephalopods, and in Australia and USA legislation is in place for some research institutes in some states. The future implementation of legislation for the ethical use of cephalopods is unclear and research scientists will be responsible for determining the legal requirements for their country and/or research institute when using cephalopods in experiments. For example, the status of cephalopods in the EU legislation for animal ethics is currently under review, and one recommendation is that all cephalopods are included in the legislation.

Legislation aside, there are a suite of reasons that cephalopod research scientists may need to consider the welfare of their study animals. These include moral and ethical issues associated with experimental manipulations and the need to ensure that obtaining information in experiments is with minimal distress to the animals. This becomes important for scientists with limited experience or restricted access to experienced researchers, who may have difficulty obtaining guidance about what may be the ''right'' or suitable method to manage cephalopods, and is critical to maximising the scientific value of animals used in experiments.

On a pragmatic level, experiments obtain information about the biology and ecology of cephalopods that cannot be obtained directly from wild animals (e.g. factors affecting growth and reproduction, movement, and behaviour), by either holding animals in captivity or handling animals prior to release into the wild. In these cases, it is essential that experiments accurately reflect the biology of the species, as there is often an explicit interest in extrapolating these results to wild populations, or at least understanding the processes that shape wild populations. To do this it is vital that the handling and maintenance conditions of these experiments are as close to ''natural'' as possible, therefore animal welfare will be an important element of these experiments. However, cephalopod researchers must also be aware of, and sensitive to, the public perception of their experiments and the animals upon which these experiments are conducted. The natural charisma of cephalopods draws significant public interest (e.g. Anderson 2000), and their complex behaviours are subject to frequent anthropomorphism.

Table 6 Examples of recent literature that has used Loliginidae as experimental animals

Life stage	Capture Handling Transport	Housing	Feeding	Anaesthetics	Treatment of diseases	Artificial fertilization	Tagging and tracking	Behaviour
Eggs/ Embryos	1, 2, 3, 4	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 22, 23, 42, 44, 46, 47			1, 4, 20	21		
Hatchlings/ Paralarvae		1, 2, 4, 5, 6, 9, 10, 16, 17, 18, 19, 24	1, 2, 4, 6, 9, 10, 16, 17, 19, 24, 25, 26, 27, 28, 43	18, 19				
Juveniles/ Adults	29, 30, 31, 32	1, 2, 4, 10, 29, 31, 32, 33, 34, 45	1, 2, 4, 10, 27, 31, 32, 33, 35, 43	1, 31, 36, 41	20, 31, 37, 38		29, 39, 40	32, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58

(1) Lee et al. (1994); (2) Lee et al. (1998); (3) Steer et al. (2003); (4) Walsh et al. (2002); (5) Nabhitabhata et al. (2001); (6) Cardoso et al. (2005); (7) D'Aniello et al. (1989); (8) Gowland et al. (2003); (9) Ikeda et al. (2005); (10) Nabhitabhata (1996); (11) Omar et al. (2001); (12) Oosthuizen et al. (2002a); (13) Oosthuizen et al. (2002b); (14) Paulij et al. (1990); (15) Sen (2004a); (16) Vidal et al. (2002a); (17) Vidal et al. (2002b); (18) Villanueva (2000a); (19) Villanueva (2000b); (20) Forsythe et al. (1990); (21) Crawford (2002); (22) Ikeda et al. (2004a); (23) Fagundez and Robaina (1992); (24) Mladineo et al. (2003); (25) Akiyama et al. (1997); (26) Navarro and Villanueva (2000); (27) Segawa (1993); (28) Villanueva (1994); (29) Gonçalves et al. (1995); (30) Ikeda et al. (2004b); (31) Oestmann et al. (1997); (32) Porteiro et al. (1990); (33) Hanlon et al. (1991); (34) Nabhitabhata and Nilaphat (2000); (35) DiMarco et al. (1993); (36) Garcia Franco (1992); (37) Hanlon and Forsythe (1990); (38) Hanlon et al. (1988); (39) Estacio et al. (1999); (40) Sauer et al. (2000); (41) Messenger et al. (1985); (42) Sen (2005); (43) Segawa (1990); (44) Ito and Sakurai (2001); (45) Segawa (1995); (46) Sen (2004b); (47) Sen (2004c); (48) King et al. (2003); (49) Dimarco and Hanlon (1997); (50) Sauer et al. (1997); (51) Jantzen and Havenhand (2003a); 52. Boal and González (1998); (53) Buresch et al. (2004); (54) Hanlon et al. (2002); (55) Hanlon et al. (1999); (56) Cornwell et al. (1997); (57) Jantzen and Havenhand (2003b)

Table 7 Examples of recent literature that has used Ommastrephidae as experimental animals

Species	Collection, handling, transport	Housing	Feeding	Eggs, embryos and juveniles	Anaesthetics and Euthanasia	Treatment of Disease	Tagging and Tracking
Dosidicus gigas				1			2,3,4
Illex spp (I. argentinus, I. coindetii, I. illecebrosus)	5	5, 6, 7, 8, 9	5, 10	11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21	8, 22		23, 24, 25, 26, 27, 28
Nototodarus spp (N. sloanii and gouldi, hawaiiensis)					29		30, 31
Ommastrephes bartramii				32			33, 34, 35, 36
Sthenoteuthis oualaniensis				32			
Todarodes pacificus	37, 38	39, 40, 41	42	43, 44	45		46

(1) Yatsu et al. (1999a); (2) Bazzino et al. (2005); (3) Markaida et al. (2005); (4) Yatsu et al. (1999b); (5) O'Dor et al. (1977); (6) Bradbury and Aldrich (1969a); (7) Bradbury and Aldrich (1969b); (8) Portner et al. (1993); (9) O'Dor et al. (1982a); 10. O'Dor et al. (1980); 11. Sakai and Brunetti (1997); (12) Sakai et al. (1997); (13) Sakai et al. (1998); (14) Sakai et al. (2004); (15) Sakai et al. (1999); (16) Boletzky et al. (1973); (17) O'Dor et al. (1982b); (18) Durward et al. (1980); (19) O'Dor et al. (1985); (20) Balch et al. (1985); (21) O'Dor et al. (1986); (22) O'Dor et al. (1990b); (23) Brunetti et al. (1996); (24) Brunetti et al. (1997); (25) Dawe et al. (1981); (26) O'Dor et al. (1979); (27) Webber and O'Dor (1985); (28) Webber and O'Dor (1986); (29) Lykkeboe and Johansen (1982); (30) Sato (1985); (31) Yamada and Kattho (1987); (32) Sakurai et al. (1995); (33) Nakamura (1991); (34) Nakamura (1993); (35) Tanaka (2000); (36) Tanaka (2001); (37) Bower et al. (1999); (38) Flores et al. (1976); (39) Flores et al. (1977); (40) Mikulich and Kozak (1971a); (41) Mikulich and Kozak (1971b); (42) Soichi (1976); (43) Ikeda et al. (1993); (44) Ikeda and Shimazaki (1995); (45) Sakurai et al. (1993); (46) Mori and Nakamura (2001)

Table 8 Examples of recent literature that has used Octopodidae and other octopods as experimental animals

	Collection, handling and transport	Housing	Feeding	Eggs, embryos and planktonic stages	Anaesthetics and Euthanasia	Health, disease, and treatment	Tagging and tracking
Coastal octopods	1, 2, 3	4, 5, 6, 7, 8, 9, 10, 11, 12	5, 7, 12, 13, 14, 15	16, 17, 18, 19, 20, 21, 22, 23, 24	10, 25, 26, 27, 28, 29	30, 31, 32, 33, 34	35, 36, 37
Deep-sea and cold-adapted octopods	38, 39, 40	38, 39, 40	38, 39, 40, 41	38, 42			
Pelagic octopods	43	44, 45, 46, 47	44, 48				

(1) Voight (1988); (2) Sánchez and Obarti (1993); (3) Smale and Buchan (1981); (4) Van Heukelem (1977); (5) Forsythe and Hanlon (1980); (6) Boyle (1981); (7) Forsythe (1984); (8) Hanlon and Forsythe (1985); (9) Forsythe and Hanlon (1988); (10) Anderson (1996); (11) Mather and Anderson (1999); (12) Anderson and Wood (2001); (13) Joll (1977); (14) Garcia Garcia and Cerezo Valverde (2006); (15) Segawa and Nomoto (2002); (16) Itami et al. (1963); (17) Marliave (1981); (18) Snyder (1986); (19) Boletzky (1989); (20) Forsythe and Toll (1991); (21) Villanueva (1995); (22) Iglesias et al. (2004); (23) Villanueva et al (2004); (24) Okumura et al (2005); (25) Batham (1957); (26) Dew (1959); (27) Brough (1965); (28) Forsythe and Hanlon (1985); (29) Seol et al. (2007); (30) Hanlon et al. (1984); (31) Budelmann (1988); (32) Adams et al (1989); (33) Forsythe et al (1990); (34) Pascual et al. (2006); (35) Robinson and Hartwick (1986); (36) Anderson and Babcock (1999); (37) Domain et al. (2002); (38) Wood et al. (1998); (39) Daly and Peck (2000); (40) Hunt (1999); (41) Collins and Villanueva (2006); (42) Boletzky (1994); (43) Seibel et al. (1997); (44) Lacaze-Duthiers (1892); (45) Boletzky (1983b); (46) Bello and Rizzi (1990); (47) Packard and Würtz (1994); (48) Young (1960)

On a moral basis, as scientists and biologists using these animals in experiments, we have a responsibility to be proactive about minimizing the distress of individuals in our care and to better understand how we can care for welfare of the animals that we are using in experiments. We recommend that collecting cephalopods humanely as possible, e.g. basket traps for cuttlefish, jigs for squid, and pots for octopuses. An anaesthetic that is commonly and successfully used on cephalopods is magnesium chloride (Messenger et al. 1985; Scimeca and Forsythe 1999). The best method for euthanising cephalopods varies among species, but the pool of information is limited. Boyle (1991) recommends decapitation; however, this is not always easy with very small or large animals, or onboard on a rolling ship. Decapitation is completely unsuitable when intact specimens are need for museum collections or collection of statoliths, as these sit at the back of the head. Chilling is suitable for tropical and warm temperate species (Anderson 1996; Moltschaniwskyj and Semmens 2000), but is not useful for cold-water species. Recent studies on fish demonstrate that live chilling is stressful (Lambooij et al. 2006). Over-anaesthesia is useful when decapitation or chilling are not logistically possible. Several anaesthetic agents have been used with success, including an isotonic solution of $MgCl_2$ (e.g. Messenger et al. 1985; Cornwell et al. 1997; Bartol 2001; Thompson and Kier 2001), although this does not work on some *Octopus* species (Anderson 1996). An alternative is ethanol with increasing concentrations from 1 to 5% over a period of hours (Anderson 1996), or clove oil (Seol et al. 2007). Whatever the end use of the animals, euthanising cephalopods should be done as rapidly as possible and decapitation and overdose of anaesthetics are suitable methods.

Given that welfare considerations of cephalopods is relatively new, particularly in relation to capture and culture (this includes handling, housing, maintenance, and rearing), this review has compiled literature that provides details of using cephalopods as experimental animals. Cephalopods are a diverse group of animals and it is not possible to provide a single set of guidelines or rules with respect to capture and culture of cephalopods as a group, or even across all life stages. Furthermore, it is not possible to provide strict guidelines about techniques or methods that minimize distress and maximize welfare, especially since limited knowledge is available or published. Published work provides a starting point, with techniques and approaches that have worked, but these techniques may be further refined especially as more information about a species comes to light. The aim of this paper is to identify welfare issues that researchers using cephalopods in experiments should consider (Table 1), and to provide sources of information that can help in making the best possible decision (Tables 2–8). The information is designed to help those scientists with limited experience or with little access to experienced researchers. It will also help research scientists needing to apply for permission from ethics committees to use cephalopods and be able to provide evidence to justify welfare decisions.

Nautilidae

Three species of *Nautilus* have been maintained in captivity over the past 30–40 years (Table 2). As a result there is a reasonable volume of information about collection, handling, and housing of individuals, as well as basic aspects of their biology (Table 2). Saunders and Landman (1987) provide the best overview of collection, maintenance, and rearing of *Nautilus* in aquariums, including housing systems. A newer publication that provides detailed specifics on the conditions and infrastructural requirements for optimum rearing in aquarium settings and for general aspects of *Nautilis pompilius* husbandry is provided by Fields (2006). Boyle and Rodhouse (2005) provide a good general summary of many facets of *Nautilus* species biology, covering form and function, ecology, predation, growth, reproduction, activity, and fisheries.

Natural growth rates of *Nautilus* are available for both wild and lab/aquarium held animals (e.g. Saunders 1983). Juvenile *N. belauensis* have the capacity to add 0.1 mm of shell per day at the ventral circumference, but this rate decreases rapidly as individuals approach maturity. Individual chamber formation is estimated to take >100 days to >1 year. Similarly, the period required for an individual animal to reach sexual maturity varies across species and individuals with a range of 2.5–15 years. Other studies by Ward (1983) and Westermann et al. (2004) review laboratory growth rates for *N. macromphalus* and *N. pompilius*, respectively and relate them to wild caught animals for age estimation.

A clear gap in our knowledge of maintaining *Nautilus* is assessment of health, besides using discoloration of the mantle and loss of ability to maintain buoyancy little is known about disease and health issues. Research is required on the best methods for euthanizing individuals in apparent poor health.

Sepiida

Due to their benthic ecology and tolerance of handling cuttlefish adapt well to life in captivity (Hanlon 1990). Methods of transport, housing, and culture of cuttlefish are reasonably well established (Forsythe et al. 1991, Table 3). One species in particular, the European common cuttlefish *Sepia officinalis*, has been studied and maintained in captivity for many years and cultured through multiple generations (Schröder 1966; Pascual 1978; Boletzky 1979; Forsythe et al. 1994). More recently, several other species have also been cultured through multiple generations, including the needle cuttlefish *Sepiella inermis* (Nabhitabhata 1997) and pharoah cuttlefish *Sepia pharaonis* (Minton et al. 2001).

Due to the ease of maintaining cuttlefish in captivity, much information on sepiid growth and behaviour has been obtained from captive individuals (Boal et al. 1999; Domingues et al. 2006). Unfortunately, few studies have related their captive conditions to the likely field environments experienced by wild individuals and this remains a significant area needing further investigation to ensure that laboratory studies are relevant to natural ecology and life history of species. Boletzky (1983a) provides a thorough review of the biology and ecology of *S. officinalis* and more recent studies on wild species include juvenile growth rates (Challier et al. 2002, 2005; Minton 2004), reproductive biology (e.g. Gabr et al. 1998), life cycles (e.g Guerra and Castro 1988), and behaviour (e.g. Aitken et al. 2005). Other areas of research specifically related to ethics that require further investigation include a critical examination of appropriate euthanasia, anaesthesia and disease treatment methods and non-invasive ways to accurately assess condition, well-being, and stress levels of individuals.

Aspects of sepiid biology that are of particular relevance to maintaining captive individuals include: their social behaviour and habitat requirements, as many species show dominance hierarchies, cannibalism or territoriality especially when reproductively active or in crowded conditions (Boal et al. 1999); dietary requirements, which are poorly understood, particularly during the early life stages when individuals require live food and are voracious feeders (Sykes et al. 2006); and water quality requirements, as cuttlefish are susceptible to skin ulceration and buoyancy malfunction in response to poor water quality and bacterial infection (Forsythe et al. 1991; Sherrill et al. 2000).

Sepiolida

The sepiolids have attracted a lot of attention from a number of research teams because of the symbiotic relationship between these animals and light-producing *Vibrio* spp. hosted within the light-organ (see review McFall-Ngai 1999). Given their relatively solitary nature and benthic mode of life, large eggs and large benthic juveniles, it has been relatively easy to culture a number of sepiolid species through several generations (Sinn et al. 2006). Detailed descriptions of culture methods, including collection, transport, housing and reproduction, are available for *Euprymna scolopes* (Hanlon et al. 1997), *Rossia pacifica* (Summers and Colvin 1989), and five *Sepiola* spp. (Bolezky et al. 1975). With careful handling and correct packing live adults and eggs of many sepiolids have been flown half-way around the world with excellent results.

Details of the biology and growth of wild animals are limited, largely due to their nocturnal and cryptic behaviour. The well-hidden eggs are rarely seen in the natural environment. Estimates of growth from natural populations have yet to be obtained due to the lack of daily growth increments on the statoliths and absence of other hard structures (Moltschaniwskyj and Cappo, in press). As much of our knowledge of the biology of these animals is being obtained from captive populations it is critical to take careful consideration of culture conditions and husbandry is made if we are to extrapolate information to wild populations (Table 4).

There are several issues to consider when culturing these species. Every 24 h, at first light, sepiolids release a high number of *Vibrio* from the light organ into the seawater. As a result, in recirculating seawater systems, the *Vibrio* levels in the seawater can reach reasonably high concentrations. It is not clear what the consequences for the health of the sepiolids are, but there is no evidence in the literature that this impacts negatively on their growth and survival. If the high densities of *Vibrio* are of concern then it is possible to reduce the density of *Vibrio* in the water using UV sterilisers. However, use UV sterilisation with caution and for limited periods, as there is the possibility of killing the biofilm in the biofilter.

Another issue that needs to be considered is that these species use a sand coat adhered to the outside of the animal and bury themselves into the soft substrate during daylight hours. Although providing sand for burying may not be essential for successful culture, the lack of available burying substrate could potentially cause increased stress (e.g. Mather 1986). The addition of sand to the tanks can cause problems with maintaining water quality and cleanliness, especially from rotting debris from prey items. On the other hand, bacteria flora building up in the sand may effectively provide a type of ''biofilter' in the tank.

Idiosepiidae

There are no papers that explicitly describe handling or care of the species of *Idiosepius*. Most of the following information is from papers that have used these species in their research; to date five of the seven described species have been collected and held in aquaria. Research has focussed on aspects of the biology of both wild and captive animals, in particular growth (Jackson 1989; Pecl and Moltschaniwskyj 1997), reproduction (Table 5), and behaviour (Table 5). For the other two species, only species descriptions are available (*I. macrocheir* and *I. picteti*). A review of the biology and ecology of this genus considers the issues and specialisation of this mini-maximalist, the smallest of the cephalopod species (Boletzky et al. 2005).

It is worth noting that adults of these species are extremely amenable to collection and maintenance, and will readily mate and deposit eggs in captivity. However, the juveniles have so far proven impossible to hold for more than five days; therefore the lifecycle has not been closed for any of the species in this group.

Loliginidae

Due to their economic value to inshore fisheries and the relative ease of capture and holding of a range of life history stages, there have been a very large number of studies that have used loliginid squids as experimental animals. Three substantial overviews of maintenance of loliginid squid have been produced (Boletzky and Hanlon 1983; Hanlon 1987, 1990). These documents are a valuable starting point to anyone wishing an overview of techniques and information about handling and holding these species. The literature in Table 6 focuses on publications since 1990 that provide additional information that complements and extends the knowledge in these earlier reviews.

Over the last six years there has been an increase in the number of species that are used for experimental work. Species which have been used extensively in experiments include: *Alloteuthis subulata, Doryteuthis gahi, D. opalescens, D. pealeii, D. plei, D. sanpaulensis, Heterololigo bleekeri, Loligo forbesi, L. reynaudii, L. vulgaris, Lolliguncula brevis, Sepioteuthis australis, S. lessoniana, S. sepioidea, Uroteuthis chinensis, U. duvauceli, U. noctiluca*, and *Uroteuthis* sp. There is extensive information available on holding and maintaining loliginid squid in captivity during all life history stages. Further, as more research teams are setting up or using land-based facilities to conduct experiments involving loliginid squids, it is evident that a diversity of seawater systems, flow through and recirculating, may be successfully used (Table 6).

Research over the last decade has provided more valuable biological detail of particular value when rearing these animals. Some examples include, the role of temperature (e.g. Oosthuizen et al. 2002a), light intensity (e.g. Ikeda et al. 2004a), salinity (e.g. Sen 2005), ionic composition of seawater on embryo growth and viability (e.g. D'Aniello et al. 1989); and rates and causes of embryonic abnormalities (e.g. Oosthuizen et al. 2002b; Gowland et al. 2003). There has also been a significant increase in the knowledge of diet and nutrition of juvenile loliginids (e.g. Vidal et al. 2002a and b).

The increase in tagging and tracking of wild loliginids means that issues of how to handle individuals are going to be critical to the success of these projects (Table 6). Such research techniques need to maximise the survival of animals upon release and ensure that data retrieved realistically represents what occurs in the wild. For example, the use of antibiotics (2–4 ml of 6 mg/ml tetracycline) at the time of tagging may benefit survival and tag retention (Moltschaniwskyj and Pecl this issue). Types of tags used include spaghetti tags inserted in the mantle or fin (Sauer et al. 2000; Moltschaniwskyj and Pecl this issue), and acoustic tags (Pecl et al. 2006).

A considerable volume of work on wild populations and individuals provides a strong base upon which experimenters can assess the performance of captive-reared animals, especially growth rates and behaviours. There is an extensive body of work on estimating growth rates for a range of loliginid squids (Jackson 2004), including measures of spatial and temporal variability. This provides a useful basis for determining what growth rates in captivity may be expected. The importance of considering captive conditions is highlighted when validation of statolith incremental structure has been conducted using captive reared animals (Jackson 2004). The use of both tagging and photographic information of wild squid has allowed an assessment of the behaviours or absence of certain behaviours in captive individuals. Hanlon and Messenger (1996) provide descriptions of behaviours associated with feeding, reproduction, and general inter-individual interactions. More recent work that is relevant to captive animals is provided in Table 6.

Ommastrephidae

The ommastrephid squids are large, oceanic species that undertake migrations between feeding and spawning grounds over thousands of kilometres. Their significant commercial importance has resulted in considerable interest in their biology and ecology (e.g. *Illex* sp.). However, their large size and continuous, active swimming make them one of the hardest groups of cephalopods to maintain in captivity. They do not hover in the water column as many sepiids and loliginids do and thus they require much larger holding tanks. Many ommastrephids also have strong cannibalistic tendencies.

Ommastrephids have not yet been successfully reared from eggs. Females produce large, gelatinous, neutrally buoyant egg masses that are difficult to find in the wild. However, techniques of artificial fertilization have allowed hatchlings of a number of ommastrephid species to be produced. Unlike many of the cephalopods discussed earlier, newly hatched ommastrephids are not functional adults; hatchlings are very small paralarvae referred to as rhynchoteuthions. Their feeding tentacles are fused into a proboscis, resulting in a diet and mode of food capture that is probably unique among cephalopods during these early stages. Feeding of these early stages has never been successful, and thus the life cycle has yet to be closed for any species.

Nevertheless, there is a significant amount of information available about certain aspects of ommastrephid life that will be of value when optimising captive conditions and conducting experiments (Table 7). This information includes details of the capture and transport of adults, the holding of eggs and observations of the rhynchotheution paralarvae, and maintenance of adults in tanks (Table 1). Researchers have successfully tagged and tracked of a number of species; details of these techniques are readily available (Table 7). For 19 of the 21 Ommastrephidae species growth rates of wild individuals has been estimated using statoliths (Arkhipkin 2004), providing a strong basis for assessing the growth rates of captive animals.

Octopodidae and other octopods

There is a long history of using coastal octopus species of the family Octopodidae for experiments in behavioural, physiological, and ecological studies, probably because this group of cephalopods is best adapted to laboratory conditions. This is due, in part, to their benthic mode of life, reclusive behaviour, and reduced swimming activity in comparison with other cephalopod groups. Recent interest in octopus as biomedical and aquaculture species has resulted in a refinement of handling and culture methods (Table 8). Studies of wild octopus populations, exploring aspects of biology, ecology, and fisheries, use traditional fishing methods, *in-situ* observations, and mark-recapture techniques with internal and external tags. This is currently the only group of cephalopods covered by Ethic Guidelines in the UK.

Reviews of information about how to maintain, rear, and culture inshore large-egged octopus species of the family Octopodidae with benthic juveniles is a function of research done during the 1980s (Boletzky and Hanlon 1983; Forsythe 1984; Forsythe and Hanlon 1988). Inshore octopus species with small eggs have a delicate planktonic stage ranging from three weeks to six months depending on temperature and species, which requires special handling methods (Table 8). Rearing benthic juveniles to adult stages for all inshore species of Octopodidae are similar for small- and large-egg species. There are species-specific requirements, as preference for temperature ranges, diurnal or nocturnal activity patterns, size and quality of food, and breeding behaviour.

In comparison with the coastal species of the family Octopodidae, little information exists for the deep-sea, polar, and pelagic octopod species represented by more than 10 octopod families. Considerably less is known about the cirrate octopods as well as families of deep-sea and cold-adapted incirrate octopods due to the difficulties of collecting and holding these cephalopods. They have very specific requirements for food, low temperature, and light levels, and high water pressure (Table 8). Pelagic octopod species have been maintained for very short periods of time, less than two weeks, and their rearing requirements are practically unknown (Table 8).

Deep-sea cephalopods

There is relatively little information on the use of deep-sea cephalopods in laboratory studies, due to difficulties in collecting and maintaining them under suitable conditions of light and temperature. Deep-sea sepiolids have been reared (Summers and Colvin 1989); however, no deep-sea squid species has been maintained for extended periods in captivity. Methods for collection and laboratory maintenance of deep-sea octopods, under suitable conditions of low light and temperature levels are available for the cirrate (Hunt 1999) and incirrate (Wood et al. 1998) octopods. Most deep-sea cephalopods seem to be long-lived species with low fecundity rates making their populations particularly vulnerable to deep-sea fishing activities (Collins and Villanueva 2006).

Concluding thoughts

It is evident that over the past 10 years an extensive volume of work done has used cephalopods as experimental animals (Tables 2–8). As a result of this research, a strong knowledge base is developing about a diversity of species and techniques. This information should guide scientists in refining their methodologies and approaches when using cephalopods in experimental systems. Refinement of experimental techniques reduces the stress of the investigation on the animals. Such refinement is achievable through careful consideration of the experimental design and procedures, housing conditions, and handling. Experiments should also be planned keeping in mind how you will monitor, assess, and manage impacts; and what procedures can be used to identify and respond to unforeseen complications. Adequate and suitable methods of euthanasia will also be points for consideration, especially when collecting animals.

Explicitly identifying how to assess welfare, the exact cause of stress, and when to terminate experiments will pose the greatest challenge to biologists using cephalopods as experimental animals. As a result of work to date with cephalopods we are gaining significant insights into their capacity to respond in adverse ways that suggests a capacity to perceive pain, suffering, and stress (Mather and Anderson in press). In a recent review of issues in fish welfare, Huntingford et al. (2006) highlighted the fact that wild fish experience stress and will suffer damage in the natural environment. Consequently, there is a conflict between what animals experience in the wild and the assessment of welfare and condition when caring for animals in captivity; we can say the same for cephalopods. Wild animals will suffer damage and stress associated with natural processes, e.g. large scale migrations, predation, interspecific and intraspecific interactions. However, in experimental conditions we expose animals to a different set of stressors and factors causing damage, which need to be minimised. One resource currently available to scientists for use as an assessment tool is a body of work on cephalopod behaviour derived from both wild and captive studies (reviewed by Hanlon and Messenger 1996, recent work in Tables 2–8). Therefore, while we continue to build upon other areas of knowledge which we are lacking, normal behaviours associated with locomotion, feeding and reproduction provide a powerful tool in the assessment of cephalopod welfare.

While disease does not cause senescence, disease is often associated with senescence (Anderson et al. 2002). Given the short life span of cephalopods a persistent question is how we identify and separate natural processes that result in senescence from health problems associated with captive conditions and handling. Tables 2–8 clearly highlight just how little we know about the health of and diseases states in these animals. There is some work on the octopus *Eledone cirrhosa* that suggests a linkage between stress and health in cephalopods (Malham et al. 2002). Furthermore, the interaction of stress and health in cephalopods is likely to be as complex as it is for fish (Huntingford et al. 2006). Evidence of disease is rarely seen in captive populations and because of this, some cephalopod species are thought to be resistant to disease (e.g. *Sepia pharaonis*, Minton et al. 2001). As a result, we know very little about causes of disease, disease progression, and the capacity of immune systems to deal with disease in cephalopods. There is anecdotal information about the occurrence of extensive skin lesions in squid by fishers, but is not clear what association the presence of these lesions has with natural senescence processes.

Given that cephalopods are invertebrates, their inclusion in animal welfare legislation is the exception not the rule; however this situation is seriously being re-considered by a number of countries. Once challenged by animal welfare legislation, cephalopod biologists will find it difficult to provide evidence and standards for techniques to collect, hold, and kill animals. Few studies that have used cephalopods as experimental animals have had to justify their decisions about animal welfare to an independent body. This is starting to change and it will be increasingly important that biologists can develop a set of welfare indicators against which we can justify decisions about experimental protocols and methods.

Not addressed in this review, but of equal importance is the issue of ecological or environmental ethics; this includes the taking of sustainable numbers of eggs, juvenile, and adults from wild populations in a way that minimizes impact to the ecosystem. This is an issue, given the collateral damage associated with the use of trawl gear to collect or sample cephalopods. It is estimated that 60–100% of cephalopods that manage to escape otter trawls will die (Broadhurst et al. 2006). Again there are no standards or guidelines for collection currently available and it is possible that in the future, scientists will have to argue that the numbers they plan to remove from the wild and the methods of collection not only have minimized impact on the animals, but also have minimal impact on the populations and environments. We recommend that targeted collection methods are preferentially used e.g. pots for octopus, jigs for squid, and hand nets for sepioids. These will ensure that both the stress on the animals is minimized and that there is limited damage to the environment. Estimating the population size of the most accessible of cephalopods (loliginids) is difficult, even when there is an established fishery (e.g. Lipinski and Soule this issue). Collection from populations that may be at risk of over exploitation e.g. giant cuttlefish in Australia or the mimic octopus in Indonesia, highlight the need to balance protection of wild populations and the benefits of developing culture techniques. Without a doubt it will be necessary to use existing studies and knowledge base as the starting point in justifying how biologists address issues of welfare and ethics (animal and environmental) when using cephalopods as experimental animals.

Acknowledgements This paper was produced as a result of a workshop held as part of CIAC '06 on Feb 2–3 2006, in which we discussed issues associated with using cephalopods as experimental animals. We would like to thank the School of Aquaculture, University of Tasmania for hosting the workshop. JEARM's participation in the CIAC 2006 Symposium was funded by the Provost's Office for Graduate Studies (USP), FAPESP, and CAPES/PROAP. RV was supported by the Centre de Referència de Recerca i Desenvolupament en Aqüicultura, CIRIT, Generalitat de Catalunya and the Programa para Movilidad de Investigadores of the Spanish Ministry of Science.

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