Combining field and laboratory study of Nautiluses enhances our understanding of their behavioral ecology

Jennifer Basil

Laboratory for Invertebrate Behavior and Ecology
Evolution, Ecology, and Behavior Program
CUNY Graduate Center
AREAC Aquatic Center

NOAA, Nautilus workshop, 2014

Pimm, *Science*, May, 2014

- **“We are on the verge of the sixth extinction. Whether we avoid it or not will depend on our actions”**
  - Species of plants and animals are becoming extinct at least 1000 times faster than before humans arrived on the scene.
- Nautilus survived 5 mass extinctions – it is up to us to ensure they survive this.
- *A main goal in our laboratory is to enhance our understanding of their mari-culture and biology to contribute to conservation efforts.*

Habitat loss is one reason

- Invasive species
- Climate change
- Anthropogenic effects
- Overfishing
- How is Nautilus not on the vulnerable list?
- What can we learn about pressures in their ecology that can inform conservation efforts? A combined approach.
  - E.g., What is affecting Juvie survivial?
  - E.g., is culturing even feasible?

LIBE lab: Synthetic Approach

- 1) Ecological hypotheses – based upon natural history
- 2) Comparative approach
- 3) Laboratory and field study
    - Focused study to understand basic biology: reproduction, foraging, environmental exploration.
    - Then test again in field.
    - *Internal and external validity*

Synthetic Approach

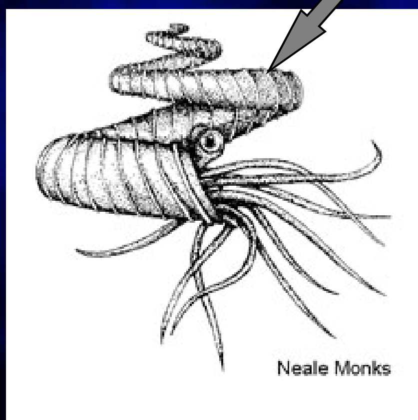
- 1) Ecological hypotheses
- 2) Comparative approach
- 3) Laboratory and field study

Synthetic Results

- First evidence for learning in this understudied, but important, group of animals.
- Characterize innate behaviors.
- Characterize plastic behaviors.
- Comparative study: behavior evolution.
- *Mariculture: keeping animals healthy, how foster breeding?*

Live slow, die old – this is the "problem".

Buoyancy
Stability
Pressure Tolerance



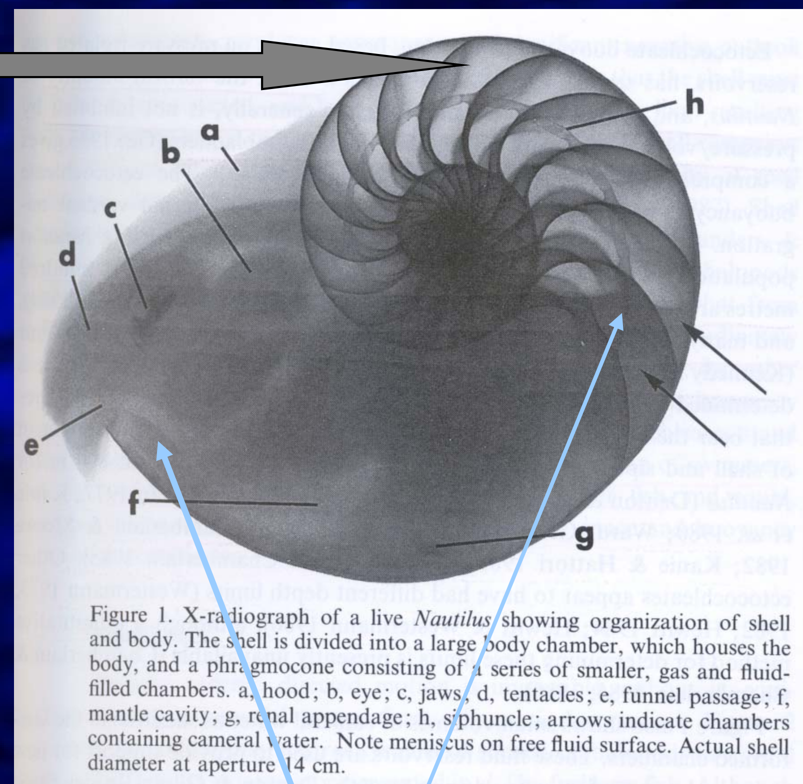
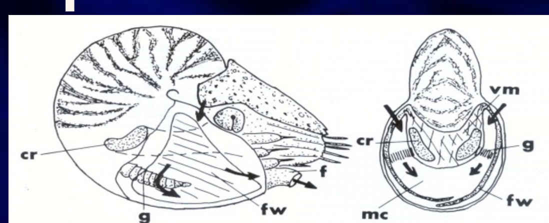


Figure 1. X-radiograph of a live *Nautilus* showing organization of shell and body. The shell is divided into a large body chamber, which houses the body, and a phragmocone consisting of a series of smaller, gas and fluid-filled chambers. a, hood; b, eye; c, jaws; d, tentacles; e, funnel passage; f, mantle cavity; g, renal appendage; h, siphuncle; arrows indicate chambers containing cameral water. Note meniscus on free fluid surface. Actual shell diameter at aperture 14 cm.

Small mantle
Little propulsive muscle
Drag



Buoyancy/Mass

Chamberlain, 1991

Recent care publications:
EU Guidelines for Cephalopods

Invert Neurosci (2014) 14:13–36
DOI 10.1007/s10158-013-0165-x

REVIEW ARTICLE

Cephalopods in neuroscience: regulations, research and the 3Rs

Graziano Fiorito · Andrea Affuso · David B. Anderson · Jennifer Basil · Laure Bonnaud · Giovanni Botta · Alison Cole · Livia D'Angelo · Paolo De Girolamo · Ngaire Dennison · Ludovic Dickel · Anna Di Cosmo · Carlo Di Cristo · Camino Gestal · Rute Fonseca · Frank Grasso · Tore Kristiansen · Michael Kuba · Fulvio Maffucci · Arianna Manciocco · Felix Christopher Mark · Daniela Melillo · Daniel Osorio · Anna Palumbo · Kerry Perkins · Giovanna Ponte · Marcello Raspa · Nadav Shashar · Jane Smith · David Smith · António Sykes · Roger Villanueva · Nathan Tublitz · Letizia Zullo · Paul Andrews

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Abstract Cephalopods have been utilised in neuroscience research for more than 100 years particularly because of their phenotypic plasticity, complex and centralised nervous system, tractability for studies of learning and cellular mechanisms of memory (e.g. long-term potentiation) and anatomical features facilitating physiological studies (e.g. squid giant axon and synapse). On 1 January 2013, research using any of the about 700 extant species of "live cephalopods" became regulated within the European Union by Directive 2010/63/EU on the "Protection of Animals used for Scientific Purposes", giving cephalopods the same EU legal protection as previously afforded only to vertebrates. The Directive has a number of implications, particularly for neuroscience research. These include: (1) projects will need justification, authorisation from local competent authorities, and be subject to review including a harm-benefit assessment and adherence to the 3Rs principles (Replacement, Refinement and Reduction). (2) To support project evaluation and compliance with the new EU law, guidelines specific to cephalopods will need to be developed, covering capture, transport, handling, housing, care, maintenance, health monitoring, humane anaesthesia, analgesia and euthanasia. (3) Objective criteria need to be developed to identify signs of pain, suffering, distress and lasting harm particularly in the context of their induction by an experimental procedure. Despite diversity of views existing on some of these topics, this paper reviews the above topics and describes the approaches being taken by the cephalopod research community (represented by the authorship) to produce "guidelines" and the potential contribution of neuroscience research to cephalopod welfare.

Graziano Fiorito, Jennifer Basil, Frank Grasso, Michael Kuba, Nadav Shashar and Paul Andrews have contributed equally to this work.

In <u>Cephalopod Culture,</u>

Iglesias et al, eds.

GJ Barord

Chapter 10
Nautilus

Gregory J. Barord and Jennifer A. Basil

Abstract Nautiluses are remnants of an ancient lineage that dates back nearly 500 million years. Extant nautiluses still exhibit many traits characteristic of the ancestral species. Nautilus culture systems should therefore take into account both the similarities between nautiloids and modern coleoids and the differences. Nautilus culture systems should be designed to maintain excellent water quality through effective filtration to promote good health. Nautiluses and coleoids differ primarily in their reproductive strategies. Whereas most coleoids are fast growing and semelparous, nautiluses grow slowly, mature later, and are iteroparous. Therefore, nautiluses may necessitate several years of care before becoming sexually mature. Successful reproduction and egg laying by a female yield only a maximum of ten eggs which take up to 1 year to develop and hatch. Currently, nautilus hatchlings have only been reared up to 1 year. The future of nautilus culture systems depends upon a better understanding of both wild and captive reproduction. The success of these culture systems would open up a brand new area of research utilizing different age groups and generations to investigate current and novel questions.

Keywords *Nautilus* culture · *Nautilus* husbandry · *Nautilus* reproduction · *Nautilus* disease · Cephalopod culture

10.1 Background

The nautilid lineage may have existed for more than 500 million years (Ward 1987; Hanlon and Messenger 1996; Strugnell and Lindgren 2007) though the most recent estimation is 416–480 million years (Kröger et al. 2011). Today, nautiluses are grouped under two different genera, *Nautilus* and *Allonautilus* (Ward and Saunders 1997). Throughout the chapter, "nautiluses" will refer to all species of nautiluses

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G. J. Barord (✉) · J. A. Basil
Biology Department, Brooklyn College, City University of NY Graduate Center,
2900 Bedford Ave, 11210, Brooklyn, NY, USA
e-mail: gbarord@gc.cuny.edu

J. A. Basil
e-mail: jbasil@brooklyn.cuny.edu

J. Iglesias et al. (eds.), *Cephalopod Culture*, DOI 10.1007/978-94-017-8648-5_10,

Housing System, Brooklyn

- 700 gallon system: three cylindrical holding tanks (1.5 m tall, 1 m diameter), a 50 gallon sump holding biological filtration, a chilling unit, ultraviolet filtration, and two protein skimmers

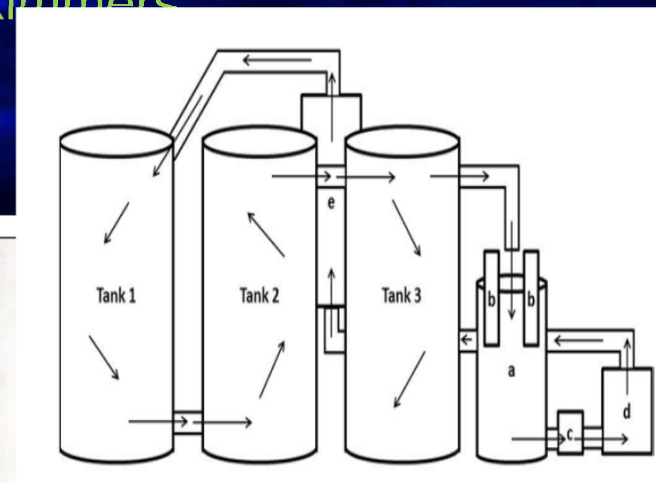
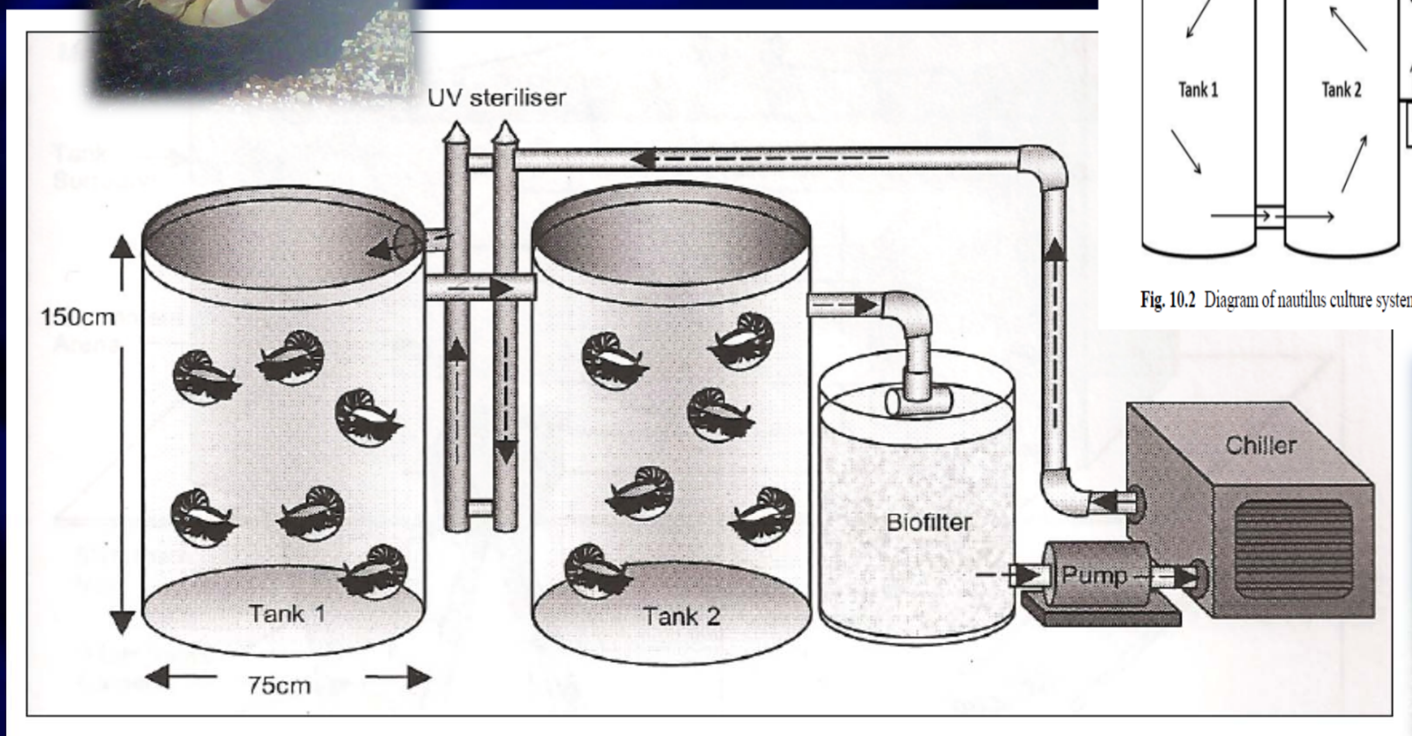


Fig. 10.2 Diagram of nautilus culture system. *Arrows* denote water flow. (Figure by G. J. Barord)



AREAC: Aquatic Research and Environmental Assessment Center

Coleoids/Fishes

Nektic

C
r
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Jawed fishes

Buoyancy
Locomotor
Velocity
Pressure
Equilibrium

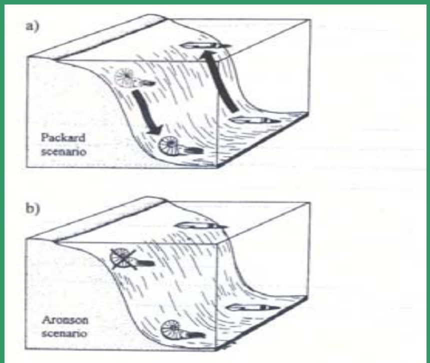

Fig. 1.6 Two schemes for the origin of the coleoids. (**a**) According to Packard competition during the Mesozoic pushed the ectocochleates into deep water, where they lost the shell prior to re-invading shallow water. (**b**) According to Aronson ectocochleates and coleoids co-existed in shallow and deep water during the Palaeozoic. Subsequently, the ectocochleates were eliminated from shallows water (from Aronson, 1991).

Ecological

Reptiles

V
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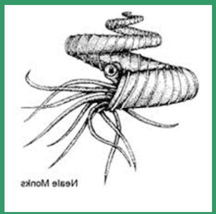
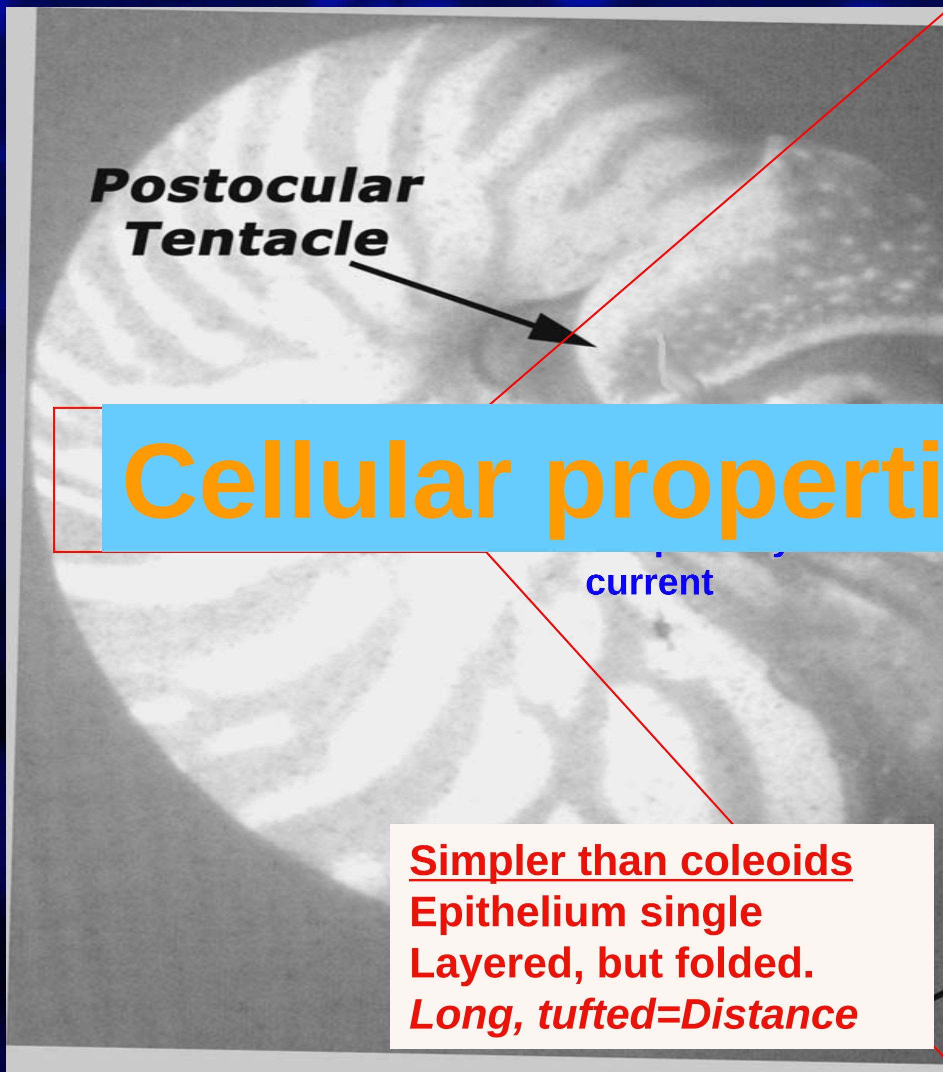


Ectocochleates

Chemosensors

Eyes: 470nm

Vertic/Nektobenthic: live slow, live long



Cellular properties: unknown

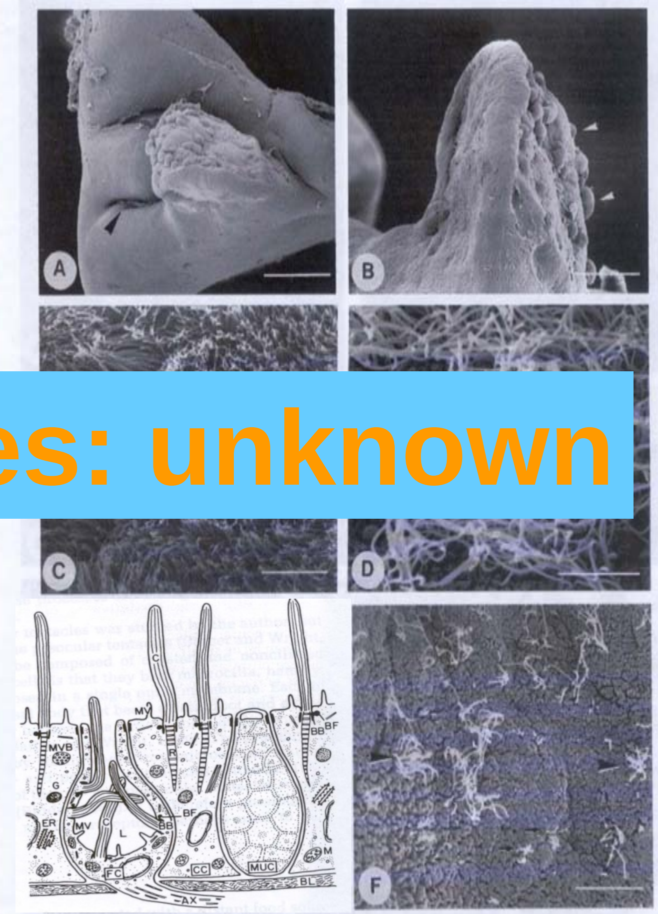
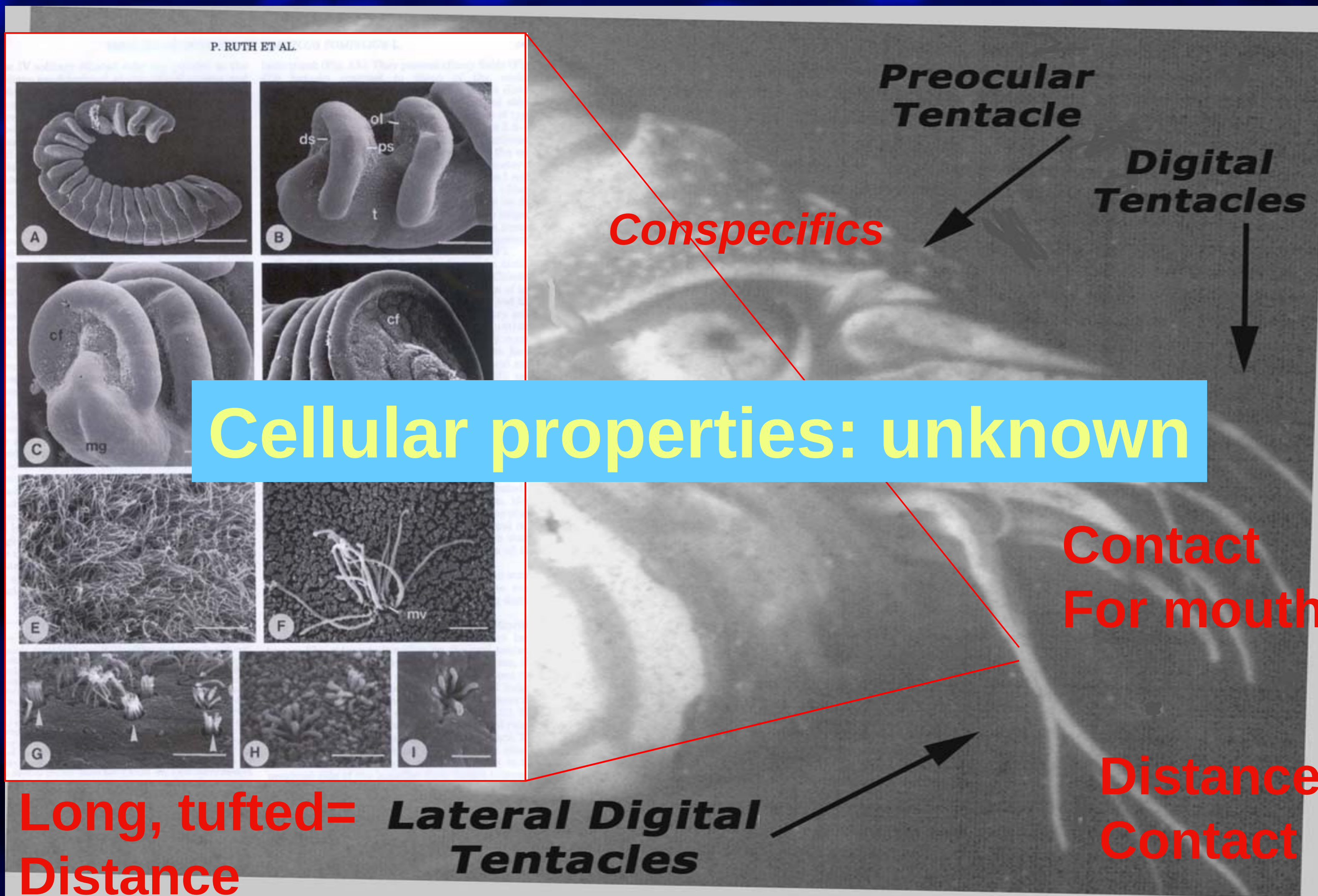


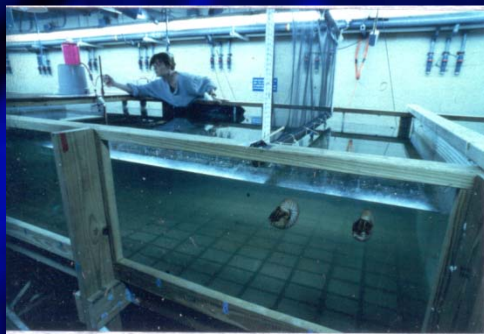
Fig. 6. The rhinophore. SEM. **A**: Overview of the tentacle-like process and the olfactory pit (arrowhead) at its base. Scale bar 1 mm. **B**: Tentacle-like process with the outer side equipped with bulges (arrowheads) while the other side, oriented toward the eyes, is relatively smooth. Scale bar 500 µm. **C**: Ciliary field of the sensory pit. Scale bar 10 µm. **D**: Type I cell (arrowhead) composing the ciliary mat: The distal parts of the cilia of cell type VII protruding out of the cell cavity are commonly covered by the long cilia of cell type I. Scale bar 5 µm. **E**: Bulges (arrowheads) at the base of the tentacle-like process with solitary ciliated cells. Scale bar 250 µm. **F**: Magnification of the bulges. Solitary type VIII (arrows) and IX (arrowheads) cells. Scale bar 10 µm. p, sensory pit.

Simpler than coleoids
Epithelium single
Layered, but folded.
Long, tufted=Distance

Barber, Ruth et al

Chemosensors
Vertic/Nektobenthic: Distance, Contact





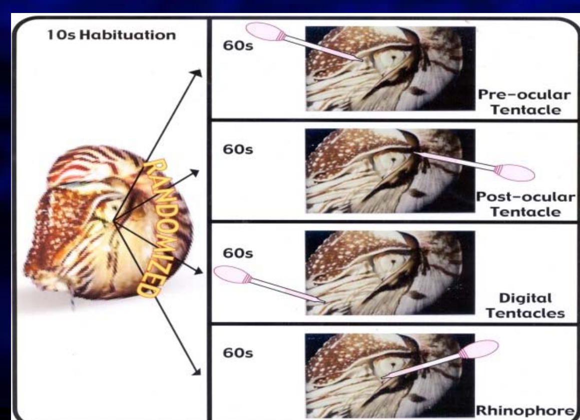
Odor Plumes: patchy, stochastic
tracking at a distance

Start position

Rhinophore blockage abolishes tracking

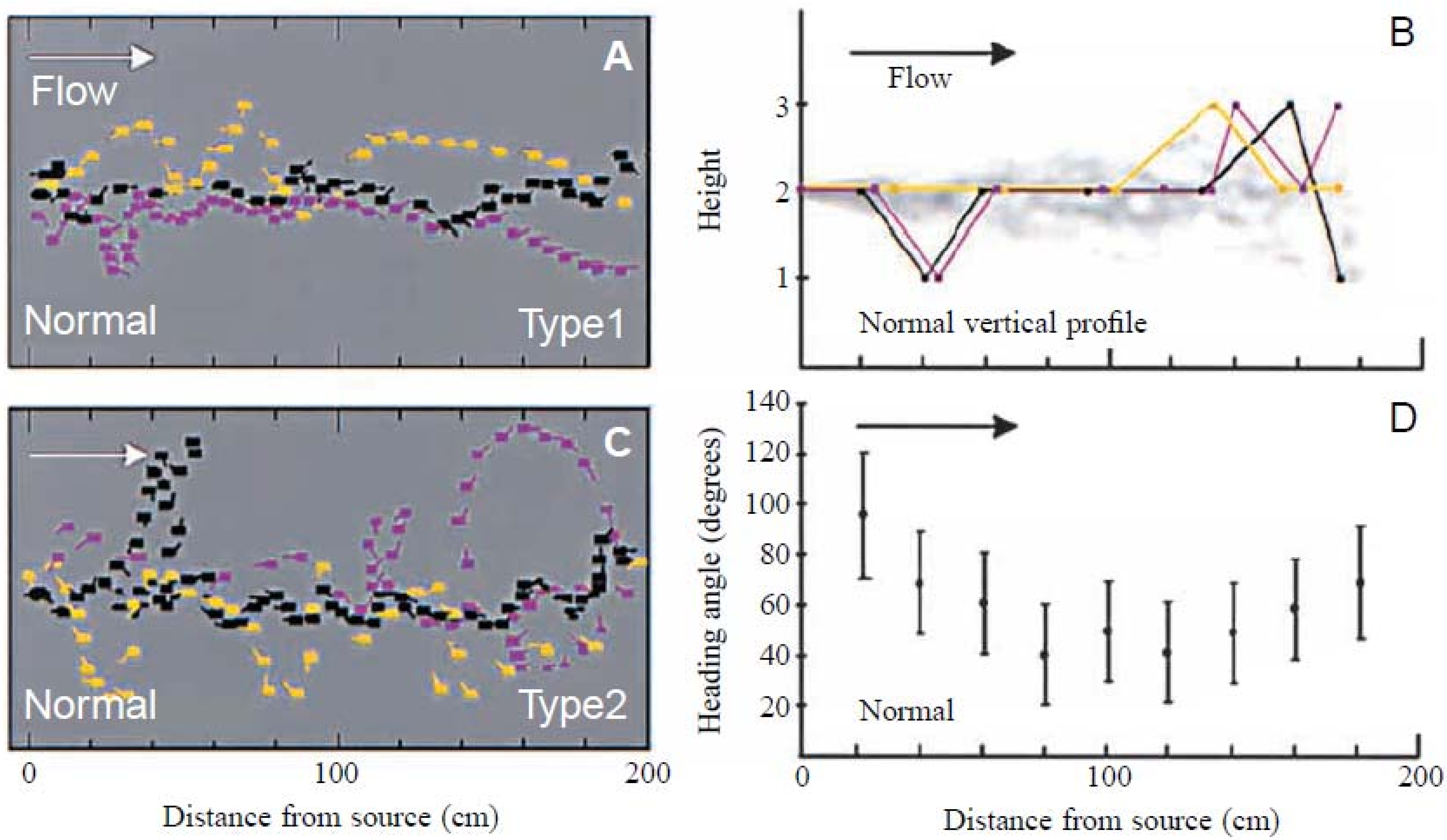
Vertic tracking

Up to 10m



Rhinophore: distance

Tentacles: both

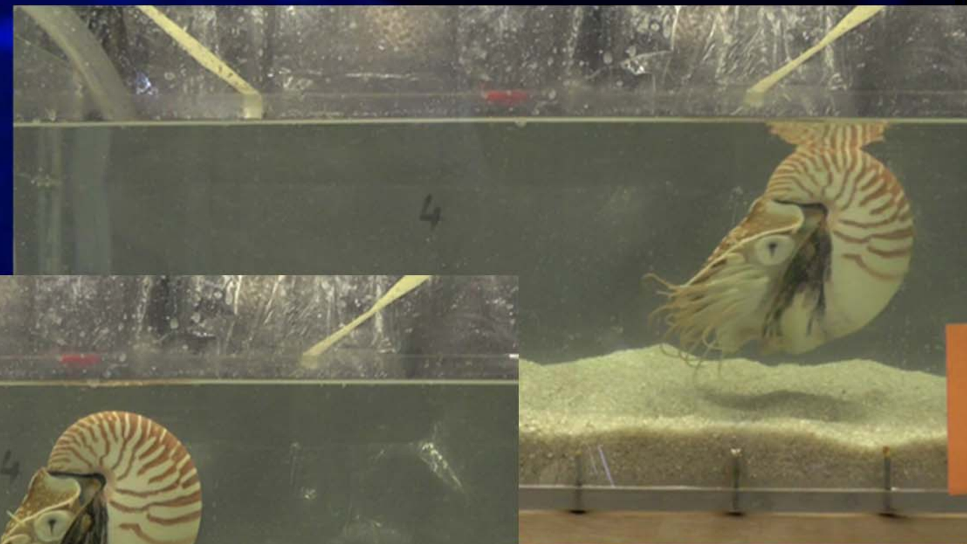

Flow
A
Normal
Type1
B
Flow
Height
3
2
1
Normal vertical profile
C
Normal
Type2
0
100
200
Distance from source (cm)
D
140
120
100
80
60
40
20
Heading angle (degrees)
Normal
0
100
200
Distance from source (cm)

Scavenging: can they detect and find food in substrate?

And…what kind of foods?

Yes!

- What is in benthic substrate?



M. Bedouyn

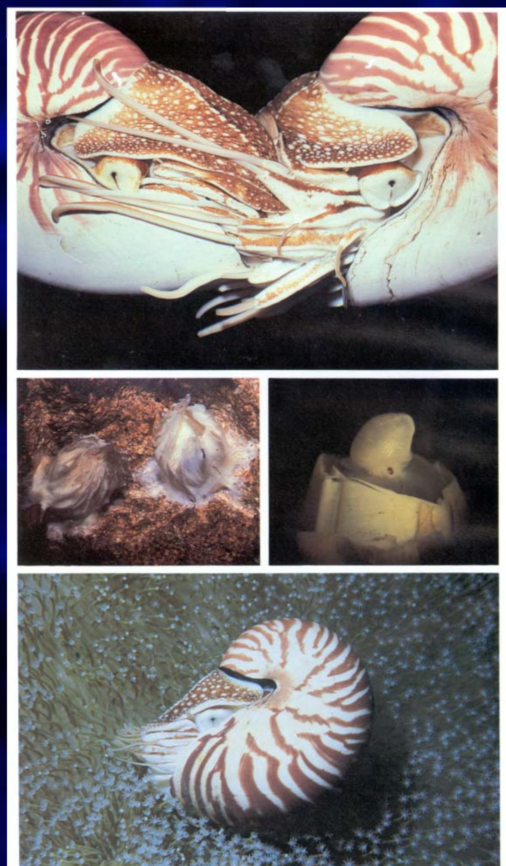
Versus live prey?

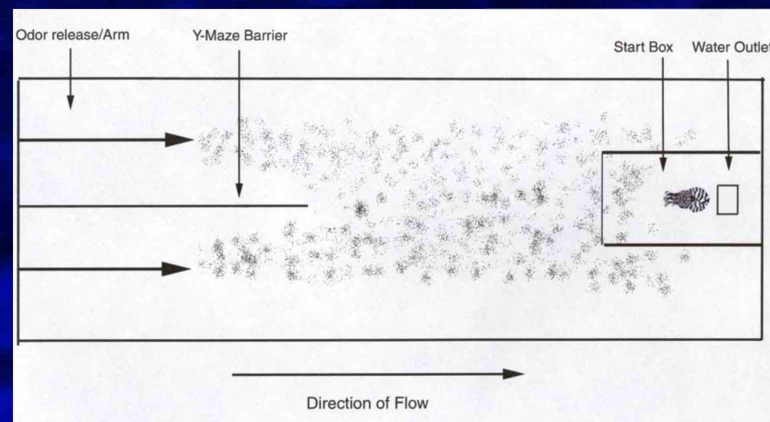
Use of hyponome in scavenging

Hyponome excavating

Finding mates

Nautiloidshttp://scrippsblogs.ucsd.edu/onboard/2013/09/05/breakfast-with-a-newborn-nautilus





Detect Conspecifics
Detect Males/Females
Different response of males and females
Female/Female avoidance?

Mating pair of Nautilus belauensis. Photo by Mark Norman. - See more at: http://taxondiversity.fieldofscience.com/2011/01/nautilaceae.html#sthash.riyJYKVi.dpuf

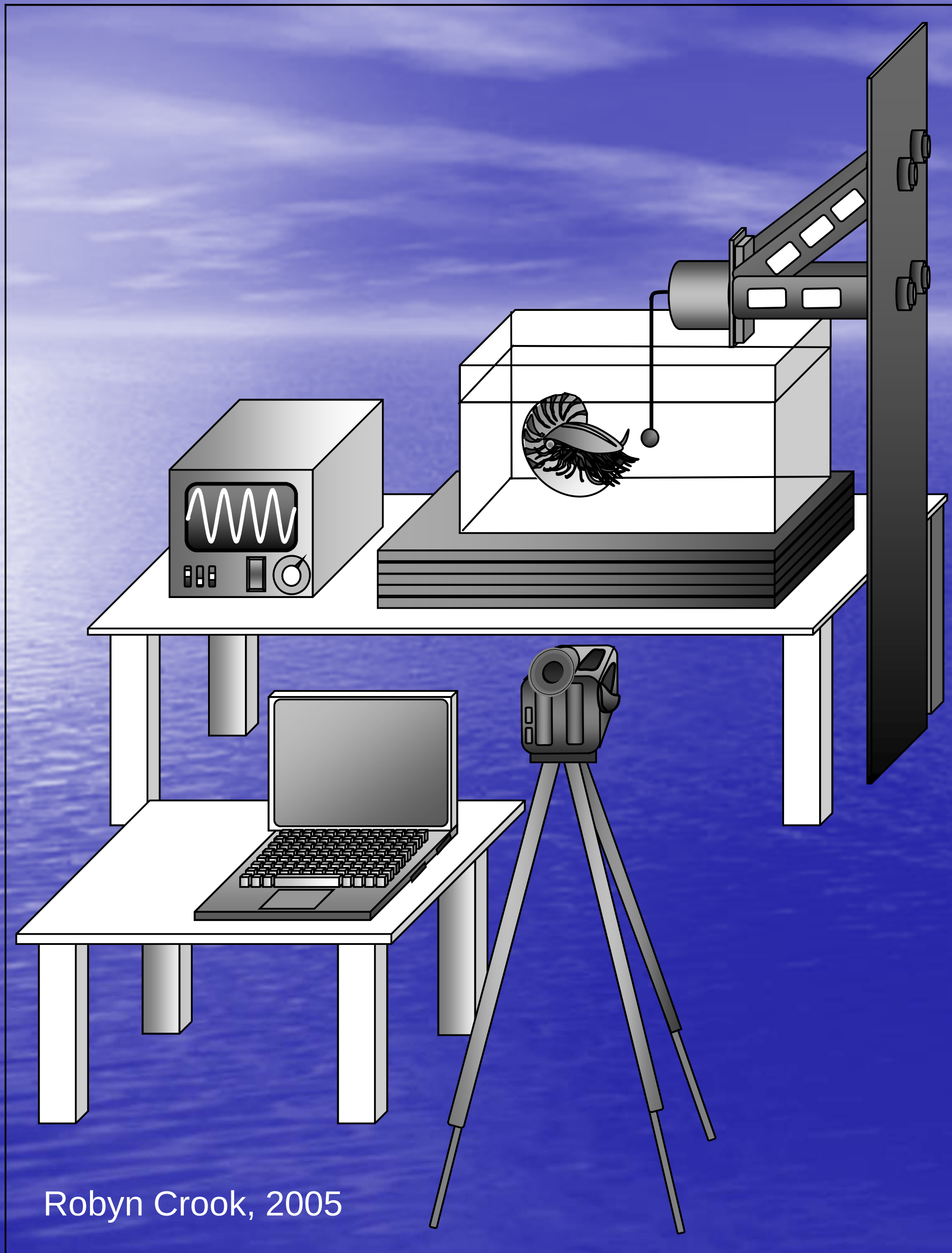
Egg wash experiments? Nautiluses, octopuses? Juvies critical

Further laboratory research

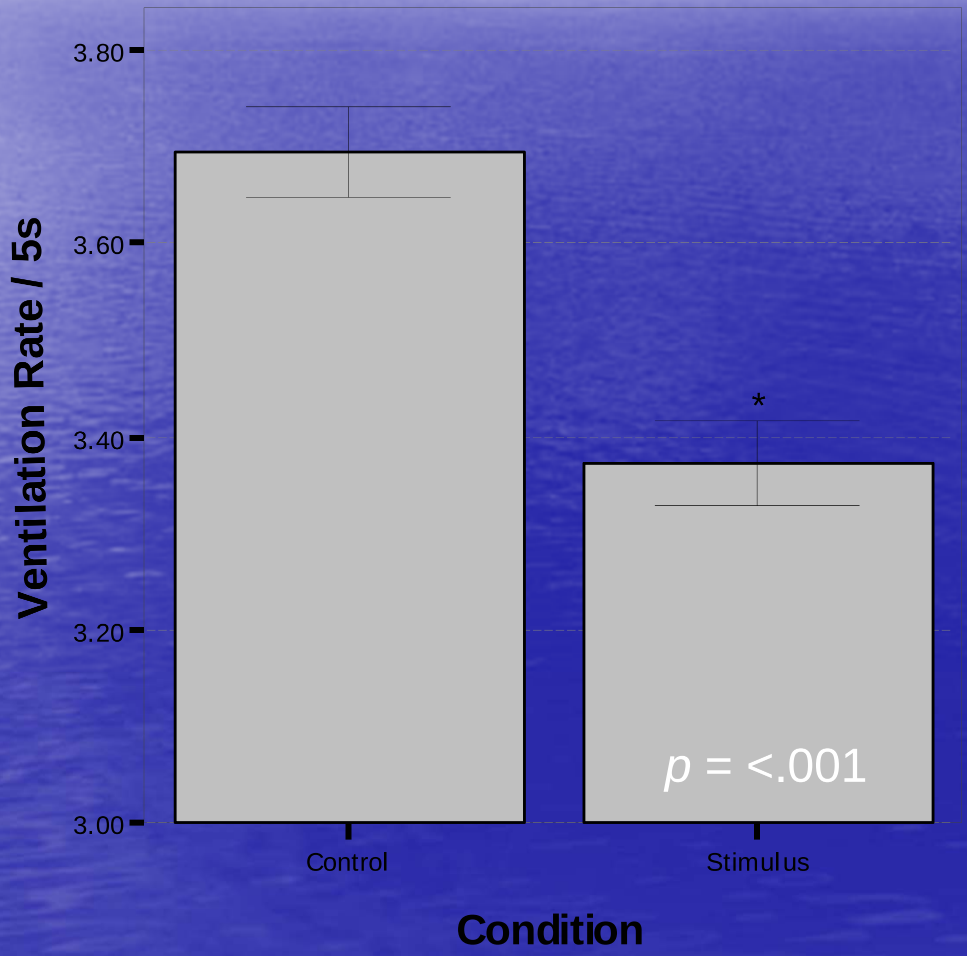
- *Egg viability in laboratory*
- *Reproductive behavior*
- *Predator detection – odor, combine with reef study (avoidance tactics?)*
- *Prey-choice experiments*
- *Field – silt samples from natural habitat*

Response to Vibrations

- Small Source-Displacement Experiment (SSDE)
- Large Source-Displacement Experiment (LSDE)
- Frequency Sensitivity Experiment (FSE)


Robyn Crook, 2005

Nautilus respond to vibration (N = 20)



8.9% decrease

- *Nautilus* respond to vibrational stimuli
  - *Nautilus* respond to a range of source intensities and source velocities (70-100hz).
  - Animals respond more strongly when the vibratory stimulus is nearby.
  - Animals respond more strongly when source intensity or source velocity increases.

Divergence -- anatomy

- Coleoids

- Nautiloids

Divergence – history of complexity

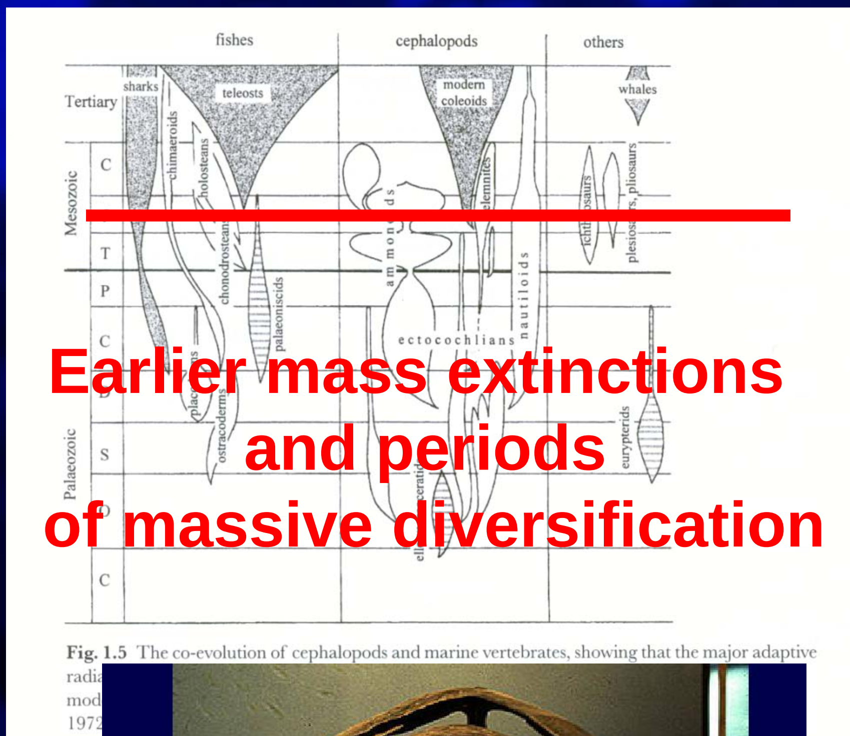


Fig. 1.5 The co-evolution of cephalopods and marine vertebrates, showing that the major adaptive radia… mod… 1972

Earlier mass extinctions and periods of massive diversification

1) Convergence with fishes?

2) Earlier?

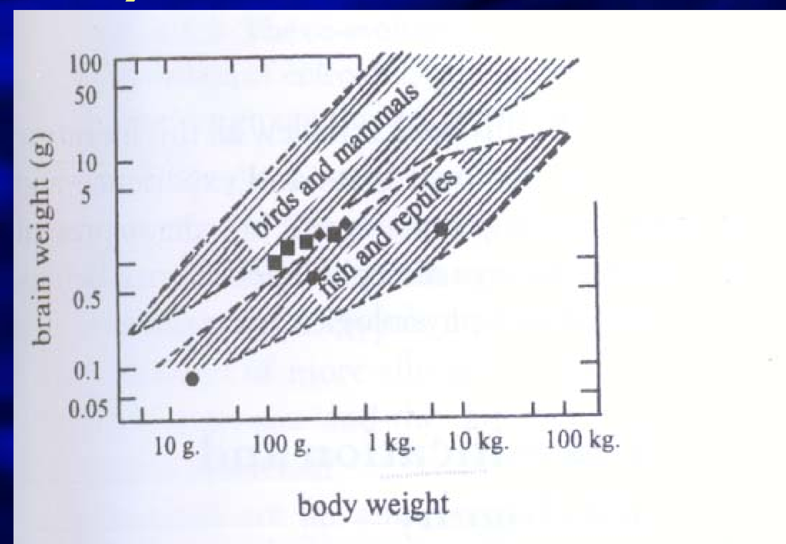
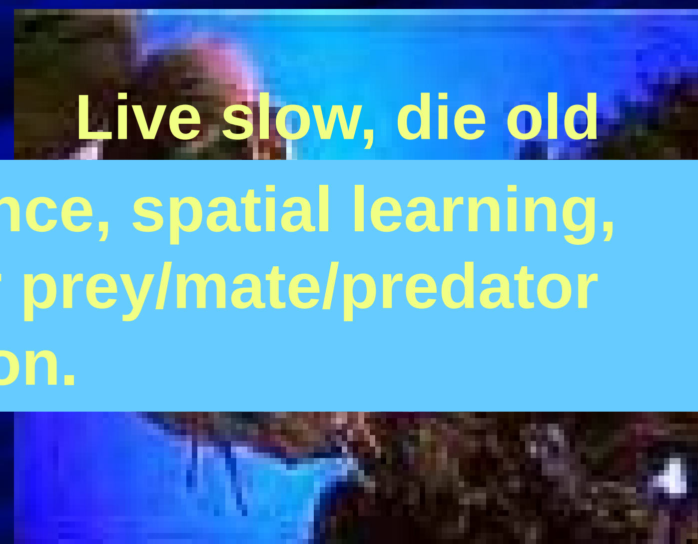


Fig. 1.3 Brain and body weight relationships in vertebrates and some cephalopods (three *Octopus* species [●], four squid species [■], and *Sepia* [◆]; from Packard, 1972).

Packard, 1972; Aronson, 1991; Hanlon and Messenger, 1996

Divergence – ecological questions

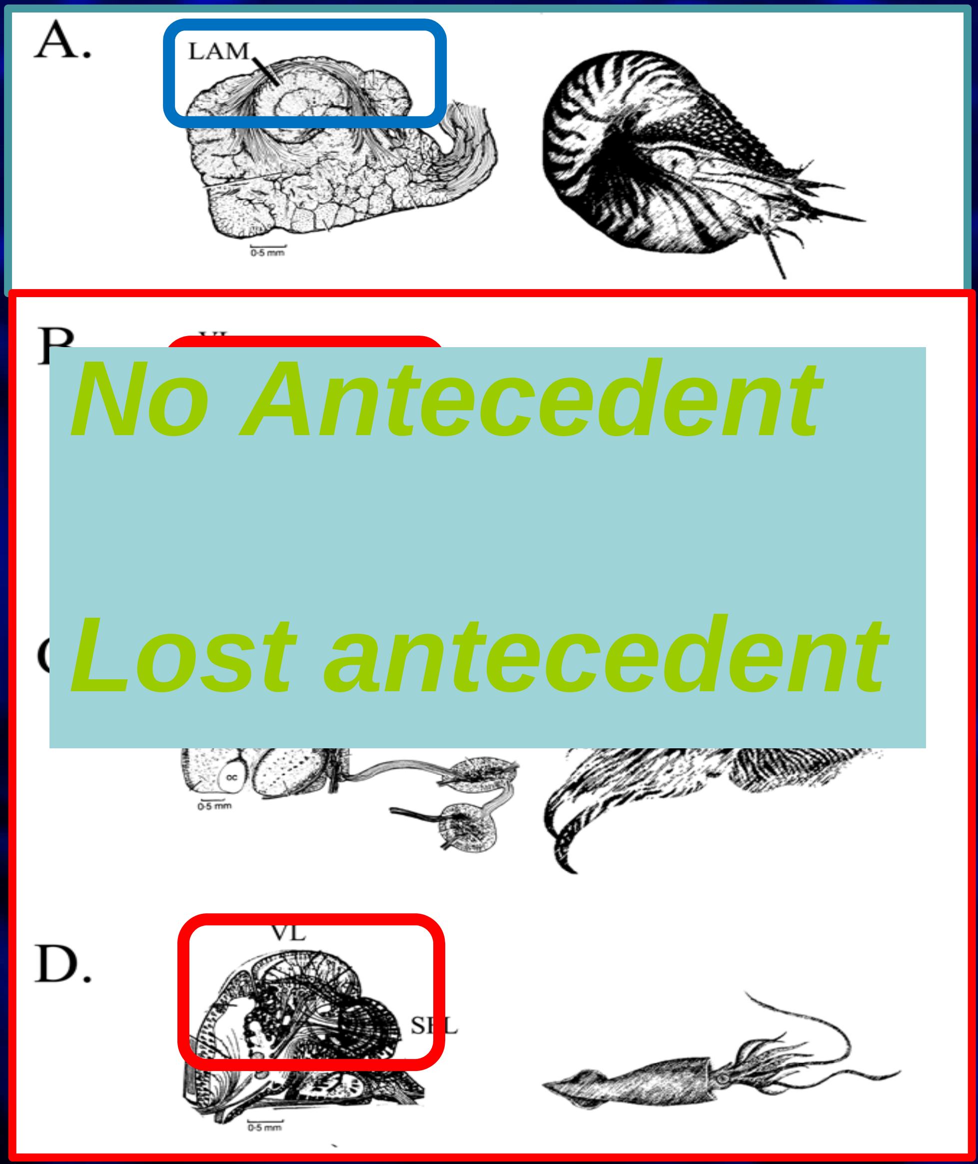
lose/reduce shells
visual predatory lifestyle
Some solitary, some group living



Learned predator avoidance, spatial learning, cross modal learning for prey/mate/predator detection.

shell for protection
less prime deeper water
slow, smellers and gropers
all solitary, nocturnal

Divergence -- brains

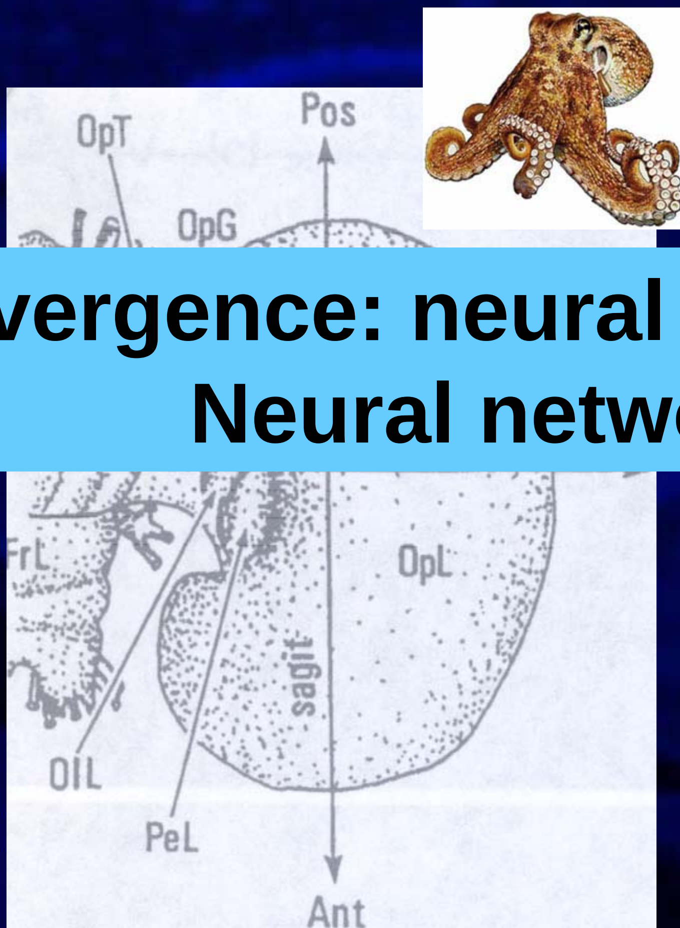


Homology: Cell bodies, neurites, neuropil, nonspiking

Ant

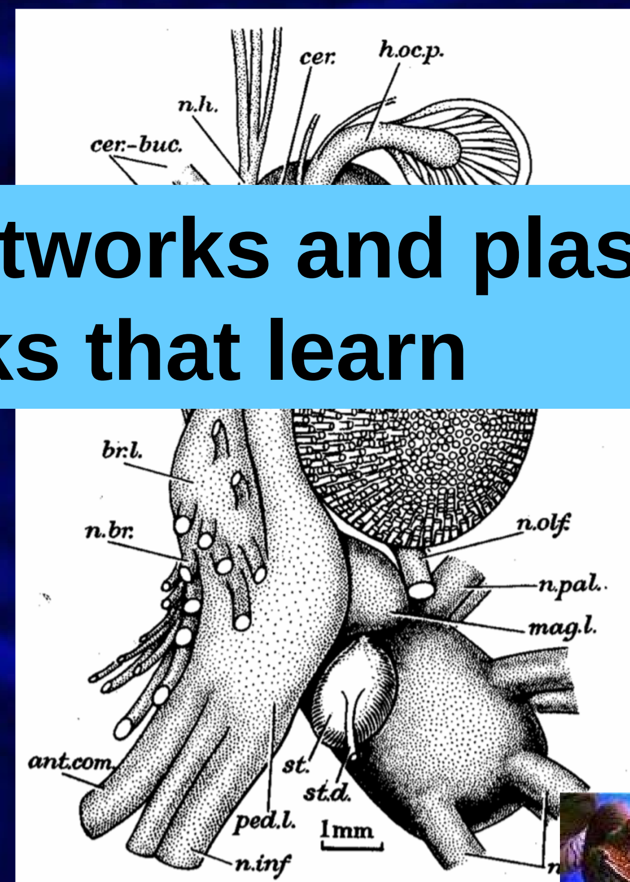
Pos

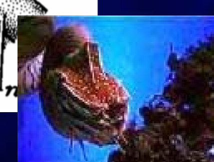
Convergence: neural networks and plasticity
Neural networks that learn



>40 lobes

Not identical scale



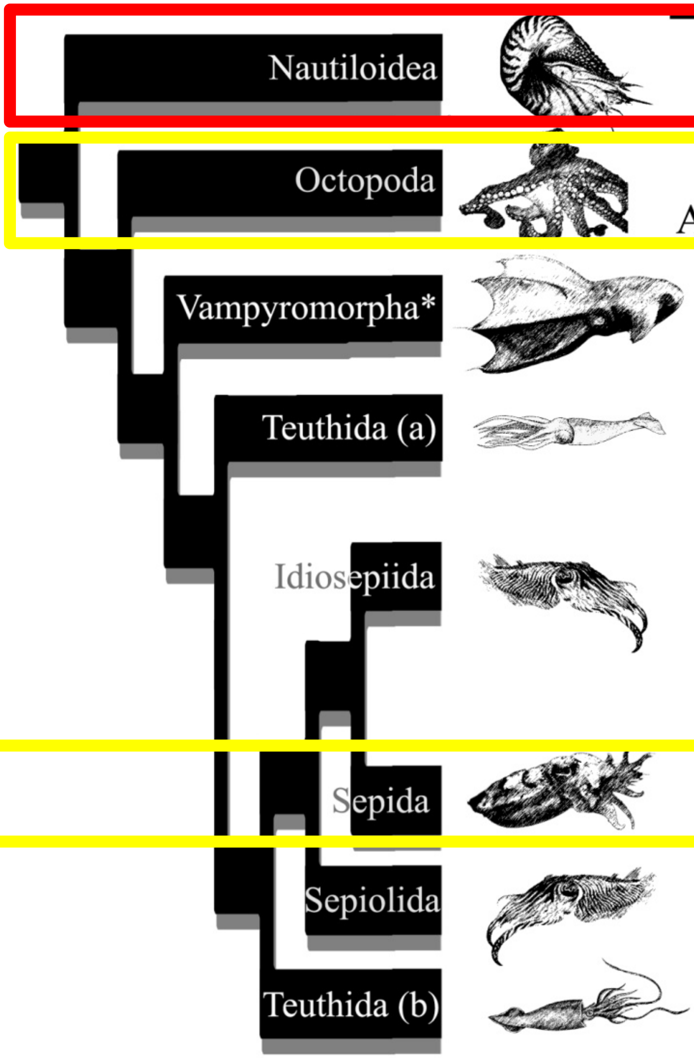


13 lobes

JZ Young

Parametric variation

A. Cephalopod Phylogenetic Relationships



(After Strugnell et al., 2004 and Lindgren et al., 2005)

B. Difference From Octopus

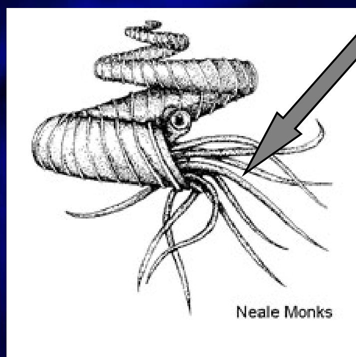
	VL %	InFF %	OL %
NAUTILUS	-100.00	-100.00	-67.88
OCTOPUS	–	–	–
ARGONAUT	0.00	+335.29	+167.29
VAMPYRO-TEUTHIS	+130.00	-34.12	+345.18
SEPIA	+95.83	-83.53	+66.94
LOLIGO	+71.67	-87.06	+295.29

(Calculated from Maddock and Young, 1987)

An old brain

Live slow, die old – time to learn

Upside



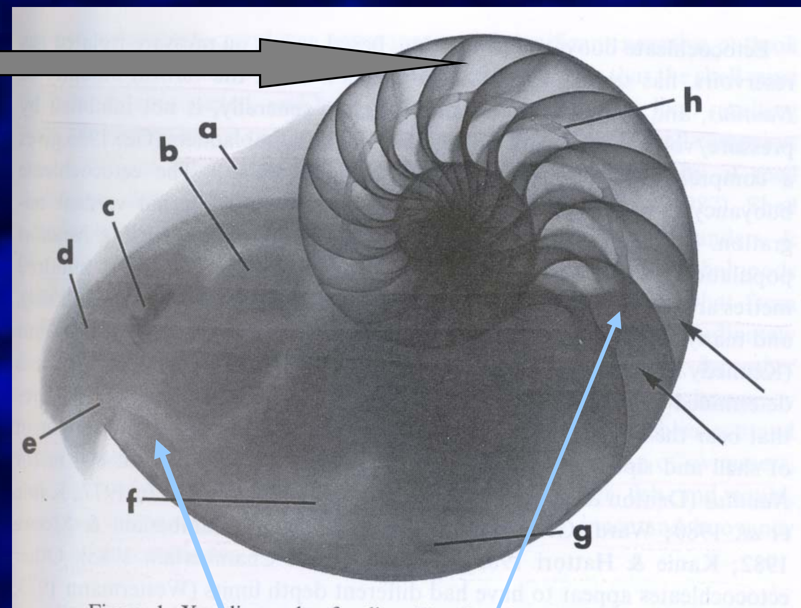
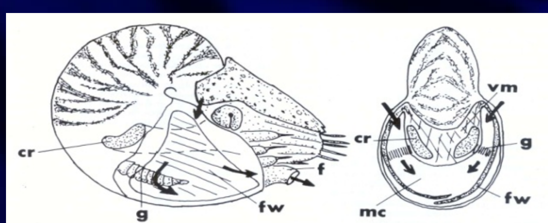


Figure 1. X-radiograph of a live *Nautilus* showing organization of shell and body. The shell is divided into a large body chamber, which houses the body, and a phragmocone consisting of a series of smaller, gas and fluid-filled chambers. a, hood; b, eye; c, jaws; d, tentacles; e, funnel passage; f, mantle cavity; g, renal appendage; h, siphuncle; arrows indicate chambers containing cameral water. Note meniscus on free fluid surface. Actual shell diameter at aperture 14 cm.

Downside



Centers of mass

Chamberlain, 1991

An old ecology

An associative problem

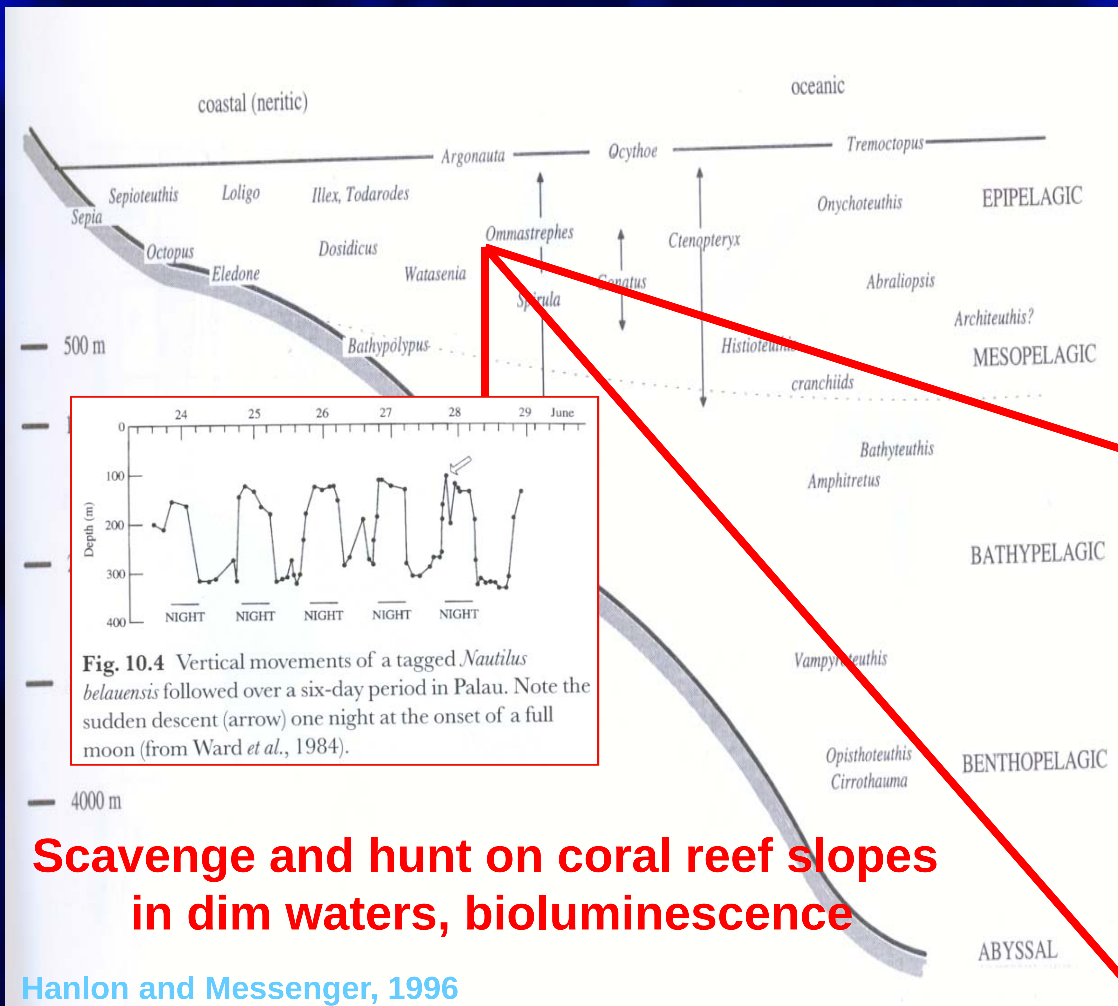
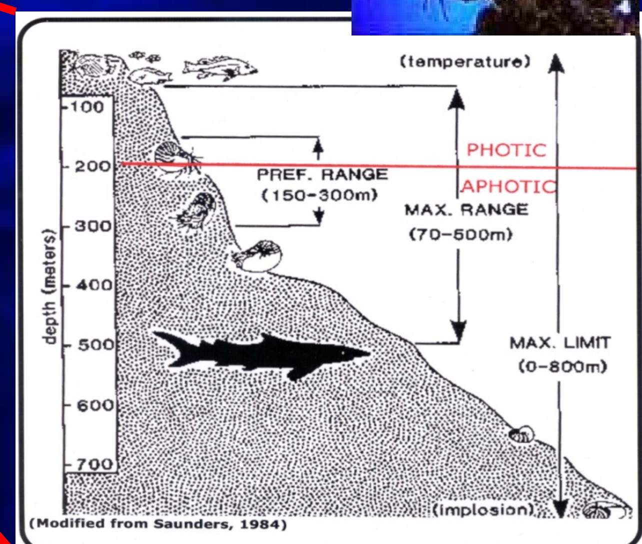


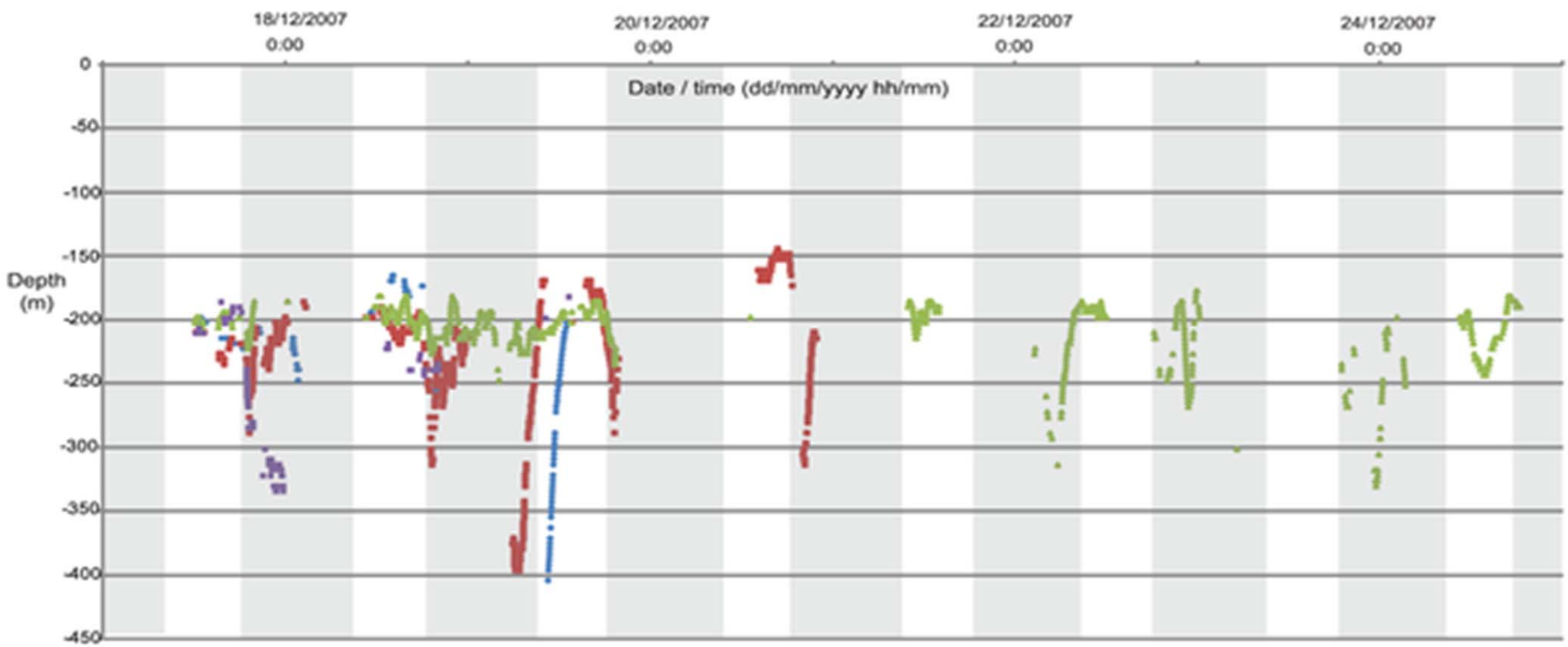
Fig. 10.4 Vertical movements of a tagged *Nautilus belauensis* followed over a six-day period in Palau. Note the sudden descent (arrow) one night at the onset of a full moon (from Ward *et al.*, 1984).



Scavenge and hunt on coral reef slopes in dim waters, bioluminescence

Hanlon and Messenger, 1996

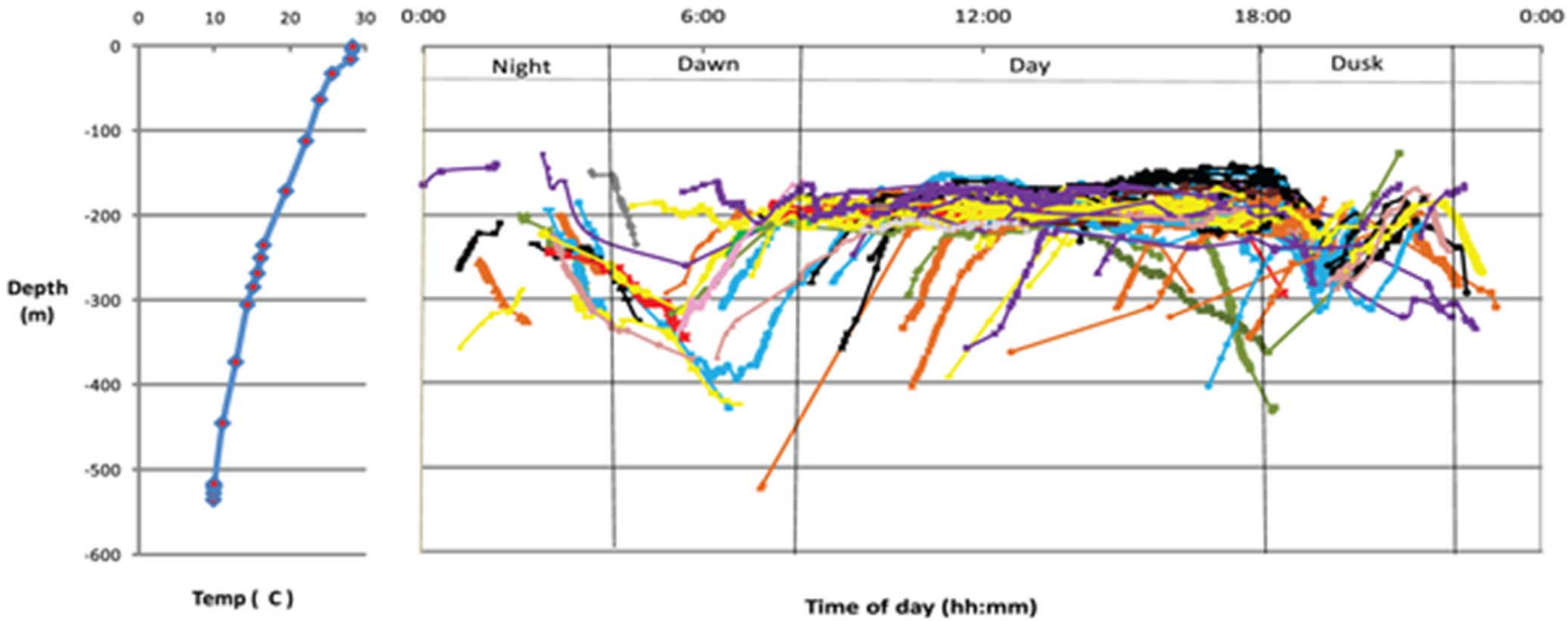
Figure 4. Long term vertical movements of four Nautilus individuals.



Shaded vertical blocks denote daytime periods (0800–1759 hrs).

Dunstan AJ, Ward PD, Marshall NJ (2011) Vertical Distribution and Migration Patterns of Nautilus pompilius. PLoS ONE 6(2): e16311. doi:10.1371/journal.pone.0016311
http://www.plosone.org/article/info:doi/10.1371/journal.pone.0016311

Figure 3. Vertical movements of tagged Nautilus with temperature/depth profile.



Dunstan AJ, Ward PD, Marshall NJ (2011) Vertical Distribution and Migration Patterns of Nautilus pompilius. PLoS ONE 6(2): e16311. doi:10.1371/journal.pone.0016311
http://www.plosone.org/article/info:doi/10.1371/journal.pone.0016311

Synthetic Approach

- First experimental evidence for learning in this understudied, but important, group of animals.
- Characterized innate behaviors.
- Characterize plastic behaviors.
- *Based on problems animals must solve in the field.*

Environmental learning
How and what do they learn?

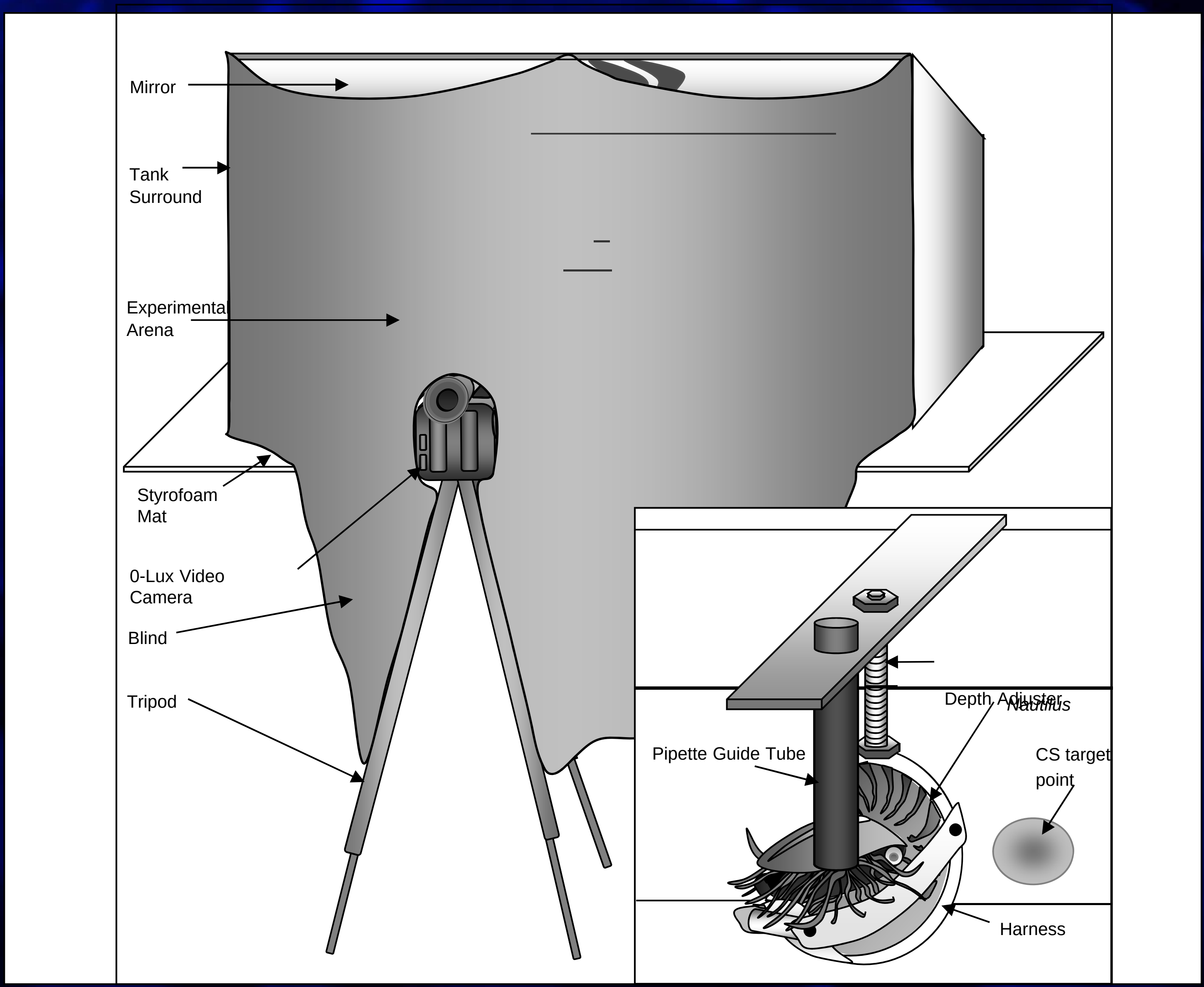
Profile

1. speed
2. retention
3. content

Content

4. sensory stimuli
5. spatial information
6. flexibility
7. memory space

Method



Mirror
Tank
Surround
Experimental
Arena
Styrofoam
Mat
0-Lux Video
Camera
Blind
Tripod
Depth Adjuster
Nautilus
CS target
point
Pipette Guide Tube
Harness

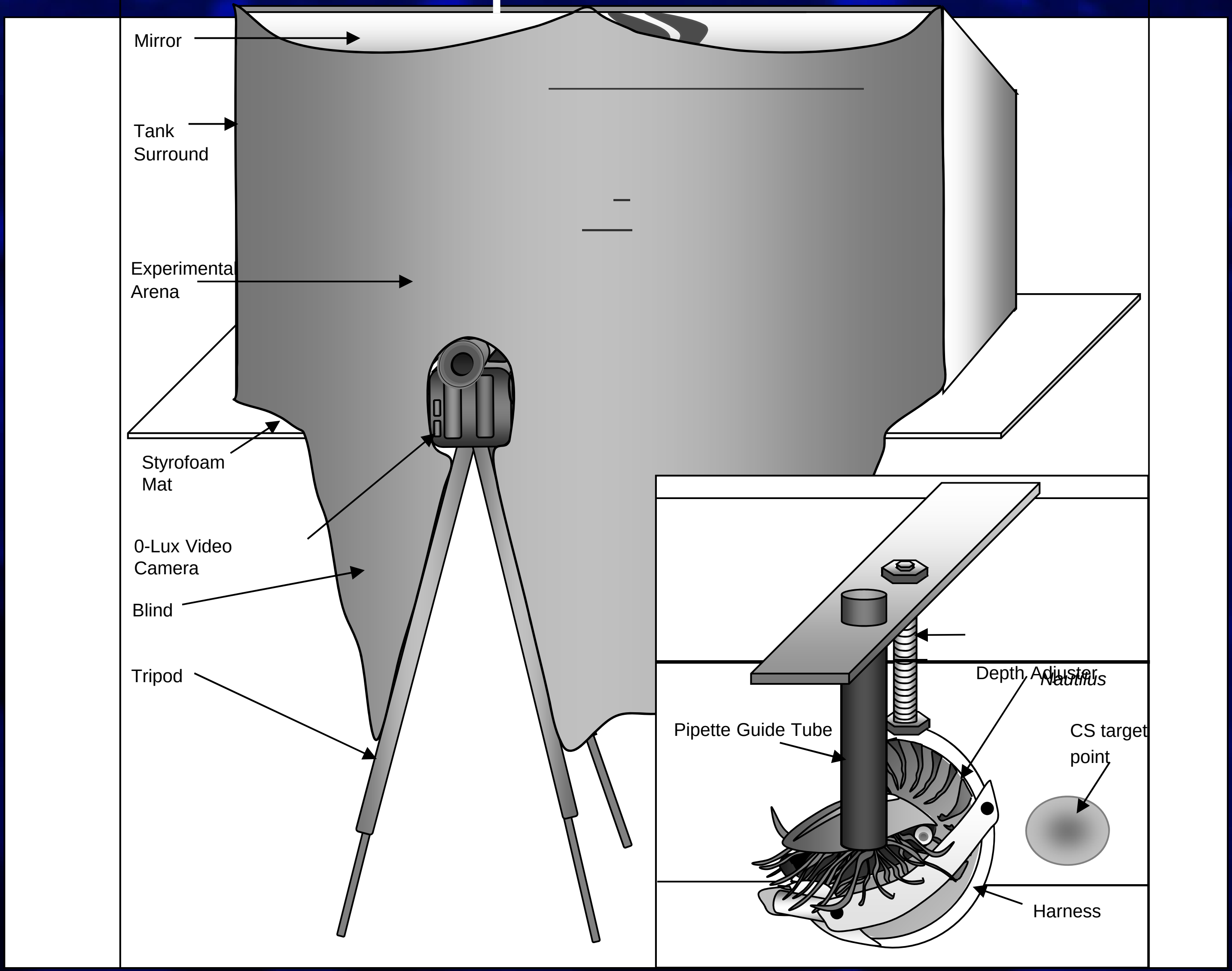
Adaptive Associations

bioluminescence-guided foraging

- Learning
  - CS+ (light)
  - US (odor)
  - CS-
  - 10 training trials
    - ISI = 1s,
    - ITI = 10 min
  - CR: tentacle extension

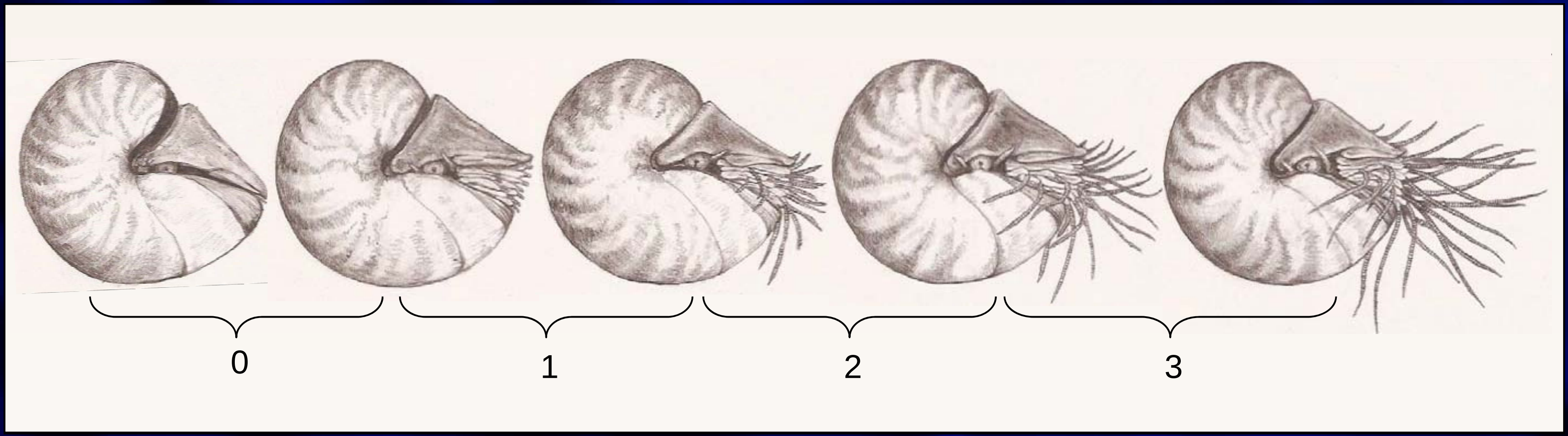
- Memory
  - 3 min, 30min,
  - 1hr, 6hr, 12hr, 24hr
  - ~single unrewarded light pulse

classical conditioning: ecological problem



CR - Tentacle Extension Response

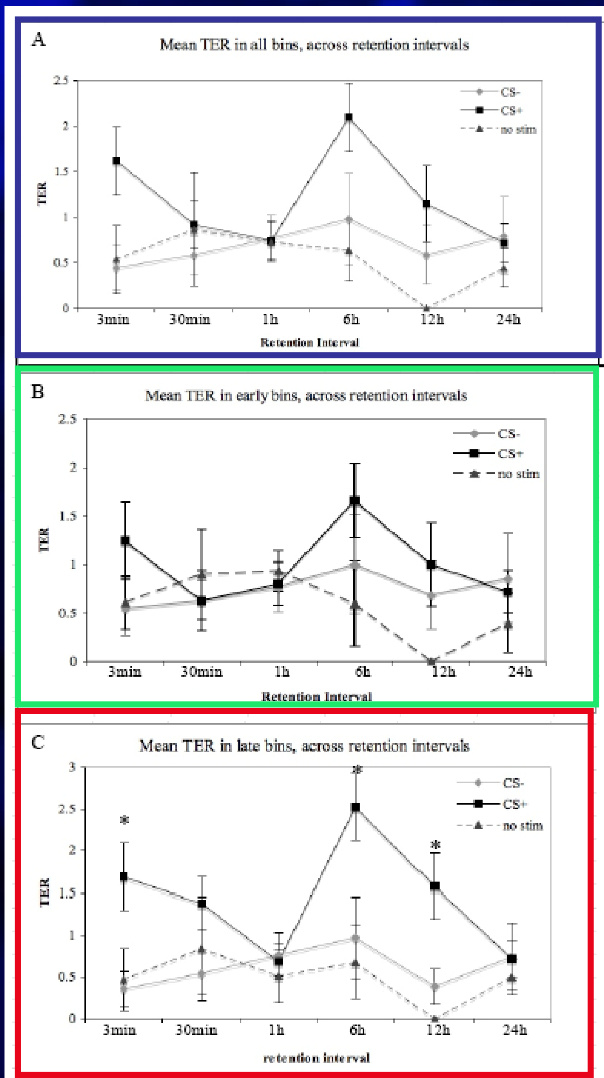
- Natural (odor)
- Arousal – retractable tentacles extend
- Percentage body length



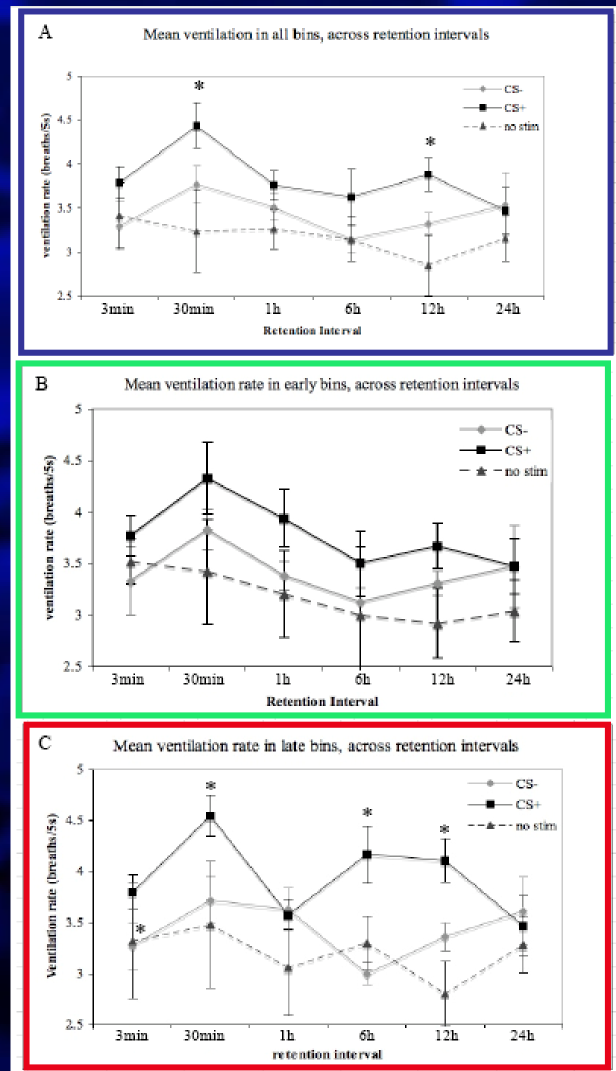
RJ Crook

Results

Tentacle Extension



Ventilation Rate

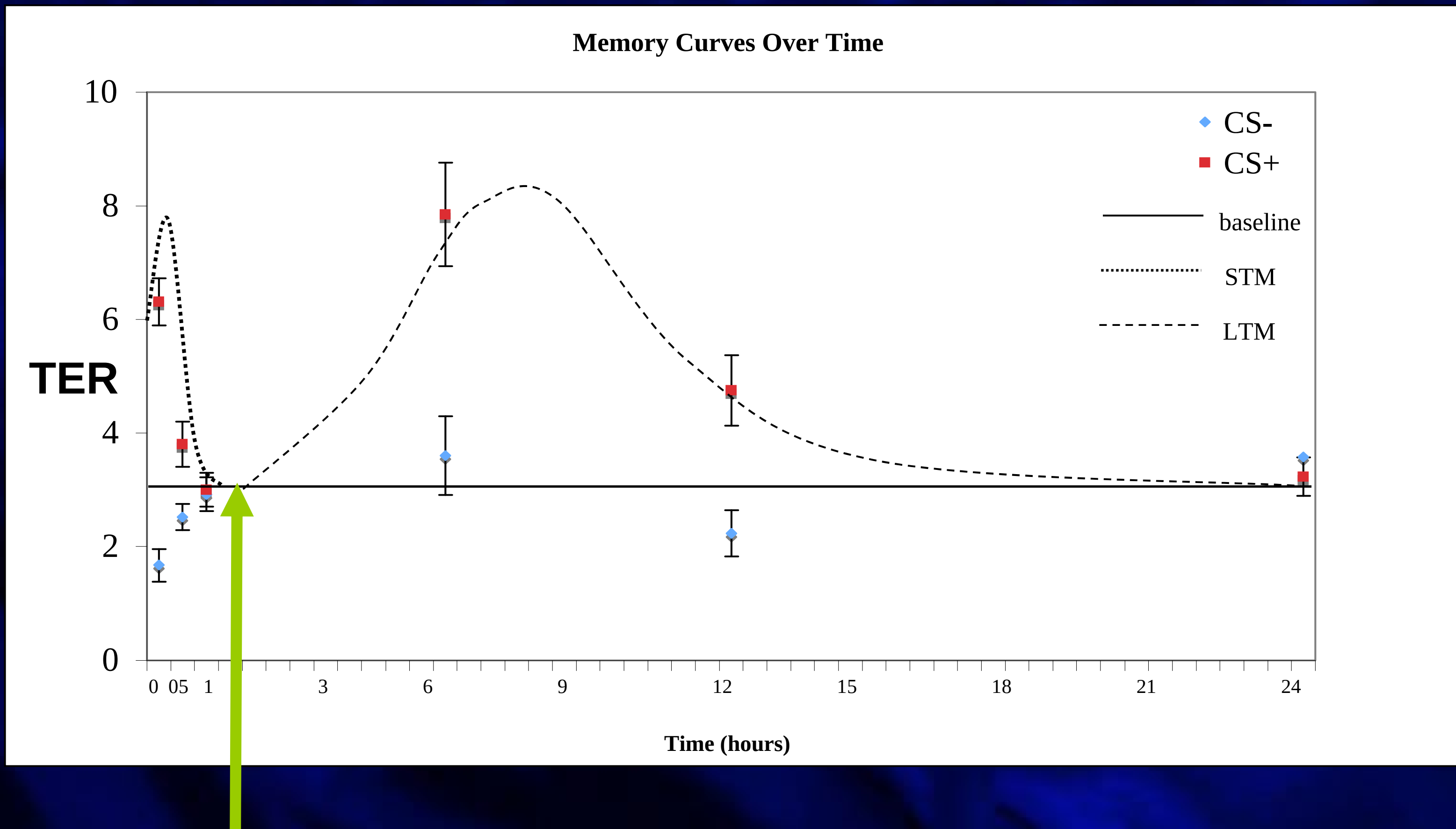


Trends were strongest in final 30 seconds

A biphasic memory curve

Memory for associations

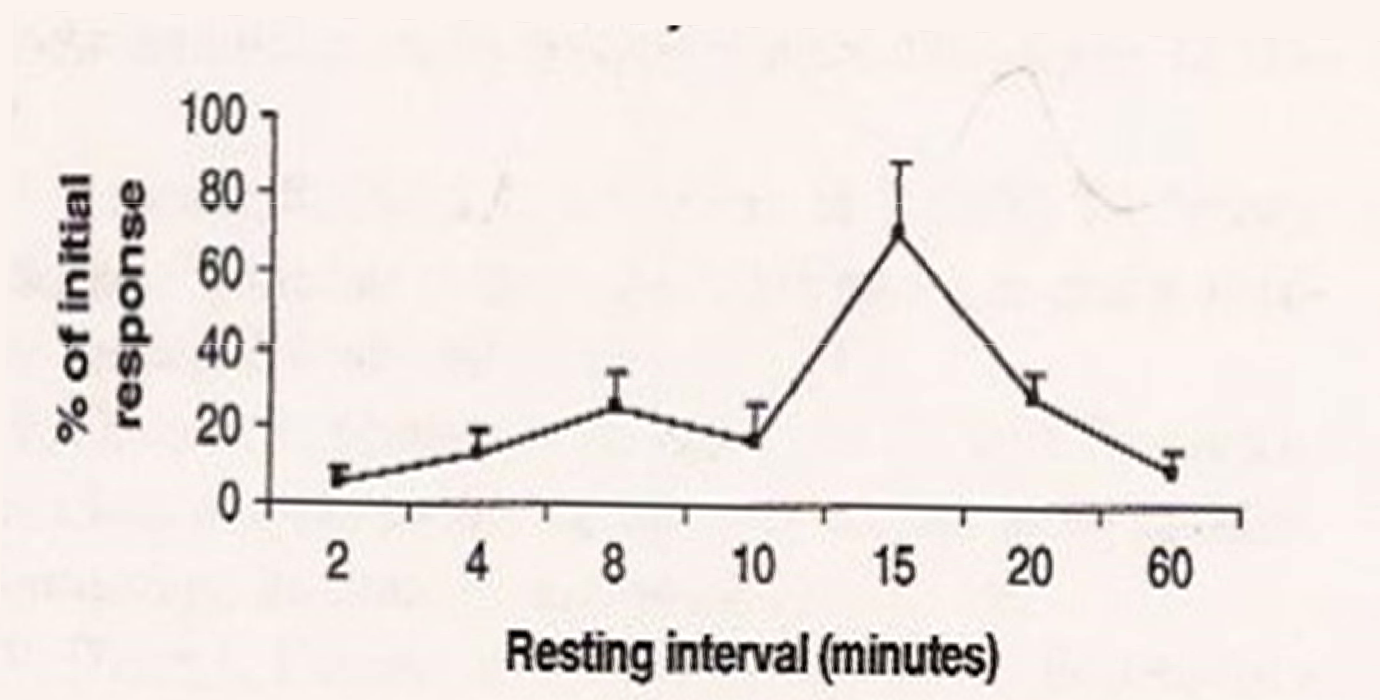
A biphasic memory curve



Consolidation (mechanism, location)

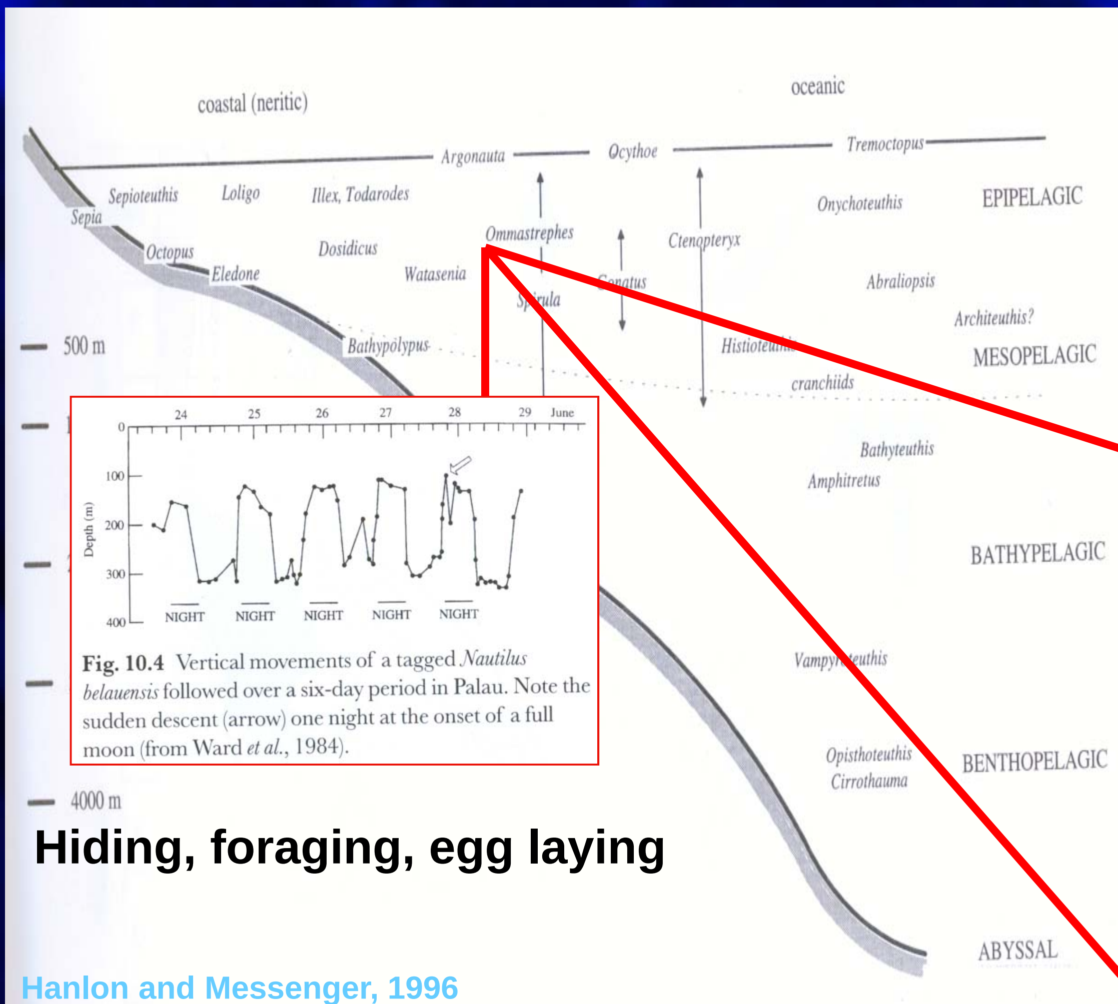
In context

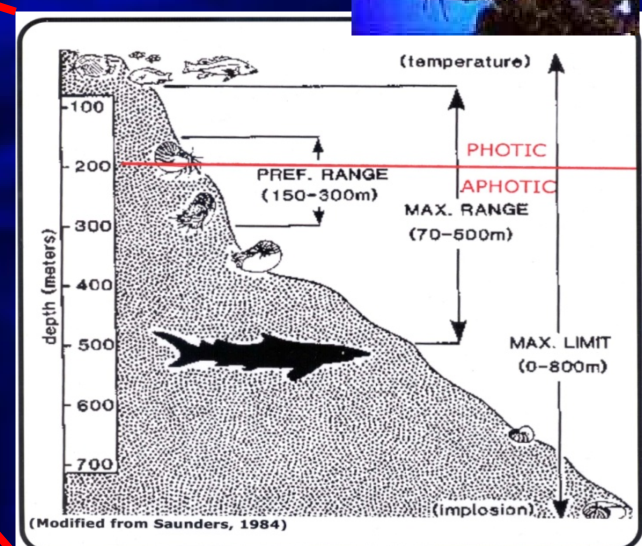
- similar to cuttlefish (*Sepia*)



Agin et al, 2006 *Developmental study of multiple memory stages in the cuttlefish*, Sepia officinalis

Spatial Ecology

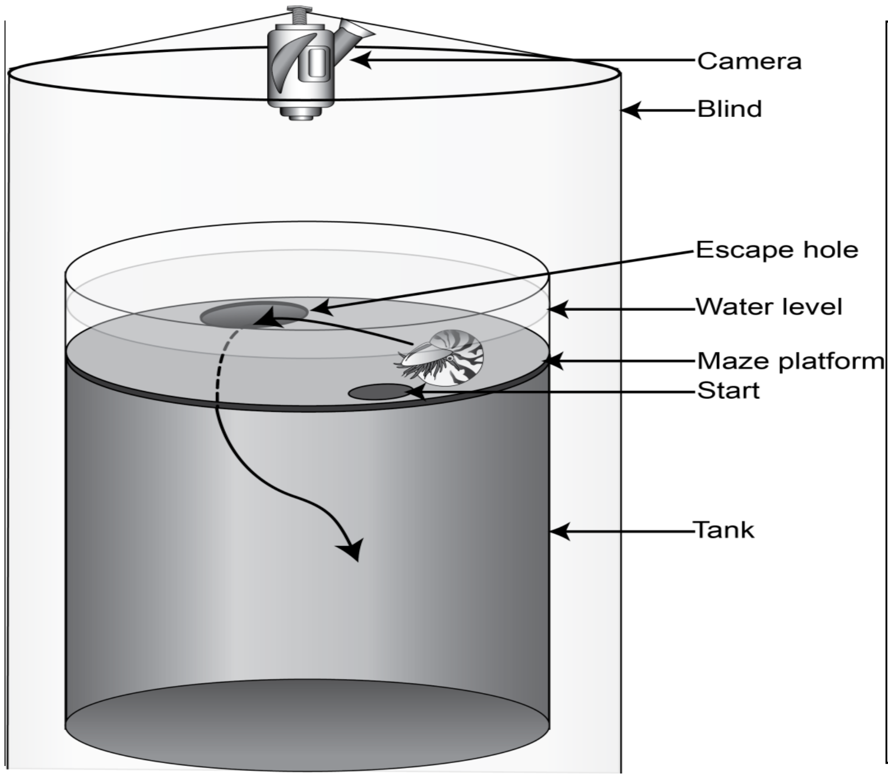


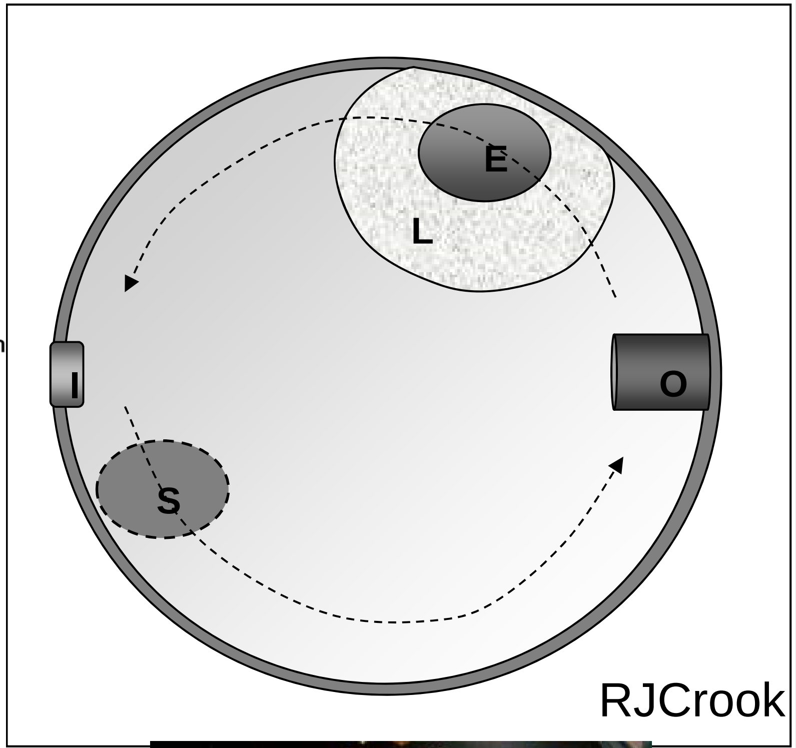


Hiding, foraging, egg laying

Hanlon and Messenger, 1996

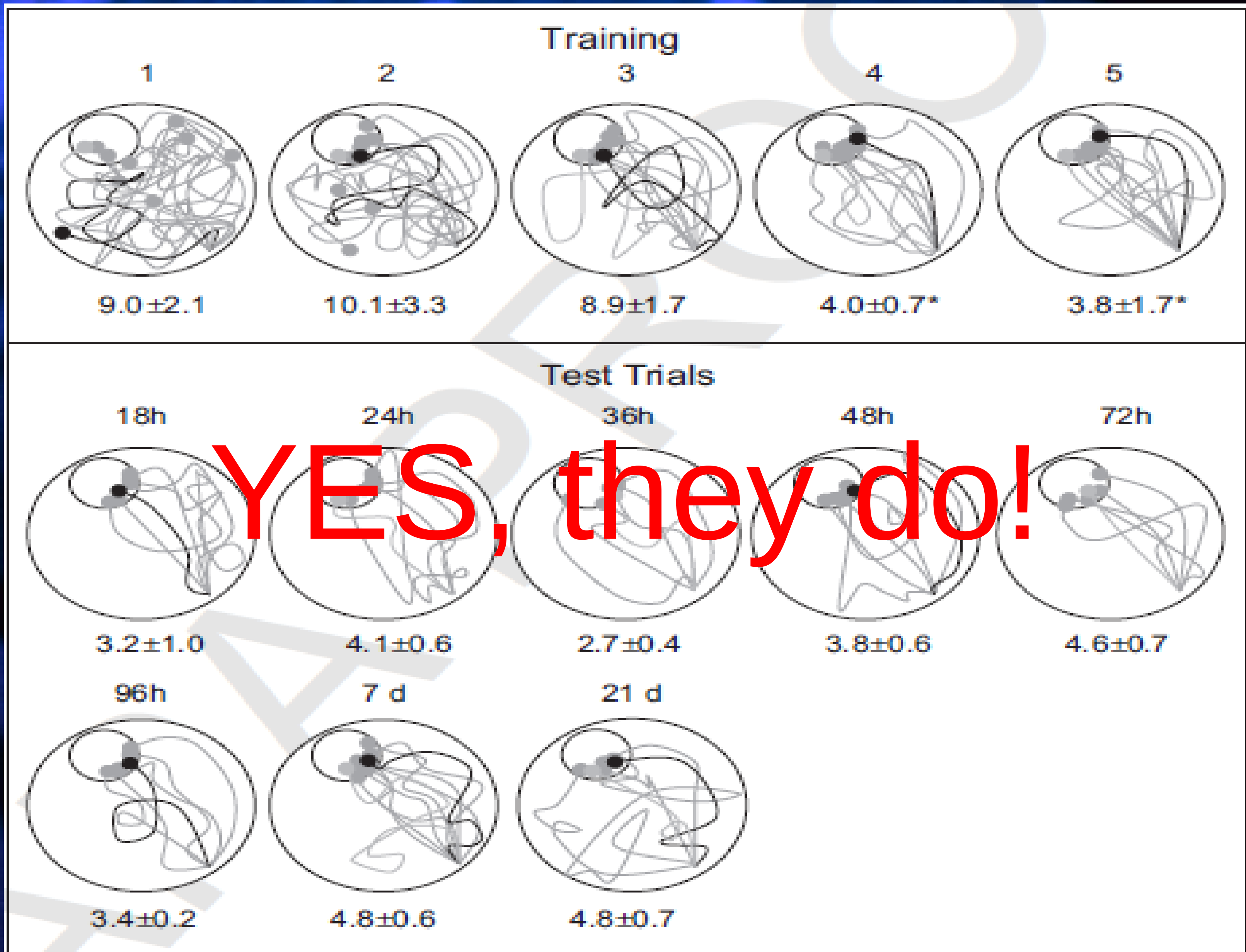
Spatial orientation: Do they learn and remember cues?



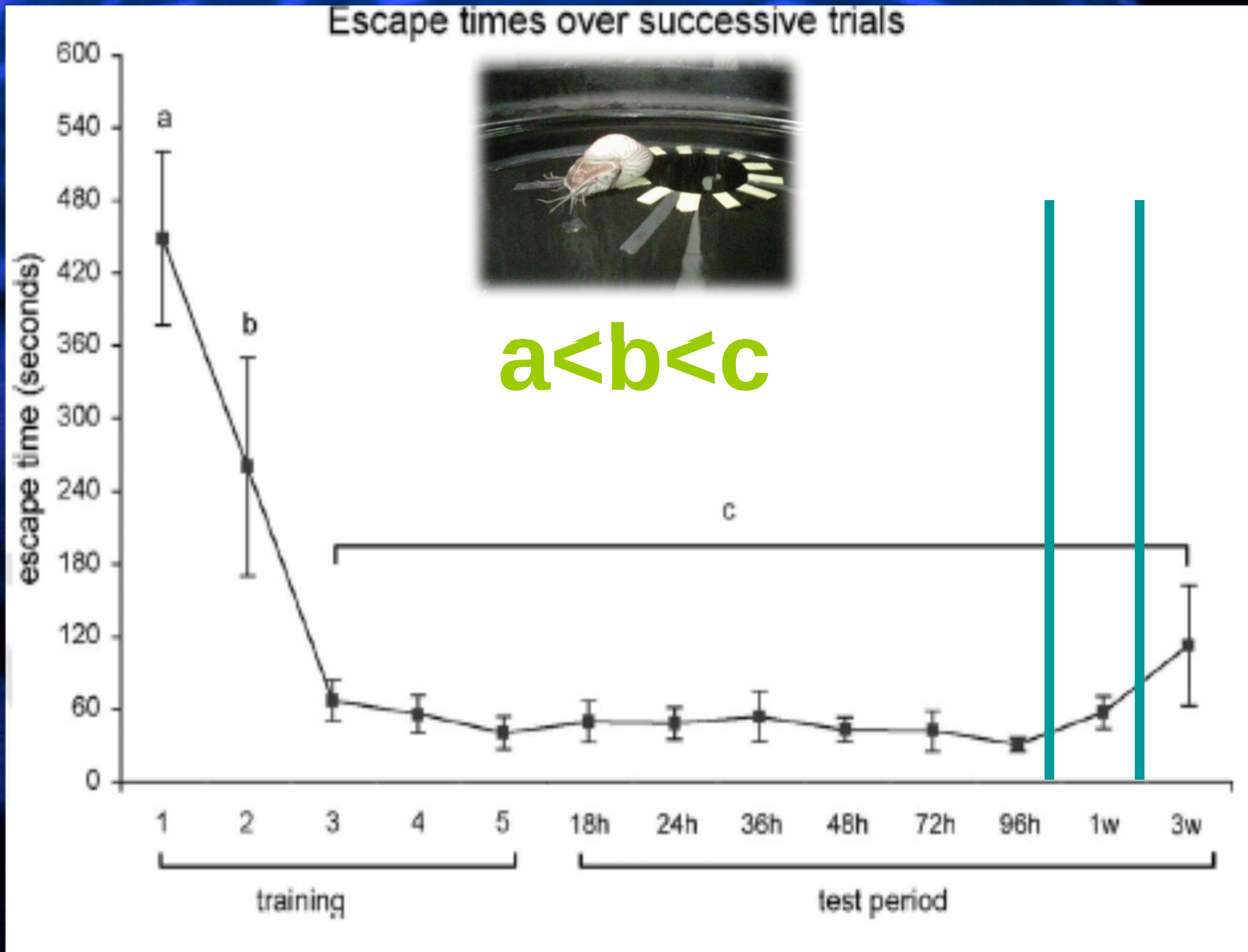


- **curtain**
- **5 trials, 5 min each**
- **10 min 'reward'**
- **Retention testing**

Solutions and corrections



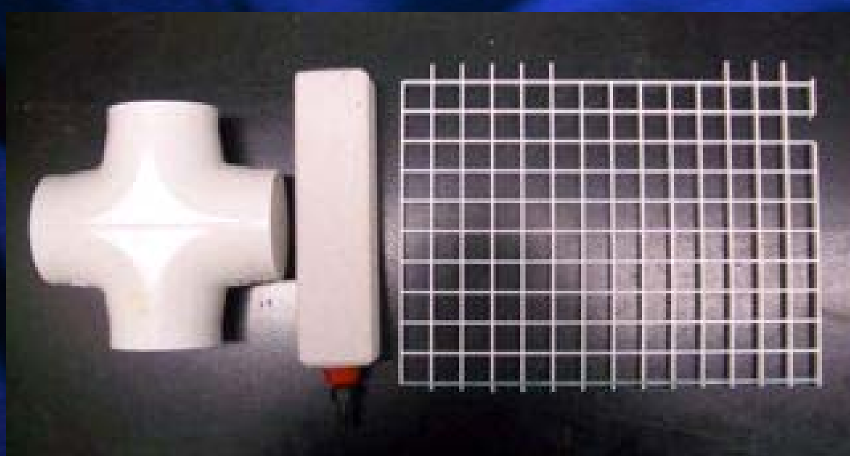
Memory lasts: for weeks!



Spatial navigation in a complex environment:

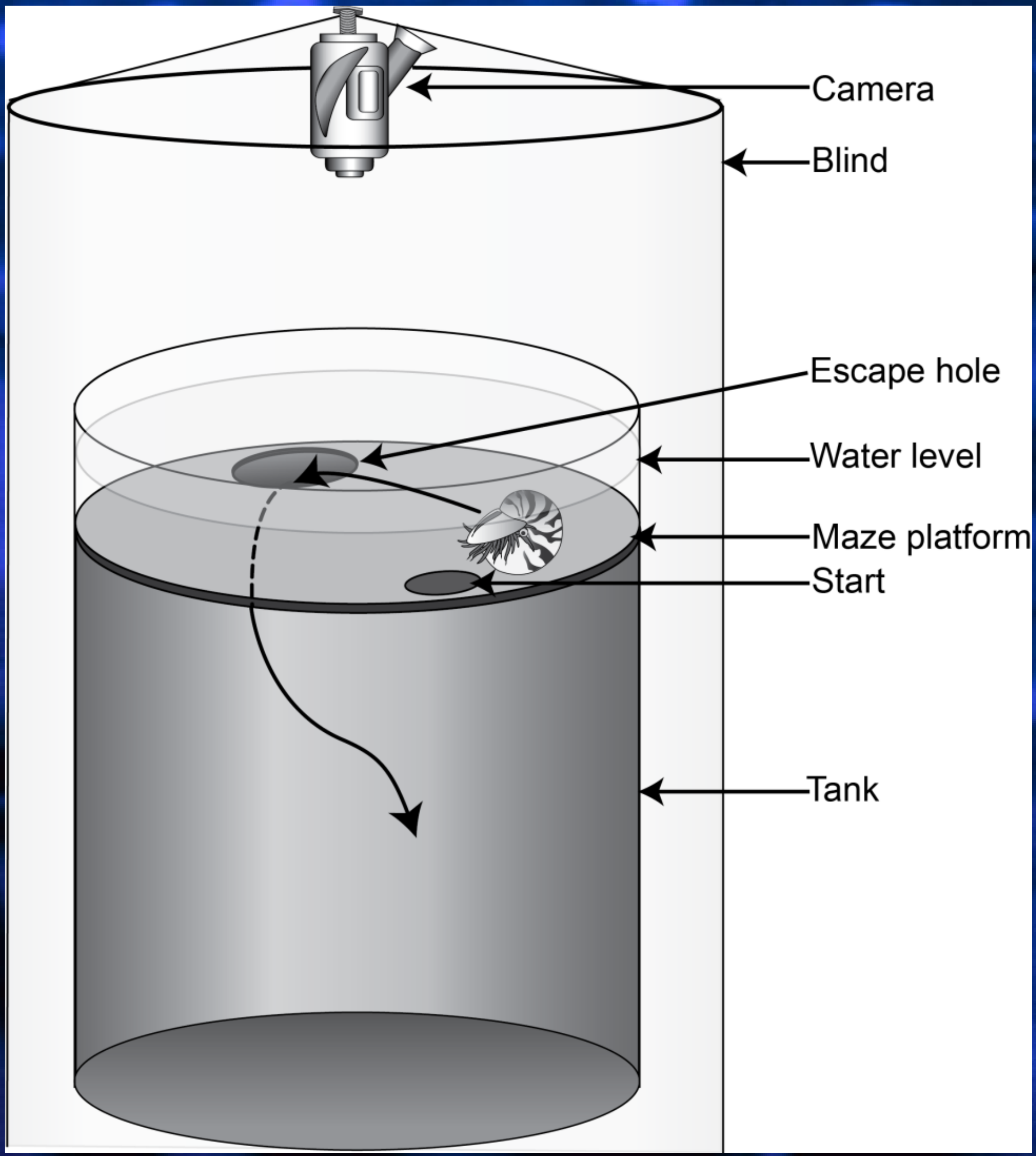
Environmental cues: local and global

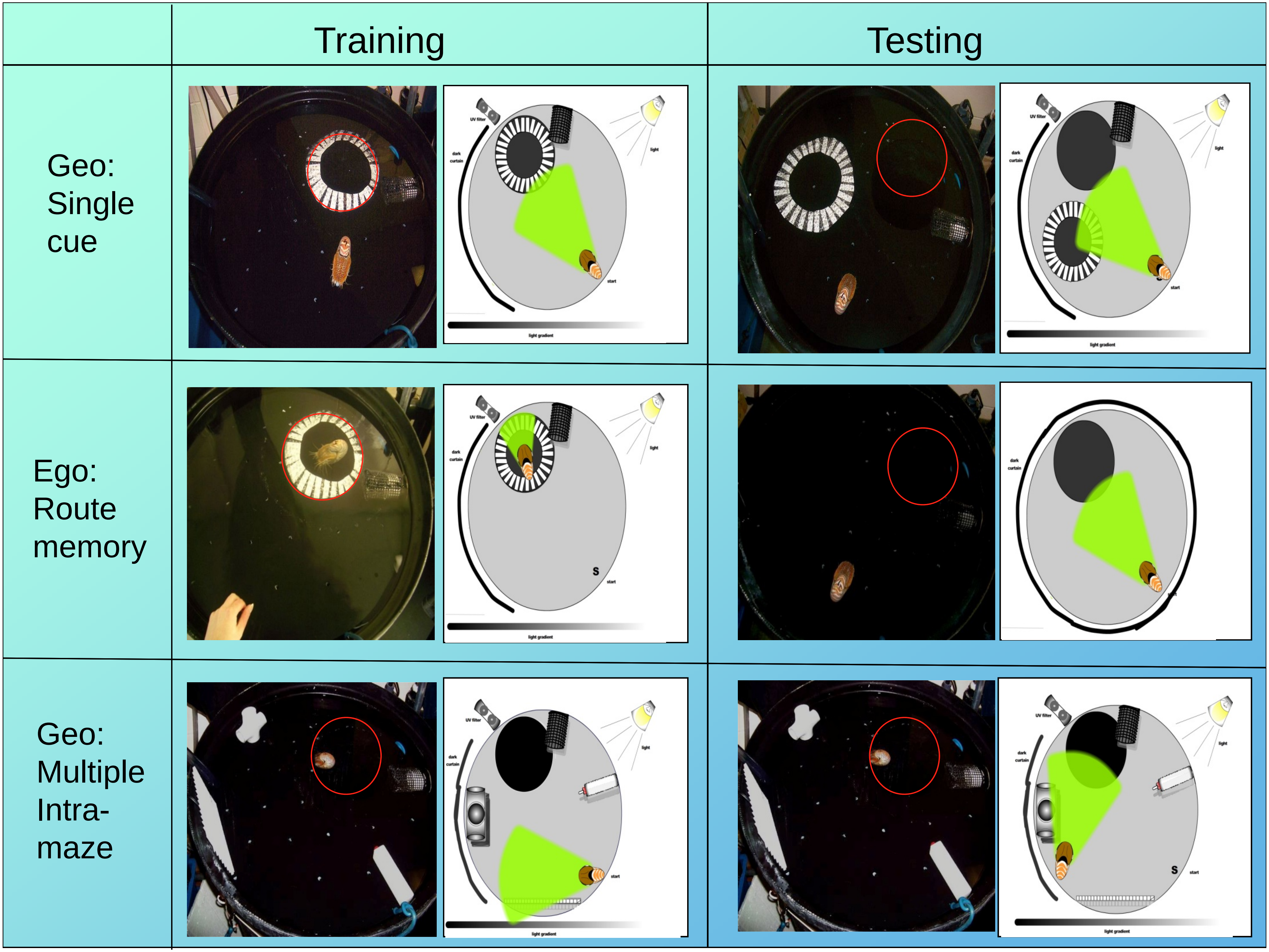
Single, proximal

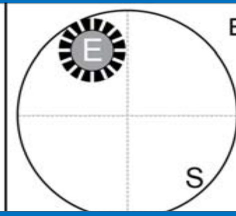
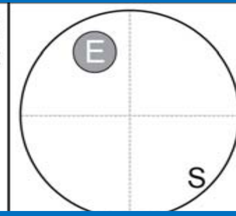
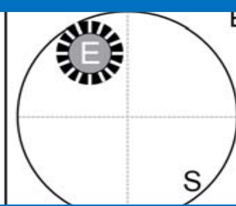
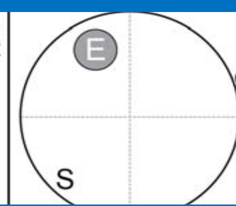
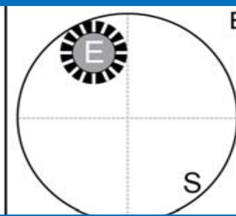
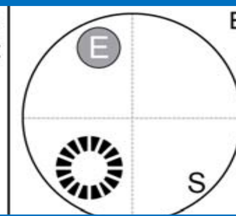
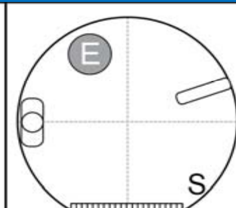
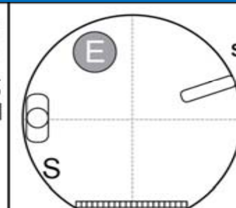
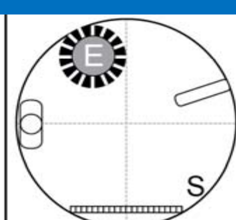
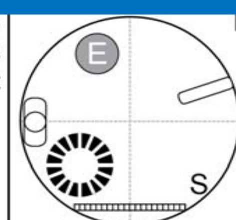
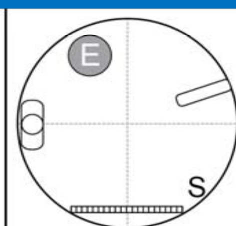
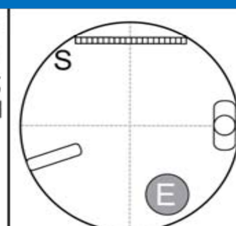


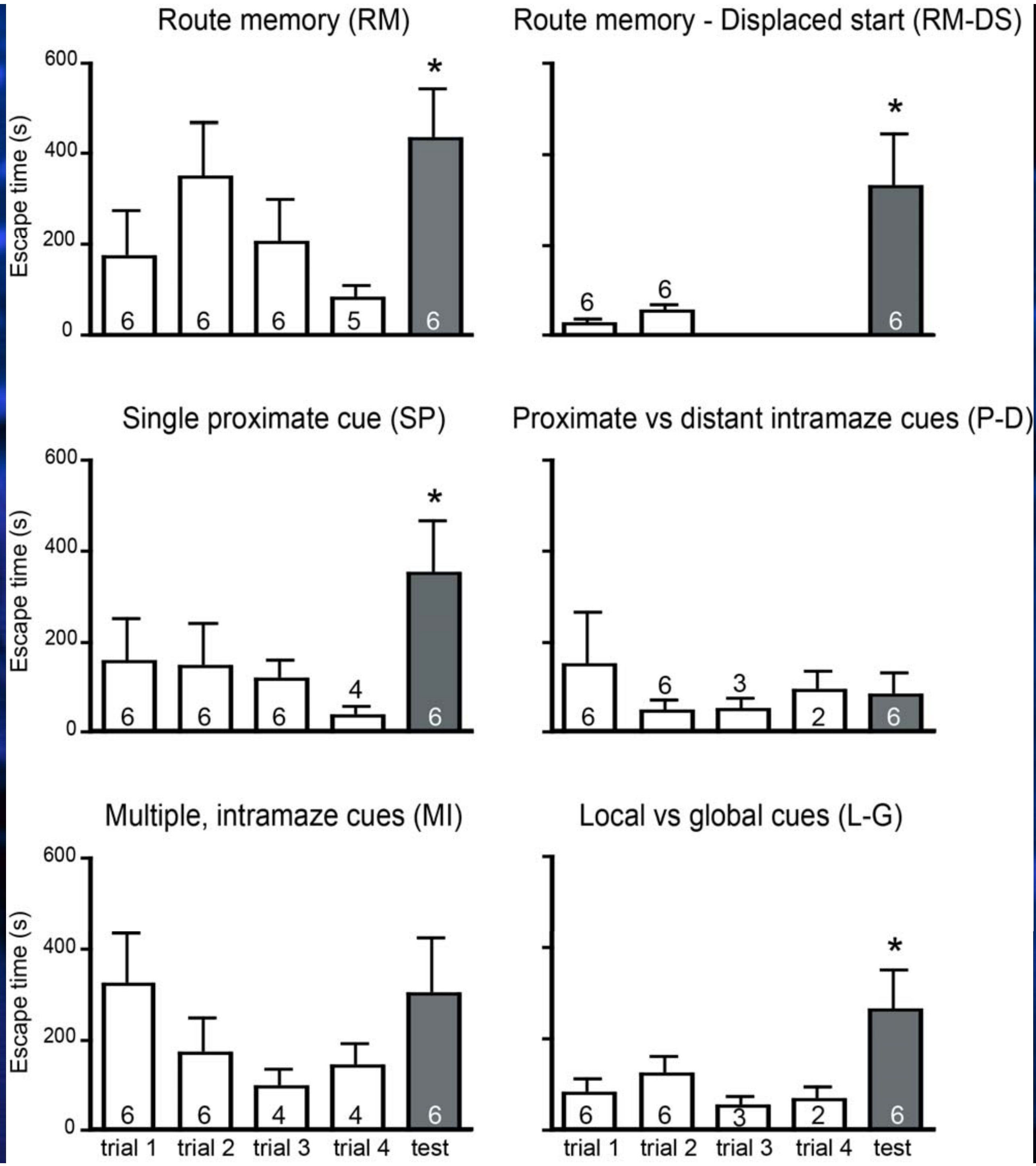
Local, global

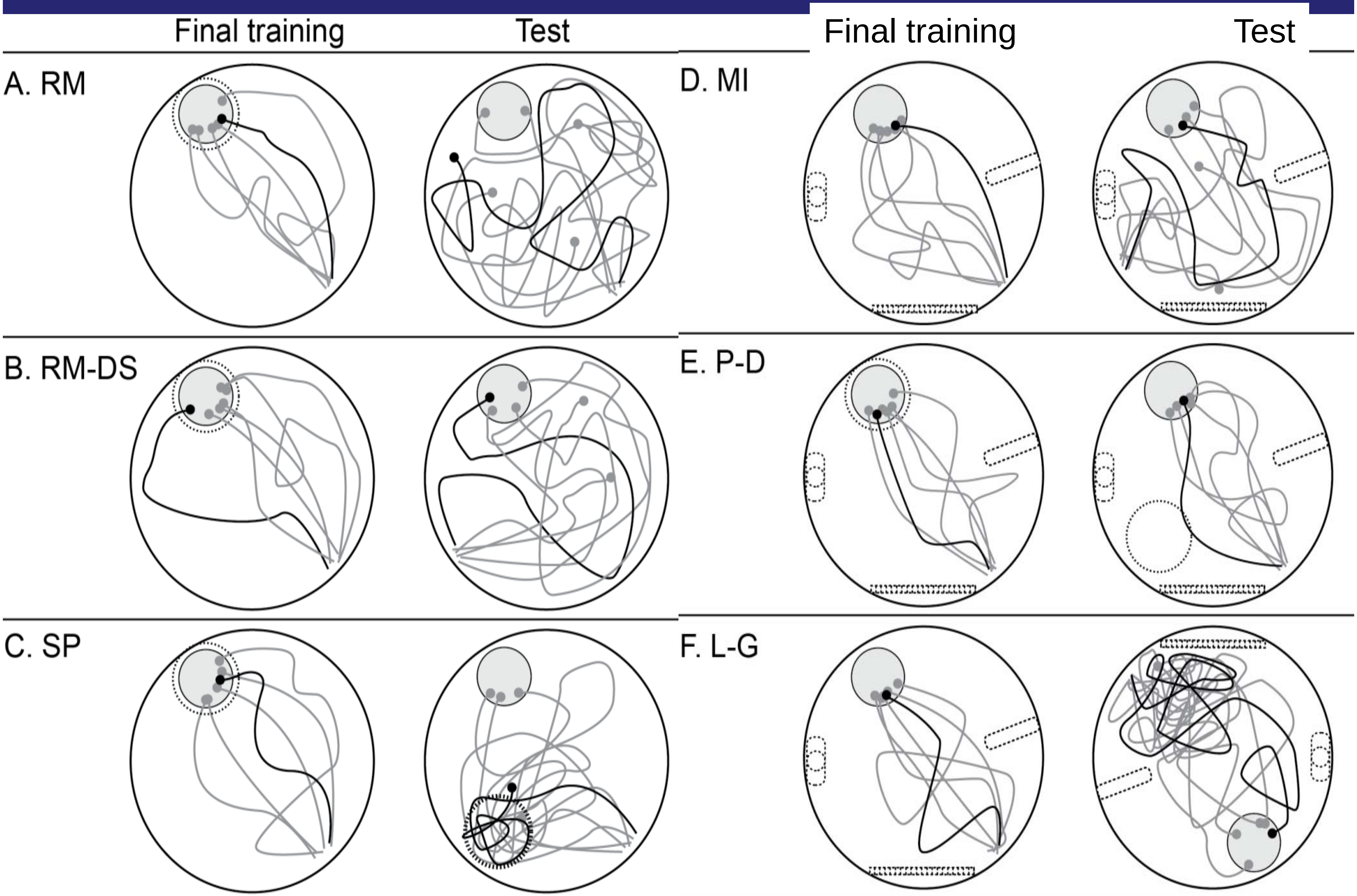
Spatial maze




Training
Testing
Geo: Single cue
Ego: Route memory
Geo: Multiple Intra-maze

Strategy being tested	Training configuration	Test configuration
A. Egocentric - Route memory (RM) Navigation tested in the absence of visual cues	 Beacon located at exit	 Beacon and extra-maze cues removed
B. Egocentric - Route memory (RM-DS) Navigation tested in the absence of visual cues and with a novel start position	 Beacon located at exit	 Beacon and extra-maze cues removed, start shifted 90° CW
C. Geocentric - Single, proximate cue (SP) A high-contrast visual cue 'beacon' signals the exit location	 Beacon located at exit	 Beacon shifted 90° CW
D. Geocentric - Multiple intra-maze cues (MI) Tests navigation based on a fixed geometric array of cues, none immediately signalling the exit	 Three distant landmarks around edge; exit unmarked	 Start position shifted 90° CW
E. Geocentric - Proximate vs. distant intramaze cues (P-D) Tests preference for a proximate cue vs. multiple distant cues	 All intramaze landmarks present	 Proximate and distant landmarks in conflict
F. Geocentric - Local vs. global cues (L-G) Tests the relative contribution of intra- vs. extra-maze cues	 Three distant landmarks around edge; exit unmarked	 Maze rotated 180° with respect to experiment room


Route memory (RM)
Route memory - Displaced start (RM-DS)
Single proximate cue (SP)
Proximate vs distant intramaze cues (P-D)
Multiple, intramaze cues (MI)
Local vs global cues (L-G)
Escape time (s)
0
200
400
600
trial 1
trial 2
trial 3
trial 4
test
*


Final training
Test
A. RM
B. RM-DS
C. SP
Final training
Test
D. MI
E. P-D
F. L-G

Vertic Ecology
Adept in vertical spatial maze

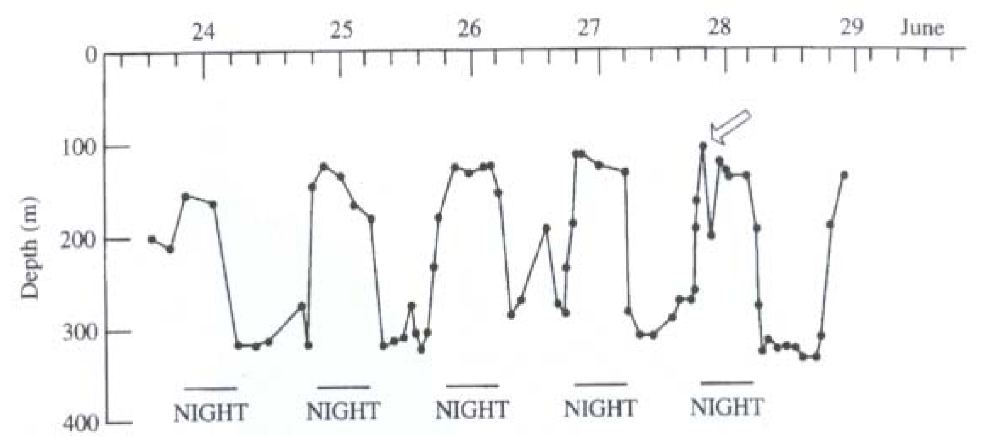
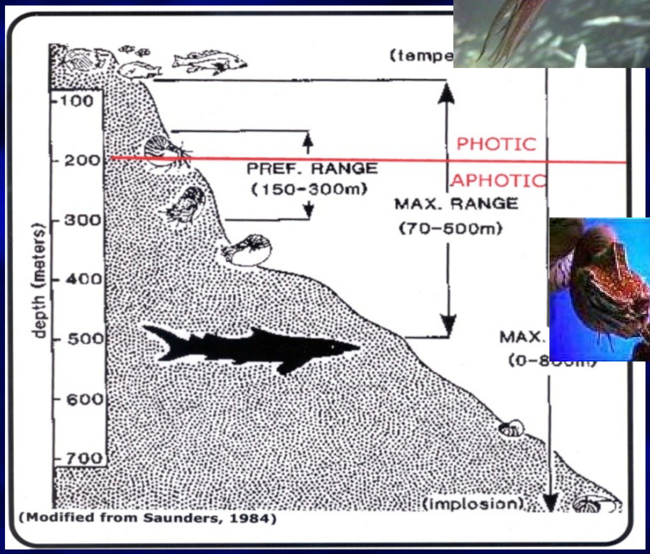


Fig. 10.4 Vertical movements of a tagged *Nautilus belauensis* followed over a six-day period in Palau. Note the sudden descent (arrow) one night at the onset of a full moon (from Ward *et al.*, 1984).

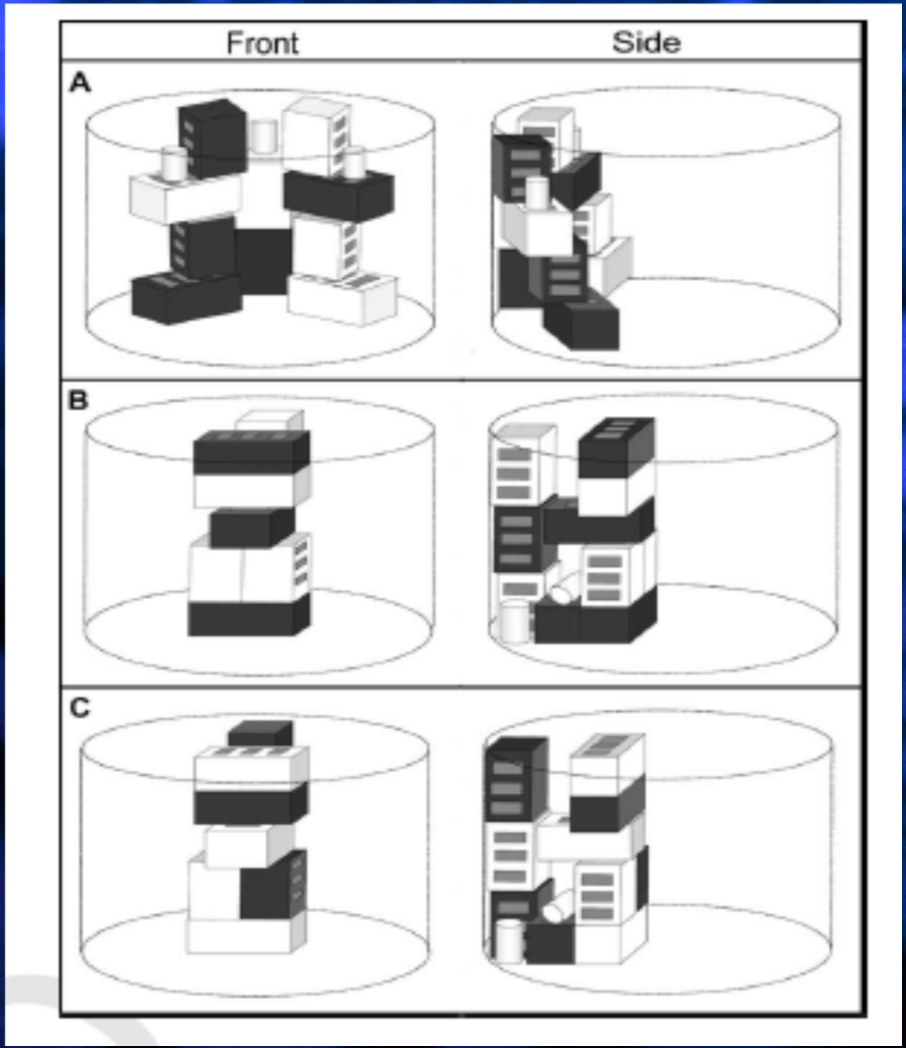


Scavenge and hunt on coral reef slopes in dim waters, bioluminescence

No defenses,
Hiding
Foraging
Hiding delicious eggs

Hanlon and Messenger, 1996

Vertic Ecology
Spatial vertical learning



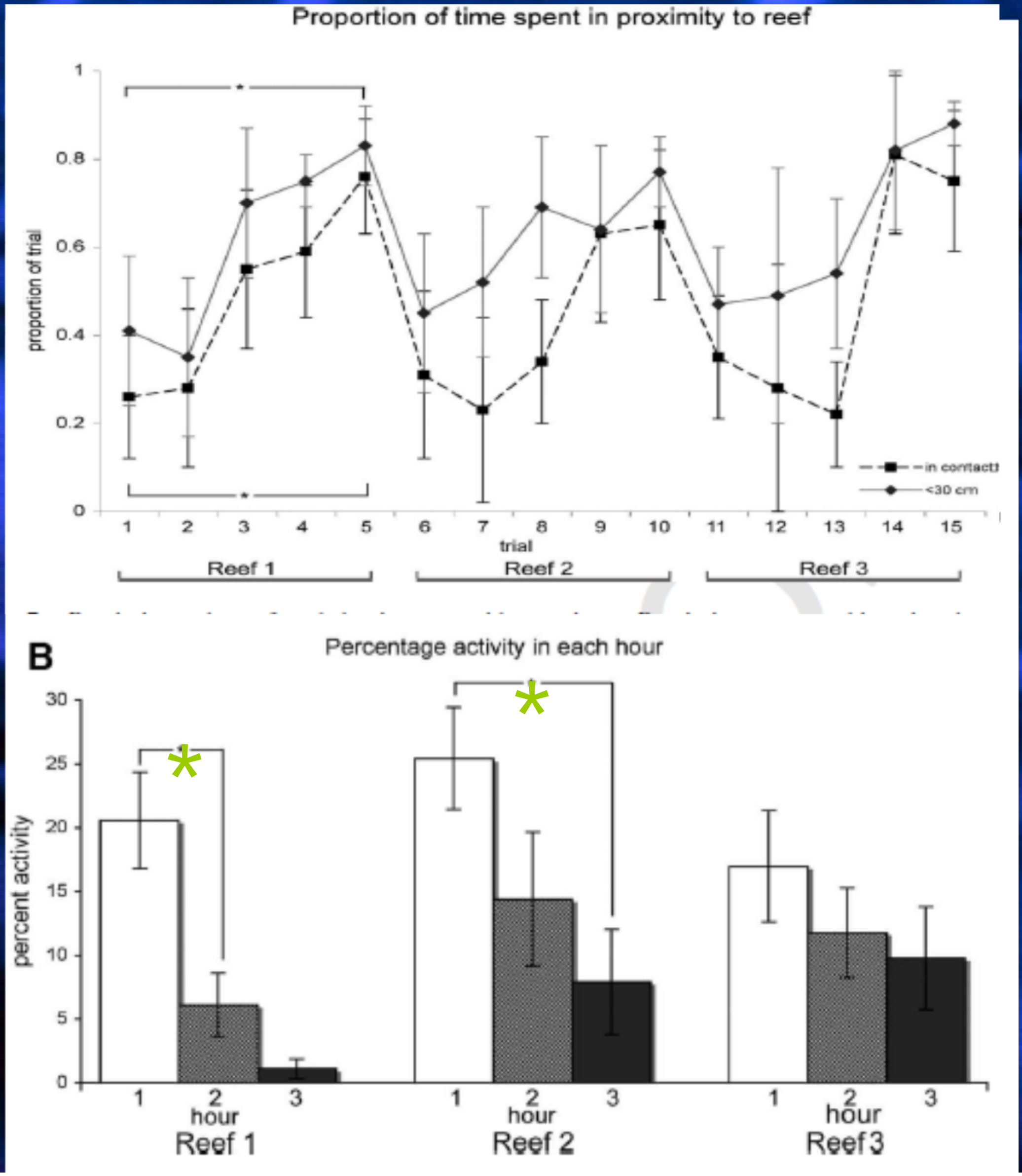
1) 3-D “reef”

2) Configurations
   A) B/W 1
   B) B/W **2**
   C) **W/B** 2

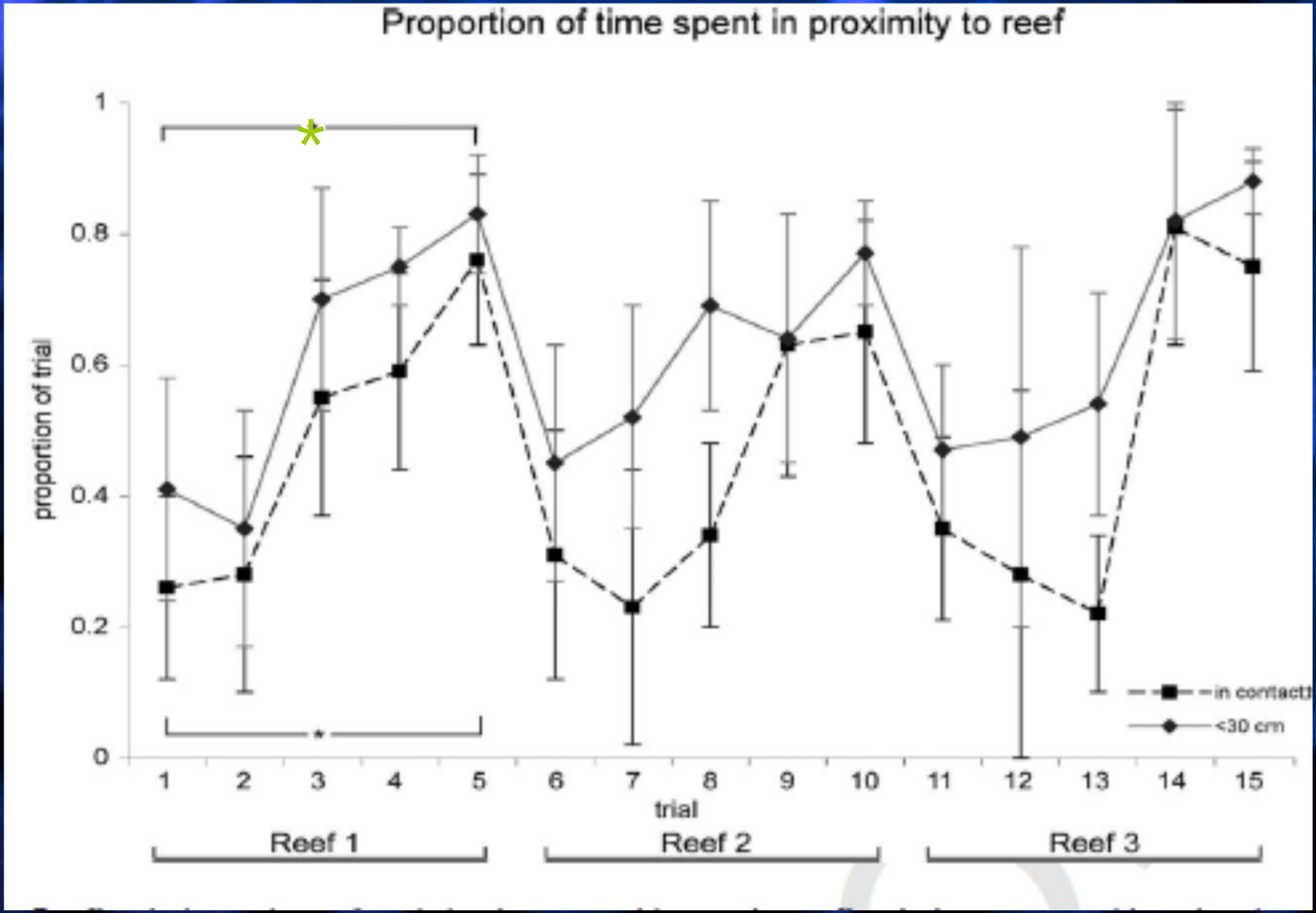
3) Exploration
   - habituation

Vertical 3D: learn and remember

Habituation: proximity and activity



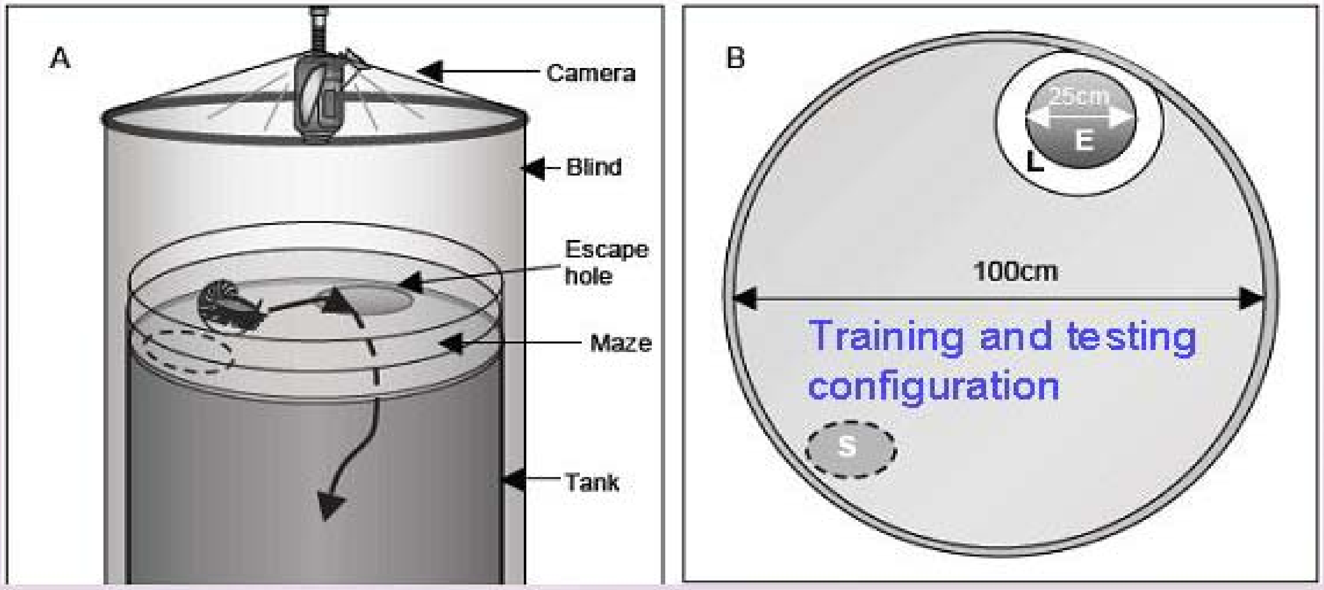
Proximity Increases



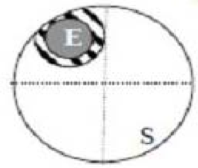
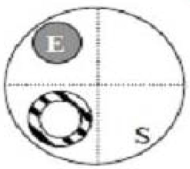
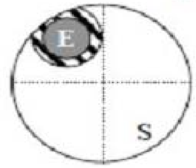
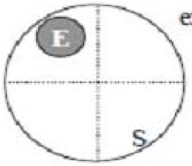
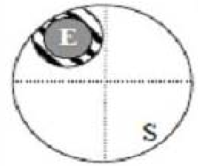
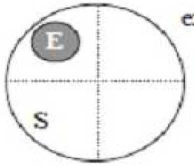
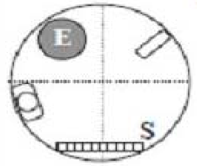
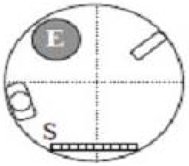
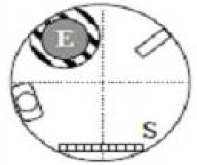
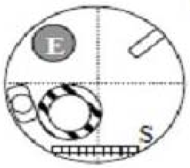
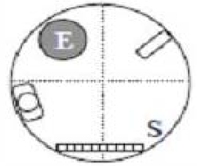
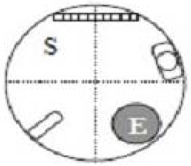
Spatial learning and memory in Nautiluses

Other cephalopods use spatial memory in their natural habitat (octopuses, cuttlefishes). Nautilus is a deep-water solitary species that must make daily migrations up and down coral-reef slopes. Memory for foraging sites and hiding places may be critical to a solitary animal with little in the way of defenses.

We tested spatial learning in a modified Morris-maze[18] where animals on a shallow platform sought an escape-hole into deep, dark water.



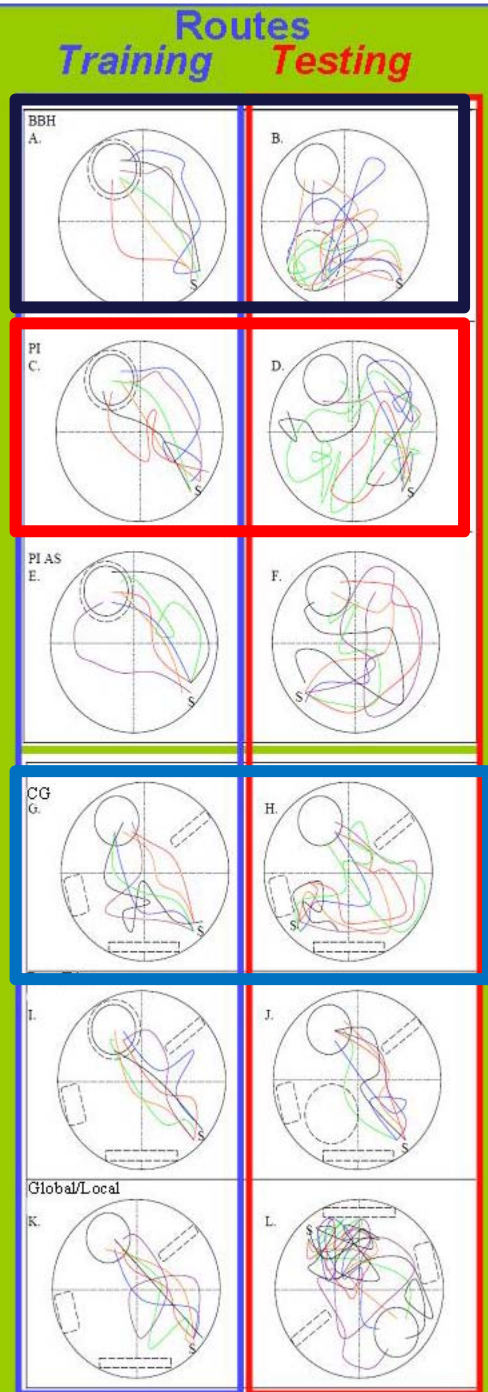
Stage 2, Path integration, cue geometry, salience

Hypothesis tested	Training configuration until criterion	Test configuration 2h after criterion
Beacon-based homing (BBH) A single landmark located proximate to the escape point.	 beacon located at exit.	 beacon moved to adjacent quadrant
Dead Reckoning Navigation tested in the absence of geocentric cues.	 beacon located at exit.	 beacon and extra-maze cues removed
Dead Reckoning AS) Tested in the absence of geocentric cues and with a novel start position	 beacon located at exit.	 beacon and extra-maze cues removed, start position moved 90°
Cue Geometry (CG) Tests navigation using known landmark array. Starting from a novel position	 hole unmarked, distant landmarks around maze	 landmarks constant, start position moved 90°
Proximate vs. Distant Cues (ALL) Navigation tested when proximate and distant cues are in conflict	 All intra-maze landmarks present	 proximate and distant landmarks in conflict
Local vs. Global Cues (L-G) Tests the relative contribution of intra- and extra-maze cues to navigation	 hole unmarked distant landmarks around maze	 entire maze shifted 180° with respect to experiment room

N=6 Animals, counterbalanced presentation

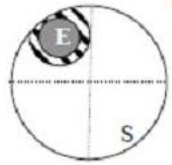
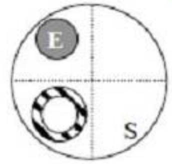
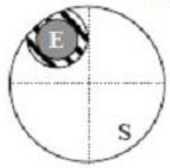
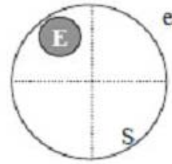
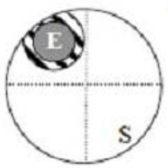
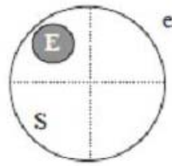
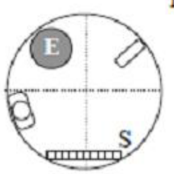
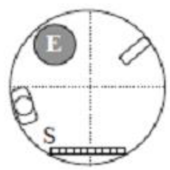
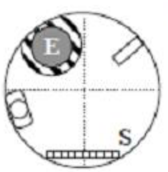
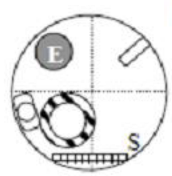
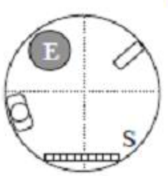
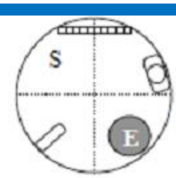
Stage 2, Path integration, cue geometry, salience

Hypothesis tested	Training configuration until criterion	Test configuration 2h after criterion
Beacon-based homing (BBH) A single landmark located proximate to the escape point.	beacon located at exit.	beacon moved to adjacent quadrant
Dead Reckoning Navigation tested in the absence of geocentric cues.	beacon located at exit.	beacon and extra-maze cues removed
Dead Reckoning -AS Tested in the absence of geocentric cues and with a novel start position	beacon located at exit.	beacon and extra-maze cues removed, start position moved 90°
Cue Geometry (CG) Tests navigation using known landmark array. Starting from a novel position	hole unmarked, distant landmarks around maze	landmarks constant, start position moved 90°
Proximate vs. Distant Cues (ALL) Navigation tested when proximate and distant cues are in conflict	All intra-maze landmarks present	proximate and distant landmarks in conflict
Local vs. Global Cues (L-G) Tests the relative contribution of intra- and extra-maze cues to navigation	hole unmarked distant landmarks around maze	entire maze shifted 180° with respect to experiment room

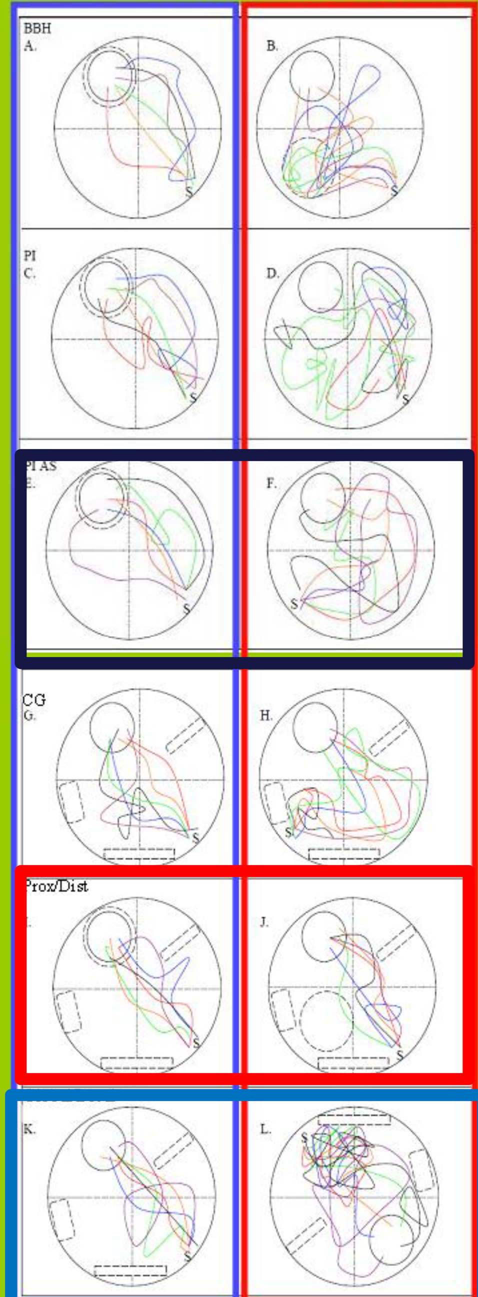


N=6 Animals, counterbalanced presentation

Stage 2, Path integration, cue geometry, salience

Hypothesis tested	Training configuration until criterion		Test configuration 2h after criterion	
Beacon-based homing (BBH) A single landmark located proximate to the escape point.		beacon located at exit.		beacon moved to adjacent quadrant
Path Integration (PI) Dead Reckoning absence of geocentric cues.		beacon located at exit.		beacon and extra-maze cues removed
Dead Reckoning -AS Tested in the absence of geocentric cues and with a novel start position		beacon located at exit.		beacon and extra-maze cues removed, start position moved 90°
Cue Geometry (CG) Tests navigation using known landmark array. Starting from a novel position		hole unmarked, distant landmarks around maze		landmarks constant, start position moved 90°
Proximate vs. Distant Cues (ALL) Navigation tested when proximate and distant cues are in conflict		All intra-maze landmarks present		proximate and distant landmarks in conflict
Tests the relative contribution of intra- and extra-maze cues to navigation		distant landmarks around maze		shifted 180° with respect to experiment room

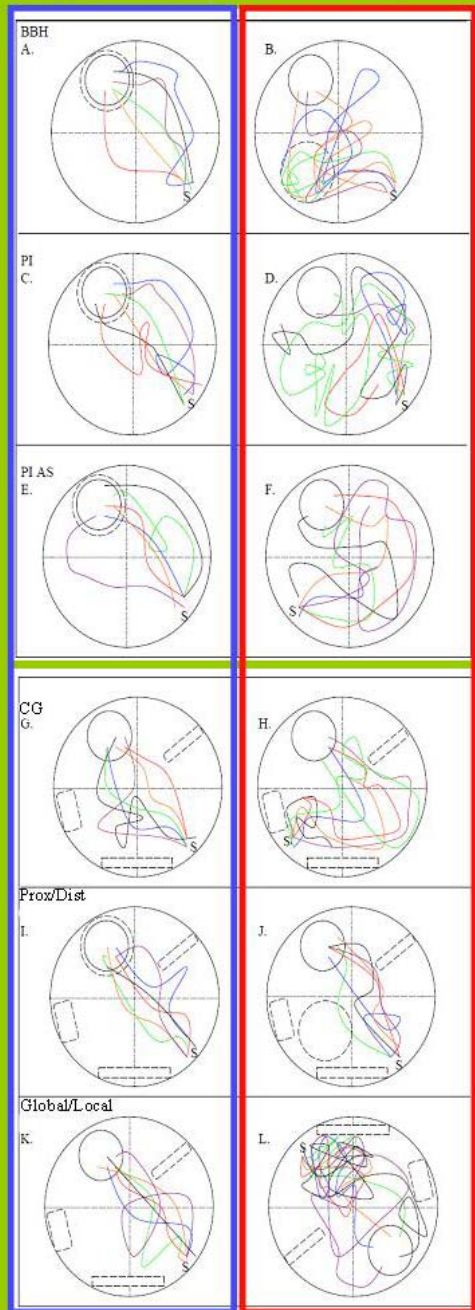
Routes



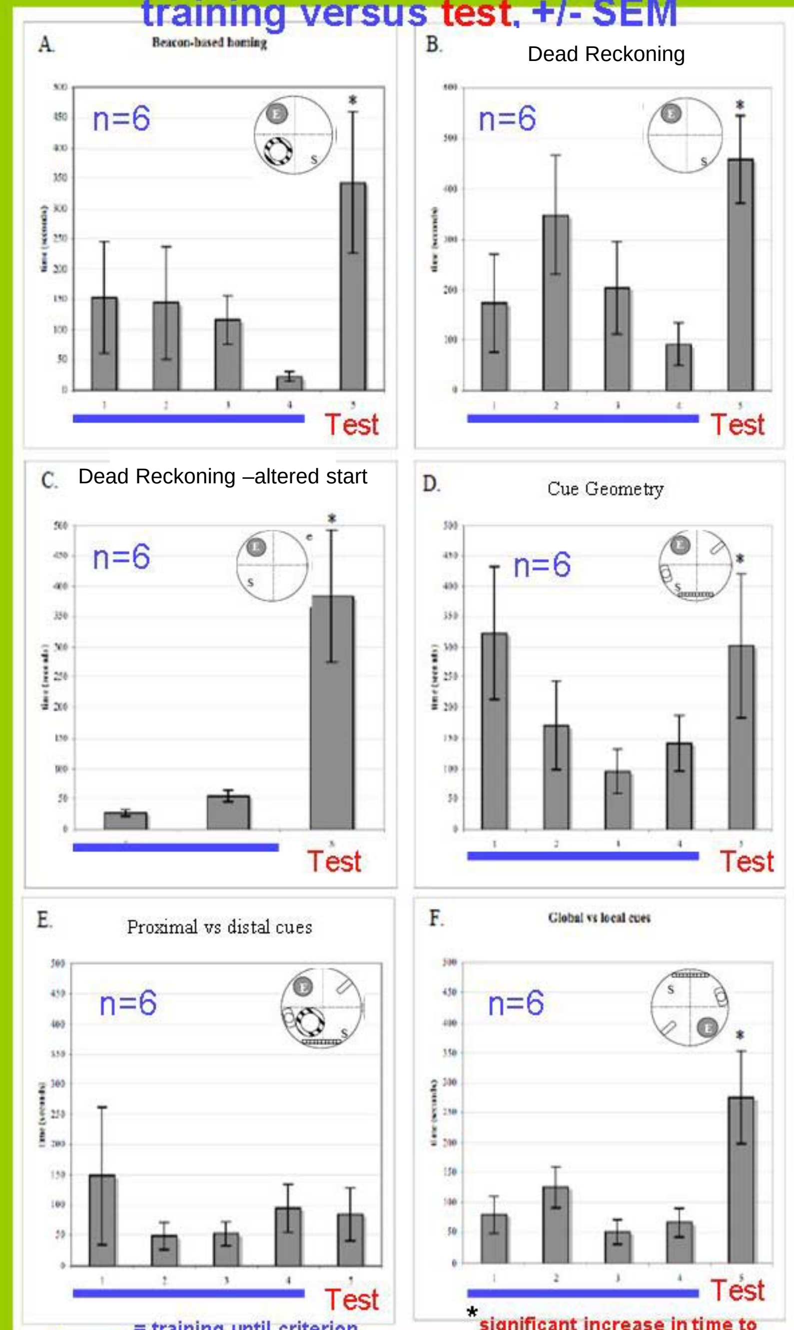
N=6 Animals, counterbalanced presentation

Routes

Training *Testing*



Latency to find spatial goal training versus test, +/- SEM



= training until criterion of 2 escapes in 2 min

* significant increase in time to find goal location

Learning: ecological reflections

- **Ecological Associations: learn to associate ecologically relevant stimuli – bioluminescent carrion matched with odor? Now test in field.**
- **Spatial Problems In nature:** Both beacon-based homing and cue-geometry navigation are plausible in the natural environment
- **Vertic:** Nautiluses learn and remember the 3-d configuration of an artificial coral reef, like complex cue arrays in their coral-reef environment. Now test in field.
- **Beacons:** Animals learn and remember BEACONS, suggesting that this was a highly salient cue. Currently testing in a vertical array and in field
- **Dead Reckoning:** At first, animals did not appear to search systematically for the exit and mostly failed to complete the test trial. *With more training, they do express dead reckoning.*
  - We further test for DR on smaller time scales, and also in a vertical array.
- **Distant Cues:** Animals were able to decode a familiar array when they were in a particular vantage point (snap-shot hypothesis?). *These cues override shifted beacon.*
- **Global Cues:** When maze shifted relative to room, animals use global cues, *overriding distant cues.*
- **Ongoing: We** now test whether dead reckoning is an underlying parallel memory module running concurrently with the use of beacons and/or cues.
- EGG cues? Versus nautiluses, octopuses, fish.
- *Culturing*
- *Acknowledgements…*

Current directions

1) Comparative cognition

2) Comparative sensory ecology

3) Comparative field studies

generate hypotheses about cognitive adaptations.

4) Care and Culture

Thank you:

Dr. Robyn Crook

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Dr. Frank Grasso

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Dr. Robert Rockwell

Greg Barord

Staff of AREAC

And…

Dr. Roger Hanlon

Dr. Binyamin Hochner

Dr. Michael Kuba

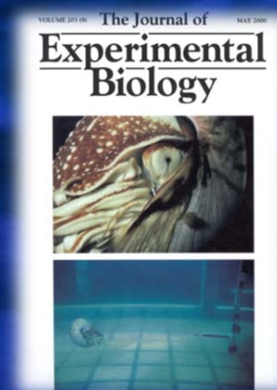
The Grass Lab

Grass Foundation

National Science Foundation

US/Israel Binational Science Foundation

Nautiluses



The LIBE Laboratory
7 days a week, cross trained!

Phylogenetic history behavioral and CNS complexity

- Comparative evidence points to evolutionary scenario:
  - Brain and behavioral complexity likely existed in the nautiloid lineage long before the parametric “cognitive radiation” in coleoids.
  - Nautiloids are critical lineage in these continuing comparative studies.



Thank you:

Dr. **Robyn Crook**

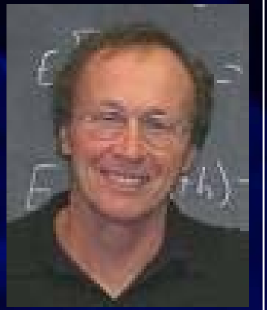
Staff of AREAC

Dr. Frank Grasso

Dr. Robert Rockwell

Dr. Chris Soucier

And…



Dr. Roger Hanlon

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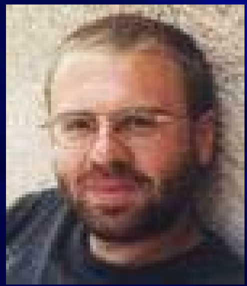

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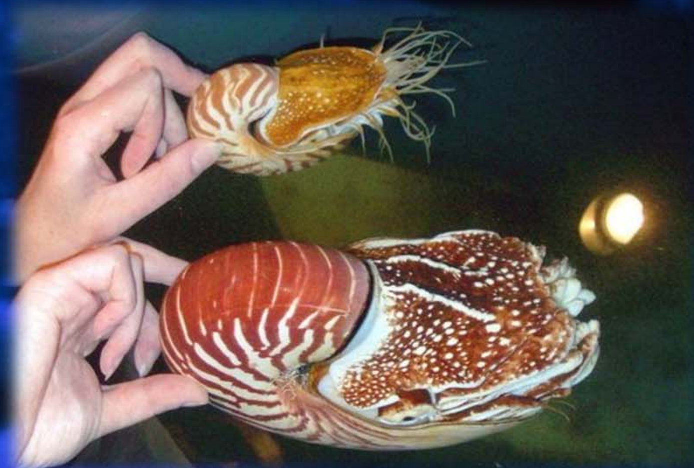
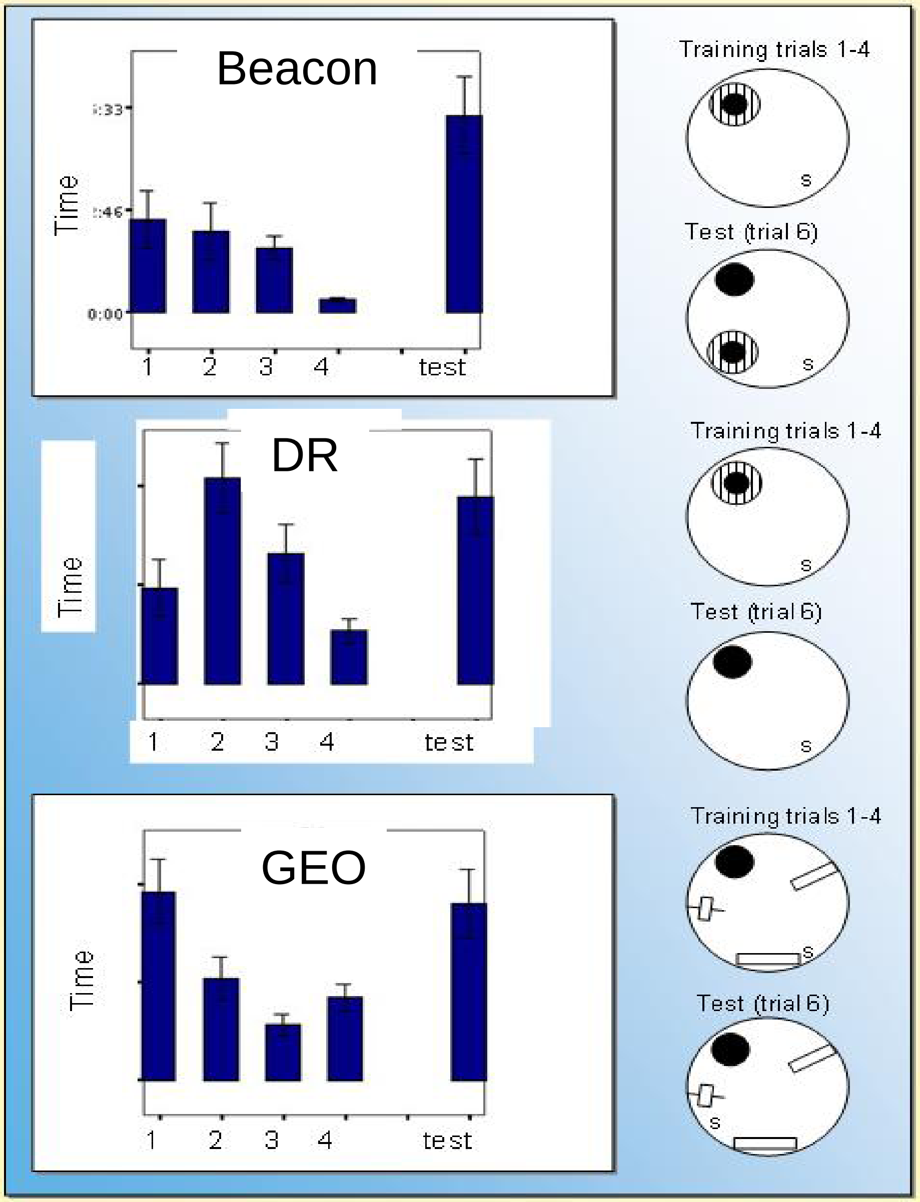


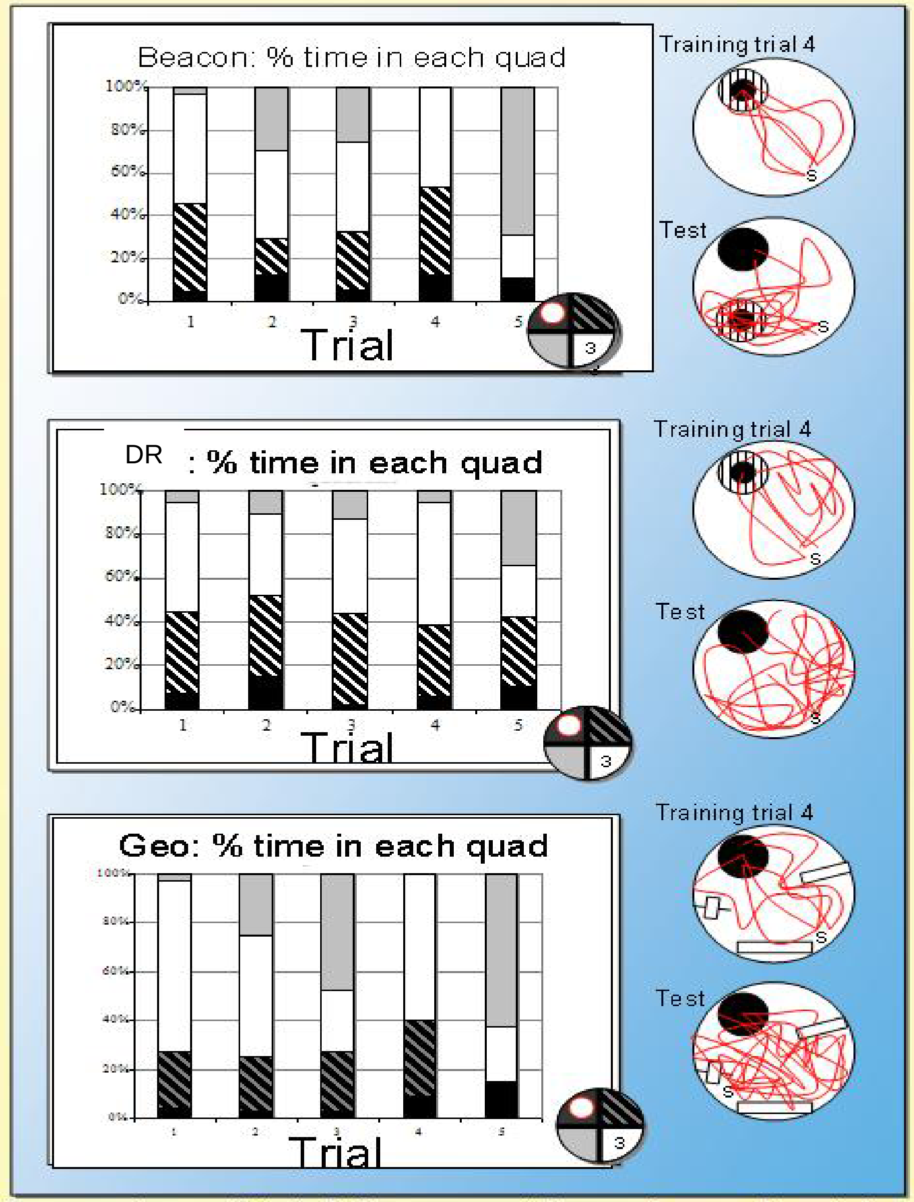
Nautiluses

The LIBE Laboratory



Training: animals learn the route to the exit, and time taken to escape decreases.

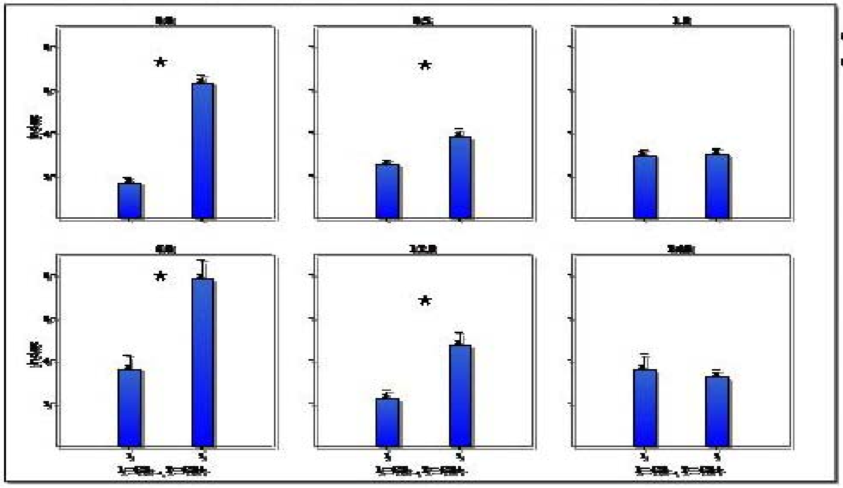
Testing: Time taken increases dramatically.



Percentage of total time spent in each quadrant. In *BH*, animals spend more time in Q4 when the beacon is shifted there during testing. In *PI* tests there is no clearly preferred quadrant. In *Geo* animals spend more time in Q4 where they start, but little in Q2. Route maps of each animal are shown for trials 4 and 5.

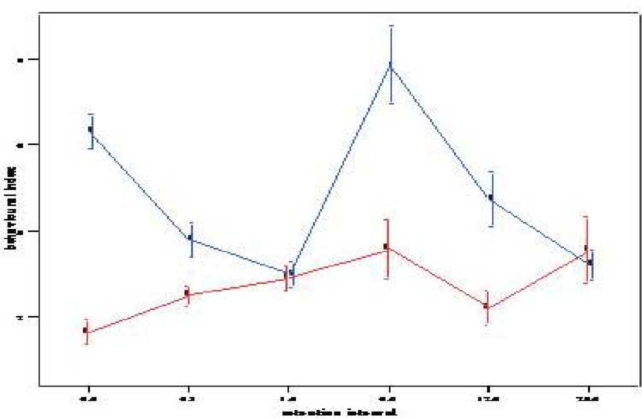
Behavioural Index scores in control (CS-) and conditioned (CS+) animals at each retention interval

A. Mean behavioural index scores at each retention interval

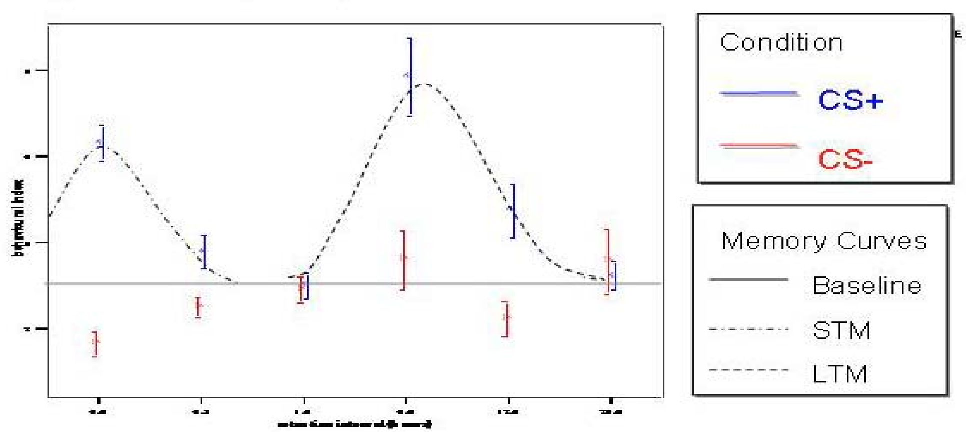


A: Graph shows mean behavioural index scores for control (CS-) and conditioned (CS+) animals at each retention interval. n=6 for all groups. Index scores are significantly different at 3 minutes and 30 minutes, indicating presence of STM in conditioned animals. There is no evidence of memory at 1 hour. At 6 hours and 12 hours post-training, scores are significantly different, indicating LTM in conditioned animals. By 24 hours there is no evidence of LTM persistence.

B.



C.

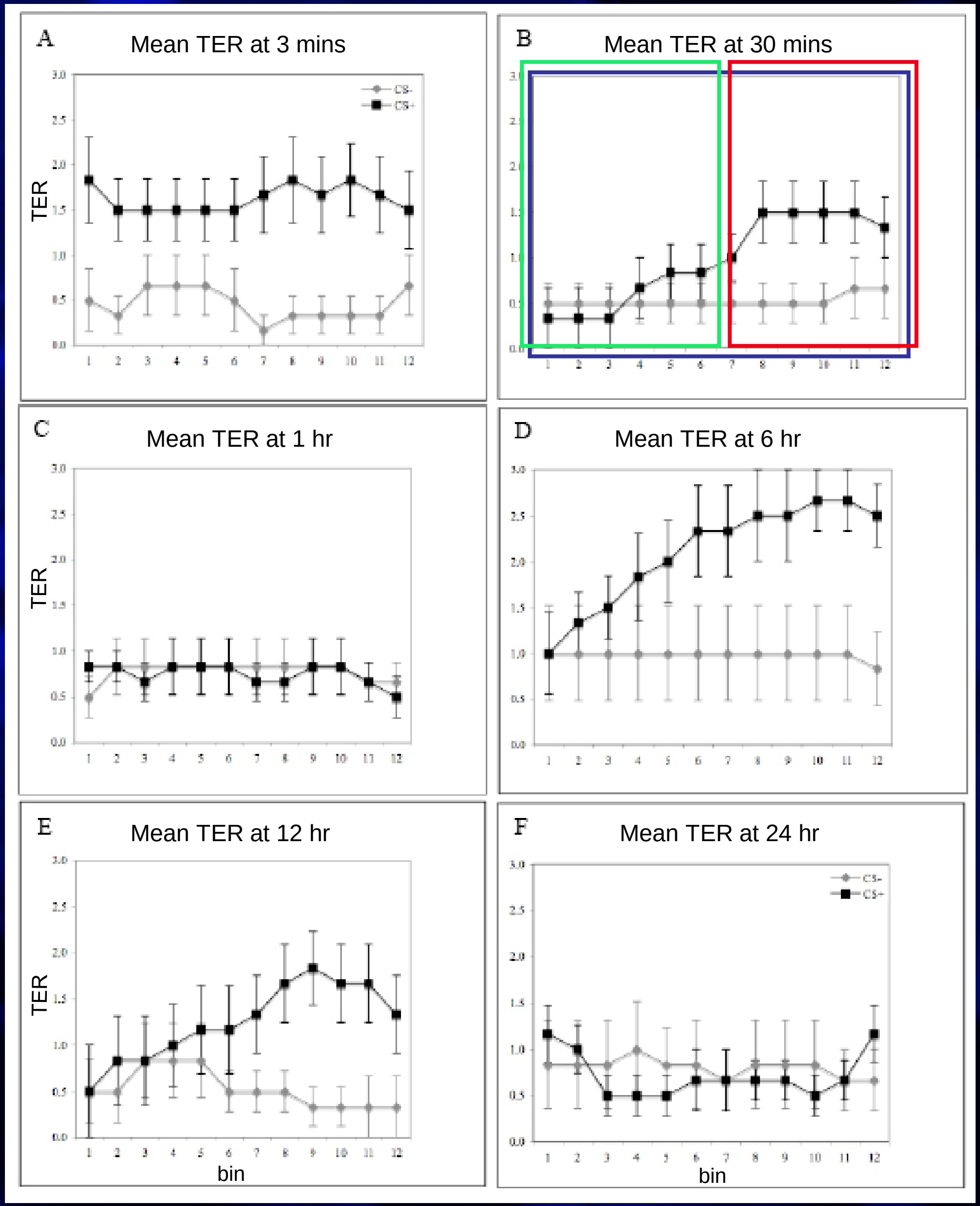


B. Mean behavioural index scores across time periods. C. Hypothetical memory curves and baseline response level, superimposed over the same points. Curves indicate the probable duration of short- and long-term memory (STM and LTM, respectively). Error bars are ± 1 SE of the mean. * denotes a significant difference between CS+ and CS- groups.

Results

- 5-s ‘bin’ after light exposure showed differential responses as a function of time

- Similar trends in ventilation data



Modern Cephalopod Relationships

Nautilus monophyletic: fewer chromasomes, longer 18sDNA

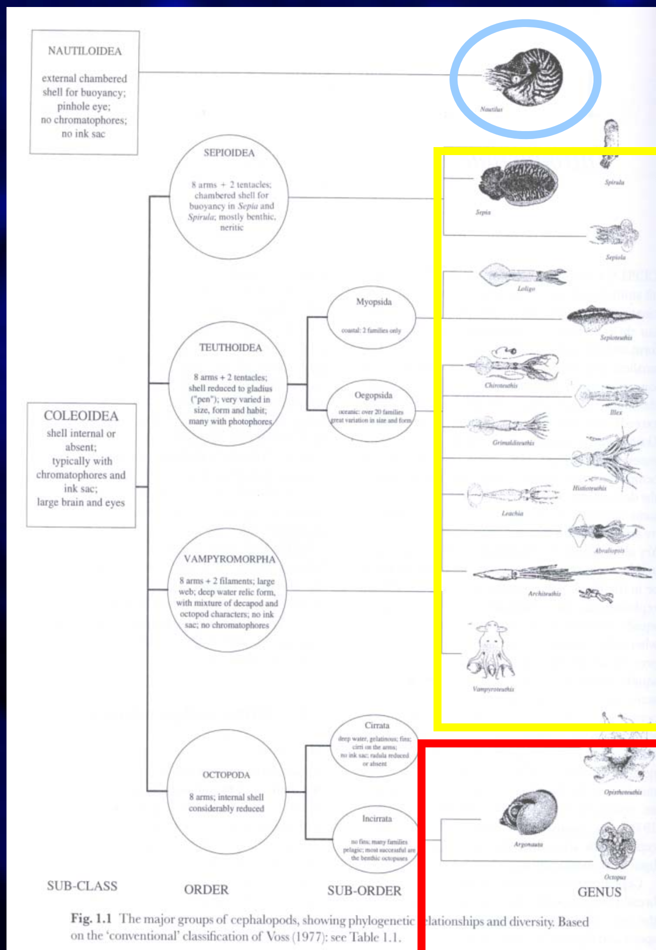


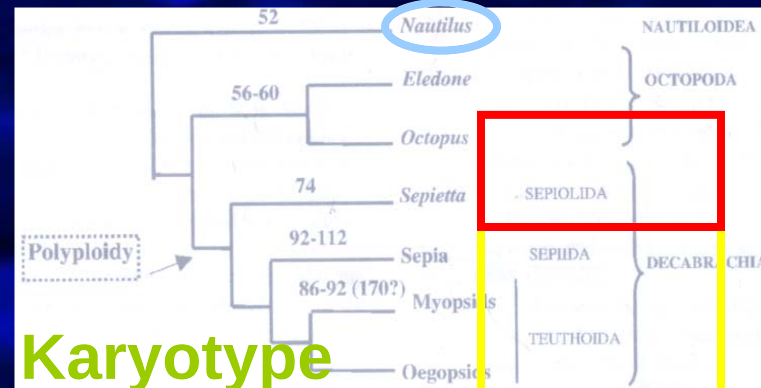
Fig. 1.1 The major groups of cephalopods, showing phylogenetic relationships and diversity. Based on the 'conventional' classification of Voss (1977); see Table 1.1.

90

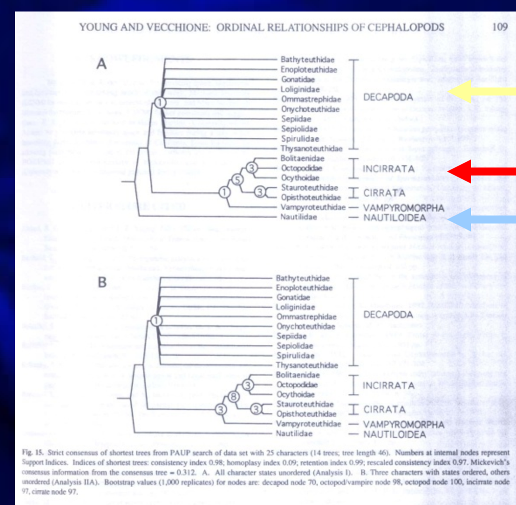
10

8

Morphological Characters



Karyotype

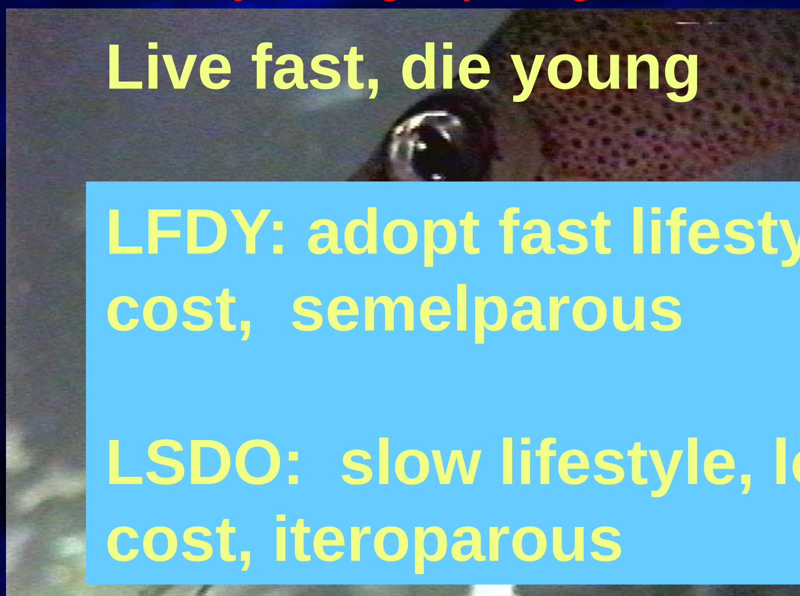


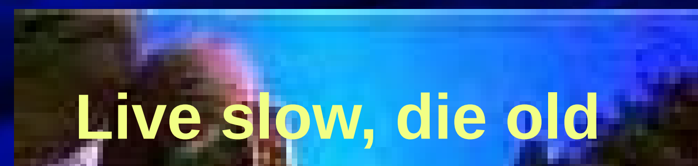
Strugnell, Bonnaud

Modern Cephalopods

Shell loss and retention:locomotion

lose/reduce shells
pelagic, nektonic
visual predatory lifestyle
avoid fishes
Some solitary, some group living





LFDY: adopt fast lifestyle, high metabolic cost, semelparous

LSDO: slow lifestyle, low metabolic cost, iteroparous

shell for protection
less prime deeper water
slow, smellers and gropers
tolerate high pressures
avoidance of nekton
all solitary, nocturnal

Live fast, die young, metabolic needs high

Coleoids/Fishes

Detection at a distance, but tracking?
Conspecifics, SW
vibration sensitivity

Taste/touch

Nektic

Cretaceous

Jawed fishes

Reptiles

Buoyancy
Locomotor
Velocity
Equilibrium

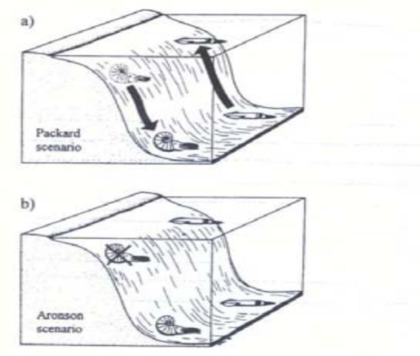
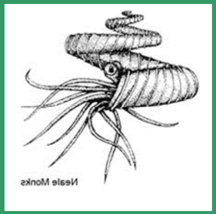


Fig. 1.6 Two schemes for the origin of the coleoids. (a) According to Packard competition during the Mesozoic pushed the ectocochleates into deep water, where they lost the shell prior to re-invading shallow water. (b) According to Aronson ectocochleates and coleoids co-existed in shallow and deep water during the Palaeozoic. Subsequently, the ectocochleates were eliminated from shallows water (from Aronson, 1991).

Ecological

Vertic

Detection at a distance *and tracking*.
seek out mates
scavenging for prey
vibration sensitivity



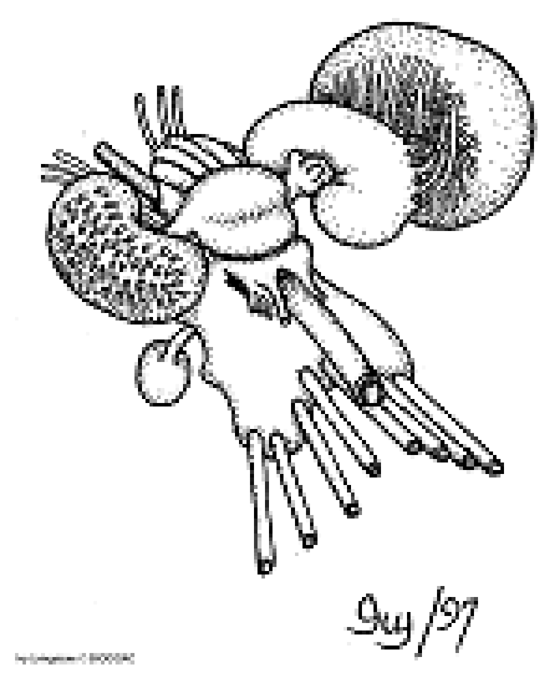
Ectocochleates

Live slow, die old, metabolic needs low

Despite these differences: they all have big brains (some bigger than others) …and they use them.

Cuttlefishes: learned taste aversion

Nautiluses: classical conditioning of light t
spatial memory up to 3 weeks.
~but no vertical lobe



Phylogenetic history: canalization due to telec
Ecological adaptations and constrants: locom
CNS: Networks that use, learn, and remember

Coleoids/Fishes

Cretaceous

Jawed fishes

Nektic

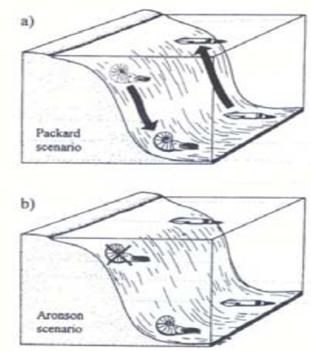
Buoyancy

Locomotor

Velocity

Pressure

Equilibrium



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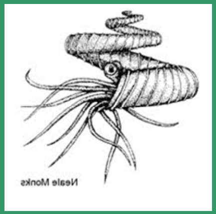
Ecological

Vertic

Reptiles



Ectocochleates