Whales as Marine Ecosystem Engineers

J. B. Nation, Joe Roman, Craig Smith, James A. Estes, Lyne Morissette, Daniel Costa, James McCarthy, Stephen Nicol, Andrew Pershing, Victor Smetacek

IWSS, UNBC, December 2021

Outline

- Sustainable harvesting
- History of whaling
- How great whales affect ocean ecology
  1. Whales as predators
  2. Whales as prey
  3. Whales as pumps
  4. Whales as detritus
- Whale-fall specialists
- Prospects for the future

Based largely on 2 papers

- J. Roman, J. Estes, C. Smith, J. Nation, D. Costa, J. McCarthy, L. Morissette, S. Nicole, A. Pershing, V. Smetacek, **Whales as ecosystem engineers**, Frontiers in Ecology and the Environment (2014)
- C. R. Smith, J. Roman and J. B. Nation, **A metapopulation model for whale-fall specialists: the importance of whale body size to species persistence**, The Sea: The Current and Future Ocean, J. Marine Research (2019)

Thanks for Joe Roman and Craig Smith for many slides and notes.

De la Cosmographie Universelle

Logistic model for a single natural population

A natural population $N(t)$ without harvesting satisfies

$$\frac{dN}{dt} = f(N) = aN - bN^2 = rN(1 - \frac{N}{K})$$

with stable equilibria at $N = 0$ and $N = K$, where
r is the **reproduction rate** = (births $-$ deaths) per capita, and
K is the **carrying capacity** of the environment.
The solution is

$$N = \frac{K}{1 + e^{-rt}(\frac{K}{N_0} - 1)}$$

which tends to K as $t \to \infty$.

(Following J. D. Murray, Mathematical Biology for this section)

Solution of logistic equation

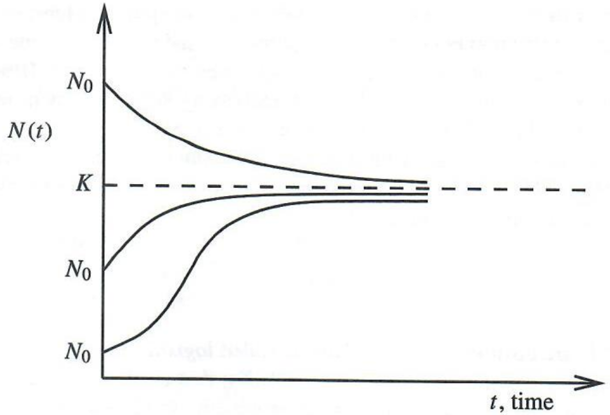


Figure 1.1. Logistic population growth. Note the qualitative difference for the two cases $N_0 < K/2$ and $K > N_0 > K/2$.

Logistic model with harvesting

Now add harvesting at a rate E, the fraction of the population harvested annually:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) - EN$$
$$= (r - E)N - \frac{r}{K}N$$

with equilibria at $N = 0$ and $N = K(1 - \frac{E}{r})$ if $E < r$, and only $N = 0$ if $E \geq r$.
The steady state yield is

$$Y(E) = EK(1 - \frac{E}{r})$$

which has a maximum yield at $E = \frac{r}{2}$ with

$$Y_{max} = \frac{rK}{4} \qquad N_{max} = \frac{K}{2}$$

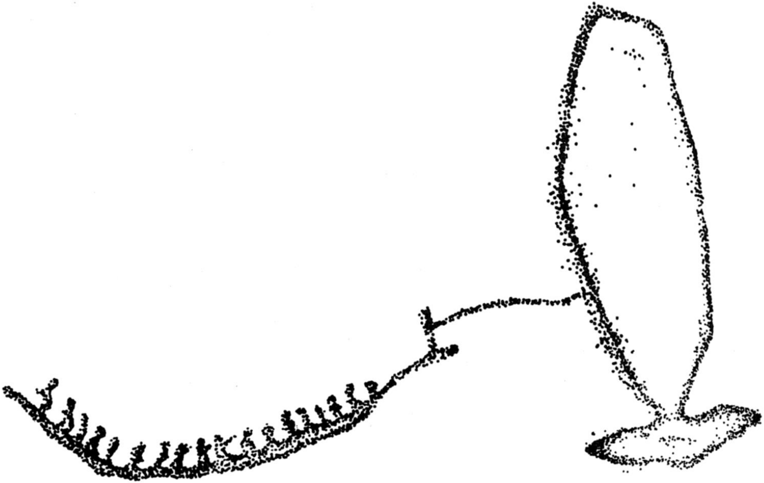
Conclusions

- The logistic model is oversimplified but makes a good starting point.
- In particular, the harvesting rate E varies with time.
- $E > r$ is not sustainable, leading to extinction.
- The maximum yield is at $E = \frac{r}{2}$ which maximizes the growth rate.
- **Pre-harvesting populations can be used to estimate K.**
- **This should be taught in calculus!**

We will look at some of the data for whales and whaling, but first ....

History of whaling

Whaling by coastal populations from around 6000 BCE



Korea ~ 2000 BC

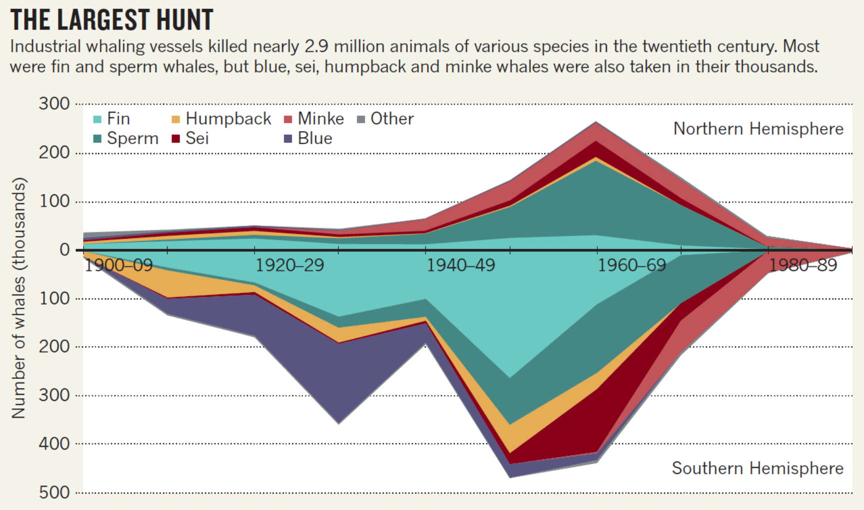
Commercial whaling

- Basques begin hunting North Atlantic right whales c. 1000 CE, slowly expanding over 5 centuries
- Whales were hunted for
  - meat,
  - oil (fuel, lubrication, and the manufacture of nitroglycerine),
  - baleen (or whalebone, prized for flexibility and strength),
  - spermacetti (from sperm whales, used for candles, ointments, and industrial lubricants).
- In the early 1600s, Europeans start hunting the Arctic for bowhead whales, joined by Japanese in 1675.
- Beginning of American commercial whaling industry in 1712 out of Nantucket.
- Sperm whales are especially valued in the 18th and 19th centuries.

Commercial whaling

- Introduction of harpoon cannon, steamships around 1870, later evolving to factory ships.
- Early 1900s sees expansion to Anarctic waters, with an emphasis on blue whales.
- Fin and sperm whales were extensively hunted.

Commercial whaling



Rocha et al. 2014 *Marine Fish Rev*

Great whales declined by ~85% since advent of commercial whali

Commercial whaling

- 1937–1949 marks beginning of international whaling regulation - but with NO effective enforcement.
- Commercial whaling moratorium actually begins in 1986.
- Some populations, such as North Pacific humpbacks and southern right whales, are well on their way to receovering from industrial whaling.
- Other species, including North Atlantic right whales and Antarctic blue whales, were so reduced that recovery may take centuries.
- Man-made hazards continue to threaten whales, including ship collisions, fishing gear entanglements, ocean noise and temperature rise, and other forms of habitat degradation.

The next slide contains a table with some

- populations of great whales in thousands, pre-whaling (N_0) and post-whaling (N_1), based on Doughty et al. (2016),
- lengths of whales in meters, pre-whaling (L_0) and post-whaling (L_1), based on Clements et al. (2017).
- Remember the desired value is $N_1/N_0 \geq 0.5$.
- Low values of N_1/N_0 mean long recovery times.
- The length entries indicate that the **size** of great whales has decreased as the larger whales were harvested.

		L_0	L_1	N_0	N_1
N. Atl					
	Right	16	16	14	0.5
	means/totals	15.9	12.3	875.1	368.9
		$L_1/L_0 =$	0.774	$N_1/N_0 =$	0.422
N. Pac					
	Gray	15	15	25	16
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S. Hemi					
	Arctic minke	7	7	670	515
	Blue	27	22	290	2
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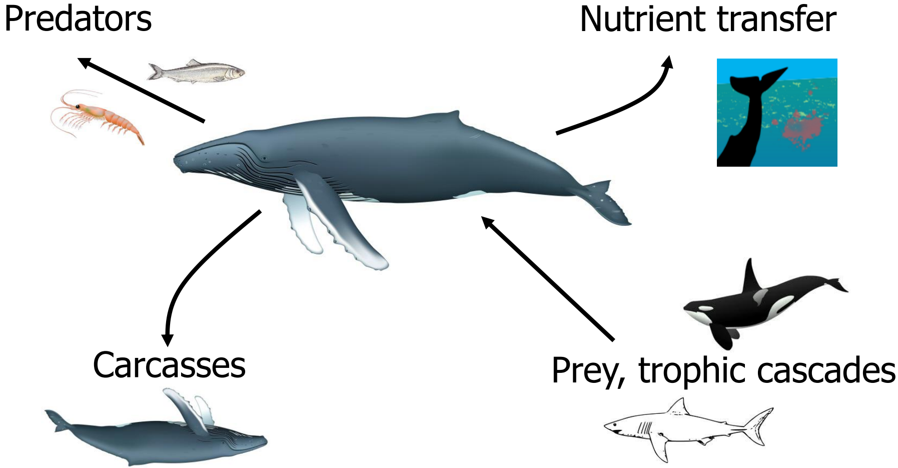
Global		L_0	L_1	N_0	N_1
		16.8	11.6	4048.5	1487
		$L_1/L_0 =$	0.689	$N_1/N_0 =$	0.367

Four Ecological Pathways



Whales as consumers

- Baleen whales include right, bowhead, humpback, blue, gray, fin, sei, Bryde's
- Toothed whales include sperm, orcas
- Baleen whales eat fish, shrimp, larvae, plankton, crabs, crustaceans, krill
- Toothed whales add squid, marine mammals such as seals, walrus, other whales
- Depending on size and season, whales consume several hundred to several thousand kg/day
- An estimated 65% of the North Pacific Ocean's primary production was required to sustain the large whale populations prior to commercial whaling (Croll et al. 2006)

Humpback whale bubble net feeding

Krill

- Phytoplankton are responsible for most of the transfer of carbon dioxide from the atmosphere to the ocean. Carbon dioxide is consumed, and oxygen released, during photosynthesis
- Krill are small crustaceans (1–2 cm) that feed on phytoplankton and zooplankton. (Photo B. Wilks)

- In the Southern Ocean, before the whaling era, whales consumed 190 million tons of krill annually.

Krill cont.

- When producing blubber, whales assimilate little of their dietary iron, and their fecal plumes have a high Fe content.
- Krill started **declining** after the depletion of the great whales; krill biomass is now a fraction of what it once was.
- The decrease in krill may have been caused, or facilitated by, the reduction of Fe fertilization needed for primary productivity.
- An iron-limited, degraded ecosystem dominates the former whaling grounds, presumably because the hard-working whales are almost completely absent.
- Distruption in the plankton-krill-whale cycle results in immense quantities of carbon not being exported from the atmosphere to deep ocean.

Lindsey and Scott, NASA, 2010; Buesseler et al., Perspective, 2019; Smetacek, Nature, 2021

Whales and fisheries

- Whales also eat fish.
- Culling whales from fishing grounds has been proposed.
- In ecosystem models, reduced whale abundances lead to appreciable **decreases** in fish stocks.
- In some cases, such as blue whales in the Southern Ocean, the presence of whales **increases** fishery yields because of their nutrient-rich feces.

(Lyne Morissette et al., PLOS ONE, 2010, 2012)

Whales and fisheries

Japanese scientific whaling and policies in Norway, Canada, and Iceland consider culling of marine mammals to reduce competition with fisheries

Whale pump: culls can be counterproductive, depressing primary productivity, reducing fish stocks

T. Wu

Whales as prey

Natural predators of great whales include

- giant shark **megalodon** (extinct) and giant sperm whales **L. melvillei** (extinct),
- humans (not yet extinct),
- large sharks and killer whales.

The **indirect** effects of removing whales from the food chain are more complicated!

- In the North Pacific, after the depletion of great whales, killer whales began to feed more on smaller marine mammals (harbor seals, sea lions, sea otters).
- **Decreased sea otters** leads to **increases in sea urchins**, leading to **decreases in kelp forests**, thence to **decreases in coastal fish populations**, and **decreased marine sequestration of carbon.**

Caveat: The above chain of events is oversimplified! Other factors are involved.

Whales as vectors of nutrients

- Iron is the limiting nutrient in the Southern Hemisphere.
- Nitrogen and phosphorous tend to be the limiting agents in the North Atlantic and parts of North Pacific.
- Whale feces have high concentrations of all three elements.
- Whale pump: Cetaceans primarily feed at depth during short dives followed by extended surface periods.
- Migration, the Great Whale Conveyor Belt: Most baleen whales feed in high-latitude productive waters and breed in lower latitude warmer waters, with the longest migration routes of any mammal.
- Thus whales redistribute nutrients to where they can be used.

Whales as detritus: whale falls

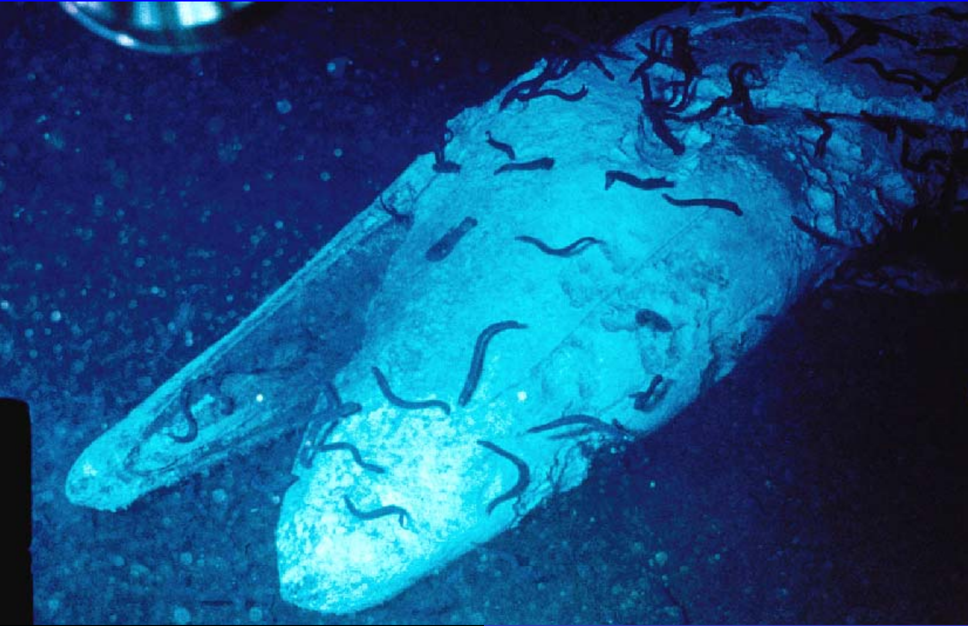
- Dead whales are big.
- Whale carcasses can wash ashore or stay in shallow coastal waters, but most sink to the seafloor.
- Sunken carcasses (“whale falls”) provide nutrient-rich islands in the food-poor deep sea.
- Whale falls provide a habitat for more than 200 species, half of which may be considered whale-fall specialists.
- Whale falls currently transfer an estimated 30,000 tons of carbon per year from the atmosphere to the deep ocean (Pershing, PLOS ONE, 2010).
- The pre-whaling estimate is 190,000 tons C per year.

Whale falls

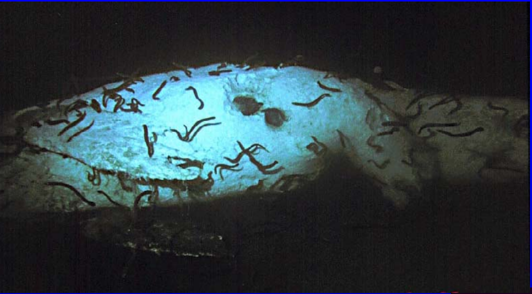
Carcasses on the seafloor pass through 3 stages:

1. a mobile scavenger stage, during which soft tissues are consumed,
   - hagfish, sleeper sharks, crabs, ...
   - duration 4–18 months
2. an enrichment-opportunist stage, when various fauna exploit organically enriched sediments and lipid-rich bones,
   - worms, mollusks, crustaceans, ...
   - duration 3–6 years
3. a sulfophilic stage, during which sulfides derived from the skeleton support another entire ecosystem.
   - bacteria mats, mussels, bivalves, limpets, snails, worms, ...
   - duration 5–100 years

Mobile scavenger phase



MSS Stage Duration?



30 ton carcass

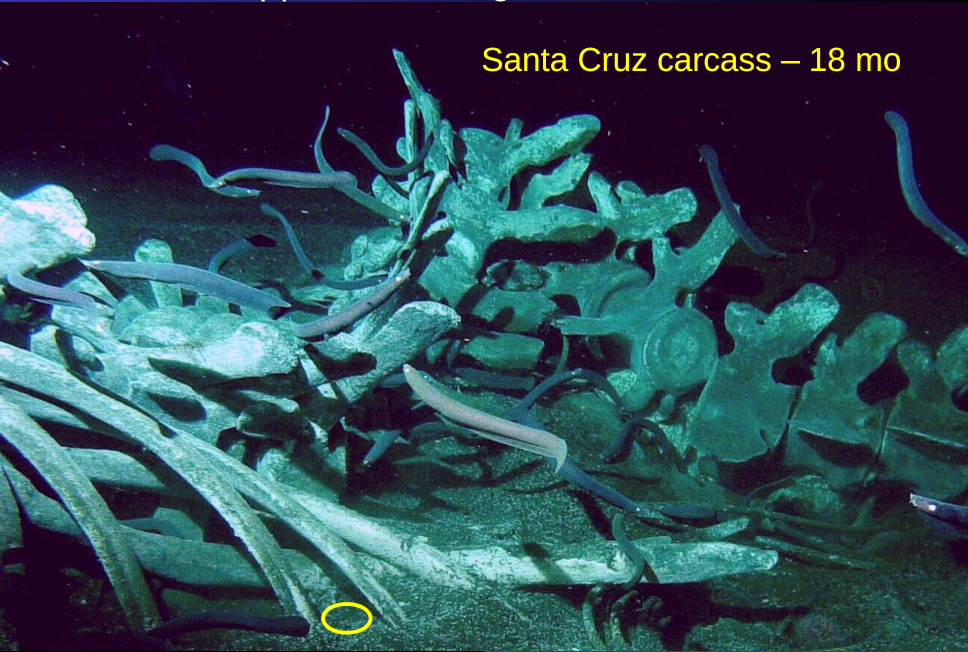
1.5 mo – Largely Intact

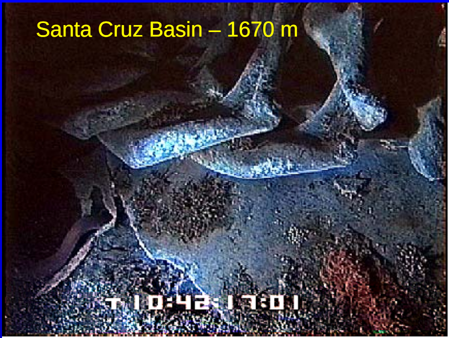
18 mo – Skeletonized!

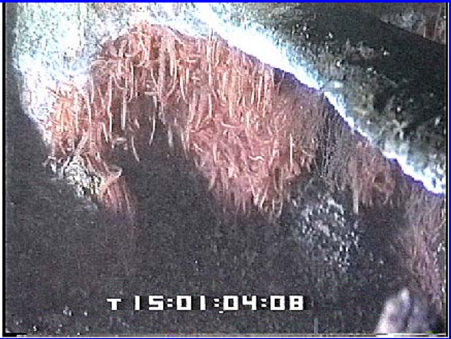
- 5 ton carcass stripped in ~ 4 mo

Duration ~ 4 – 18 mo

Enrichment opportunist stage







Evolutionary novelties

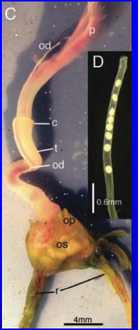
Carpet worm = *Vigtorniella flokati*

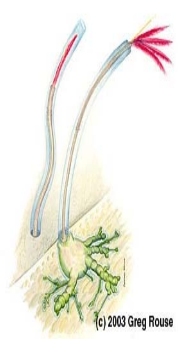
- new to science
- reduced gut
- bizarre behavior
- only found at whale falls

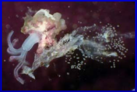
18 new species of dorvilleids!

Bone-eating siboglinid snot worms ≥ 27 species

Monterey Canyon – *Osedax rubiplumus* *O. frankpressi*, & 14 other spp. (Rouse et al. 2004; Lundsten et al., in press)







Santa Cruz Basin - *Osedax* sp. n.

Japan - 8 new species of *Osedax*

West Antarctic Peninsula – 1 new species of *Osedax*

→ **World Wide Whale Worms?**

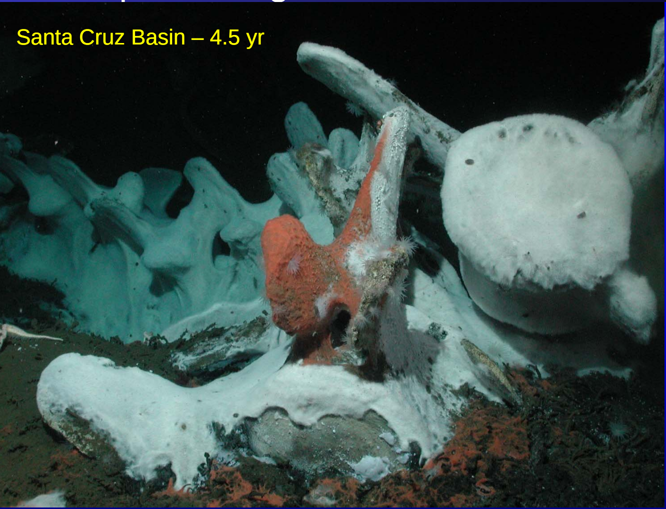
Evolutionary novelty :

- no gut or trophosome
- heterotrophic endosymbionts
- Oceanospiralles-like in MC species
- *Hyphomonas*-like in S. Cruz species
- lipid or protein degraders

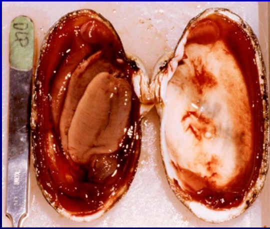
Sweden – *Osedax mucofloris* (Glover et al., 2005)

(Goffredi et al., 2005, Goffredi, Smith et al., unpublished)

Sulfophilic stage



Clams with chemo-autotrophic endosymbionts



Mats of sulfur oxidizing bacteria

Idas washingtonia and *Cocculina craigsmithi*

Estimated Population Sizes of Whale-Fall Fauna in Sulfophilic Stage

Taxon	San Clemente (3.4 yr)	San Nicolas (70 yr)	Santa Catalina (54 yr)
Mytilid			
Idas washingtonia	> 20,000	> 10,000	> 10,000
Limpets			
Cocculina craigsmithi	-	300	1,100
Pyropelta corymba	-	1,200	1,000
Pyropelta musaica	-	280	1,000
Other Limpets	-	1,800	1,200
Snails			
Mitrella permodesta	3?	1,800	1,800
Provanna lomana	-	1,500	-
Eulimella lomana	~1,000	-	-
Juveniles and Others	1,800	1,700	800
Crustaceans			
Illyrachna profunda	900	500	1,800
Amphipods	< 400	800	500
Galathaeids	800	~50	~100
Misc. Crustaceans	9,000	8,000	4,000
Polychaetes			
Nereid sp. 1	~50	~50	~50
Ampharetids	50?	2,500	100
Misc. polychaetes	1,800	10,000	8,000
Total Individuals	>40, 000	>40,000	> 30,000
Total Species	>103	>201	>180

The sex life of bone-eating snot worms

1. Release larvae to drift in the current.
2. If they reach an occupied whale fall, they join the colony.
3. If they reach an unoccupied whale fall, they form a new colony.
4. Otherwise, they float off and die.

Classic Levins metapopulation model

- $\dfrac{dP}{dt} = cP(1 - P) - eP$

  where P is the fraction of occupied sites, c the colonization coefficient, e the rate of site removal
- The solution is $P = \dfrac{1 - \frac{e}{c}}{1 + De^{-(c-e)t}}$ where $D = \dfrac{c - e}{cP_0} - 1$
- Equilibrium occurs at

$$P^* = \begin{cases} 1 - \dfrac{e}{c} & \text{if } e < c \\ 0 & \text{if } e \geq c \end{cases}$$

- That is, in order to survive, the colonization rate must exceed the rate at which habitat islands become depleted.
- **This should be taught in calculus!**

Whale-fall metapopulation model

- Some modifications required for whale falls since the habitat islands can last for decades.
- The condition for a whale-fall specialist species **not to go extinct** depends on $\left(\frac{N_1}{N_0}\right) \cdot \left(\frac{L_1}{L_0}\right)^4$.
- That is, survival depends on the number of whales and their sizes **to the 4th power!**
- This can be expressed in terms of the fraction of whale-fall sites that would need to be occupied pre-whaling by the species in order for it to not become extinct.
- Whale-fall specialists may well be in danger of extinction.

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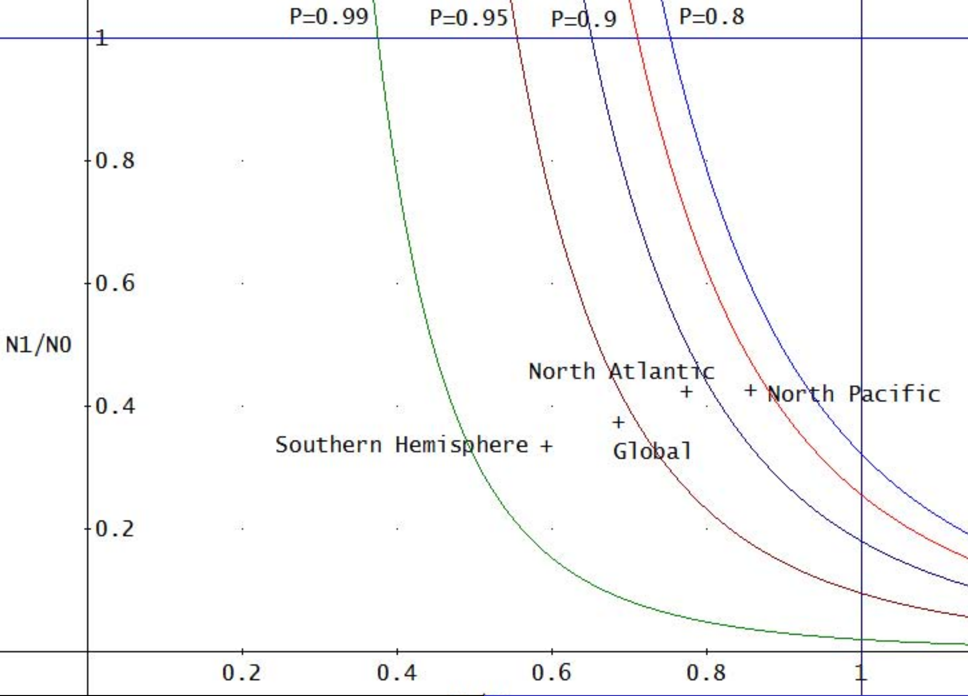
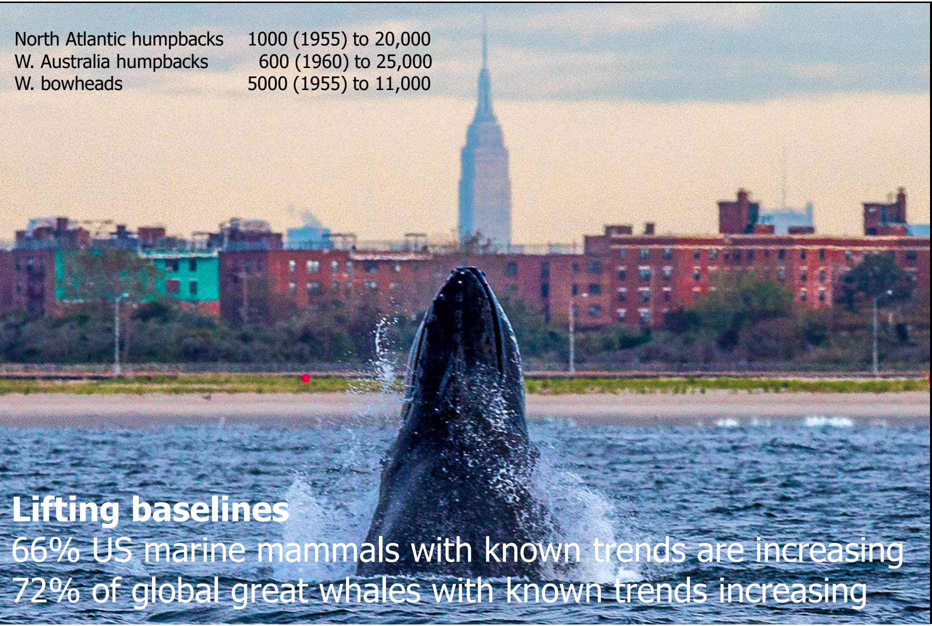

P=0.99
P=0.95
P=0.9
P=0.8
1
0.8
0.6
0.4
0.2
N1/N0
North Atlantic
North Pacific
Southern Hemisphere
Global
0.2
0.4
0.6
0.8
1

Good news



Roman et al 2013 *NYAS*, Roman et al .2015 *TREE*

Mahalo!

P. Colla