The Role of Whales in Southern Ocean Ecosystems

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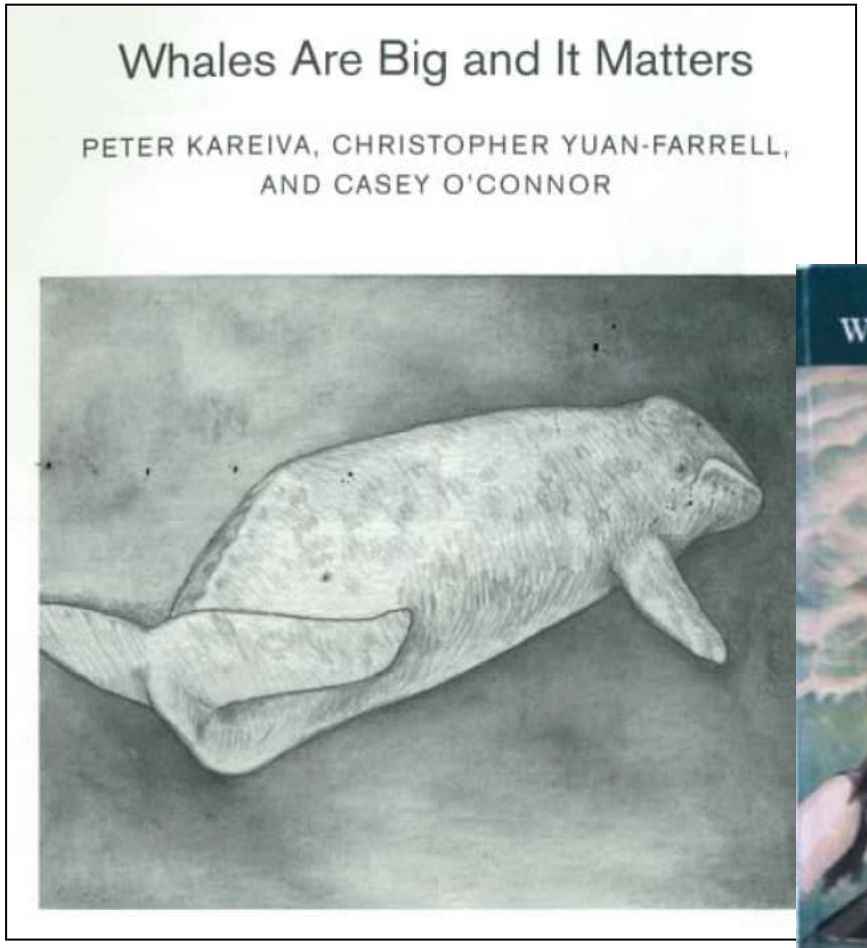
Preface: The Take-Home Message



	Current Population Estimates					
	Southern Hemisphere	North Pacific	North Atlantic	Total	Mean Body Mass (tons)	Tons of Whale in the Ecosystem
Humpback Whale	56,000	20,000	12,000	88,000	31.8	2,798,400
Right Whales	12,000	550	450	13,000	53.0	689,000
Gray Whales	20,000	---	---	20,000	25.0	500,000
Blue Whales	4,600	2,000	2,000	8,600	69.2	595,120
Fin Whales	15,000	11,000	37,000	62,000	42.3	2,622,600
Sei Whales	10,000	10,000	12,400	32,400	19.9	644,760
Bryde's Whales	50,000	39,000	5,000	94,000	13.2	1,240,800
Minke Whales	500,000	30,000	185,000	715,000	7.0	5,005,000
Bowhead Whales	---	12,000	8,000	20,000	80.0	1,600,000

Sources: RL Brownell pers. comm.; synthesis by Hewitt and Lipsky 2009

~15.7 million tons of whale in the world's marine ecosystems

This sheer tonnage implies that whales can play significant roles in marine ecosystems.

- Cetaceans in the California Current are estimated to consume ~12% of the ecosystem's net primary productivity (Barlow et al. 2008).
- Benthic feeding by gray whales provides habitat for benthic scavengers, prey for seabirds, and mixes sediment, with the potential to alter primary production (Oliver and Slattery 1985, Obst and Hunt 1990, Pilskaln et al. 1998).
- Whale carcasses support 350+ species and can be havens of deep-sea biodiversity (Jones et al. 1998, Smith 2006).
- A decline of sperm whales in the tropical and subtropical Pacific may have resulted in a shift toward ecosystems dominated by squids and tunas (Essington 2006).
- Killer whales may have sequentially depleted marine mammal species in the Bering Sea (Springer et al. 2003).

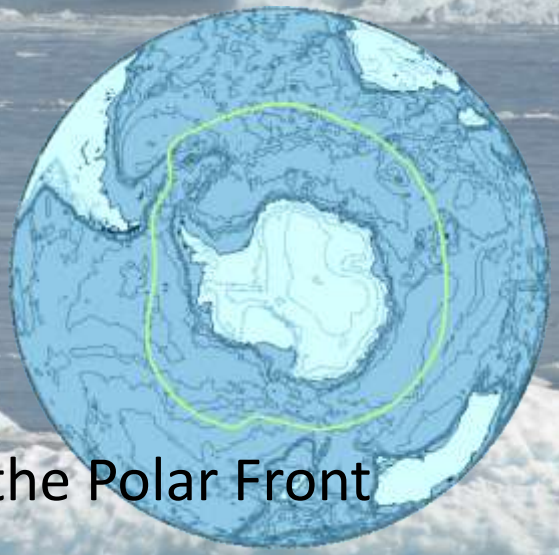
"The irony is that, although whales have become a symbol of the human capacity for greedy overharvest and a rallying point for environmental activists, we know surprisingly little about their ecological role."*

	Total Number of Publications	Number (%) Addressing Whale Ecology, Species Interactions, Effects on Ecosystem Processes
Marine Ecology (1999-2003)	106	0 (0%)
Marine Mammal Science (1985-2003)	94 (focused on whales)	17 (18%)

Kareiva et al. 2006

*remember for later

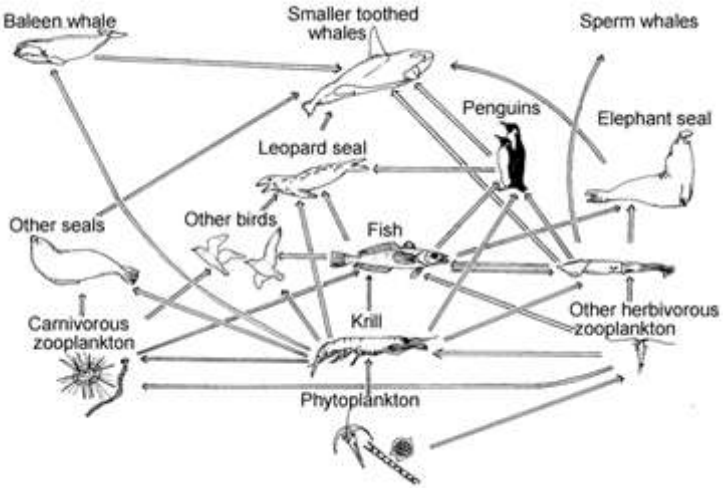
The Southern Ocean* Ecosystem



*South of the Polar Front

Whales* and the Southern Ocean Ecosystem: A trophic interactions perspective

- Whales as Consumers
- Whales as Competitors
- Whales as Prey



* = Cetaceans

Whales as Consumers

"The combination of great abundance, large body size, and endothermic metabolic demands make odontocete and mysticete whales some of the most voracious consumers in the oceans. As such, they have the potential to place extraordinary pressures on marine resources." (Williams 2006)

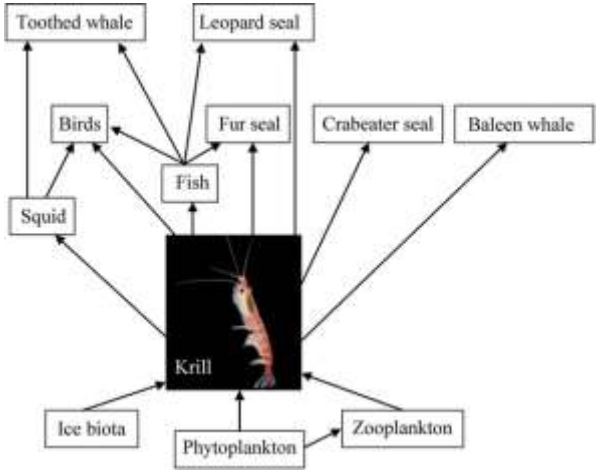
When we think of consumers in an ecosystem context, we ask questions like:

- What is eaten?
- How much?
- How does this consumption impact the ecosystem?

Krill

E. superba, E. crystallorophias, T. macrura

"Krill-based ecosystem" in about one quarter of the ~32 million sq. km of the Southern Ocean (Siegel & Loeb 1995)



How much krill is consumed?

	Estimated Abundance	Mean Mass (tons)	Ingestion Rate/Day (1,000 kcal)	No. Days Spent Feeding	% Krill in Diet	Total Krill Consumed Annually (millions of tons)
Antarctic Blue Whales	2,300	83	3,708	120	100	1.1
Fin Whales	15,000	48	2,415	120	100	4.7
Sei Whales	20,000	17.5	1,096	120	80	2.3
Humpback Whales	55,000	26.5	1,517	120	100	10.8
Antarctic Minke Whales	500,000	7	535	120	100	34.5
						53.4

Sources: RL Brownell pers. comm.; synthesis by Hewitt and Lipsky 2009

~53.4 million tons krill consumed annually by 5 species of whales

- For some perspective, annually:
  - 104,182 – 211,984 metric tons harvested: 2000 – 2011 (SC-CAMLR 2011)
  - 190 million tons consumed by baleen whales alone prior to commercial exploitation (Laws 1985)
  - 250 million tons consumed by current populations of all krill predators (whales, birds, pinnipeds, fish, squid: Miller and Hampton 1989)

- Despite much careful attention, estimates of krill consumption are invariably associated with a **great degree of uncertainty** (e.g., Leaper and Lavigne 2007)

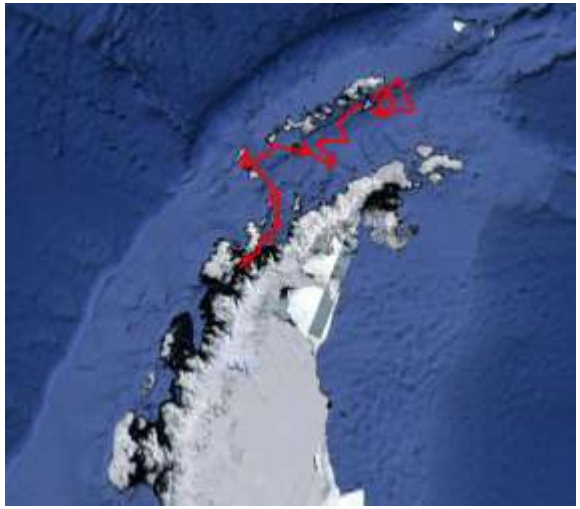
- How does this consumption impact the ecosystem?*

*remember for later

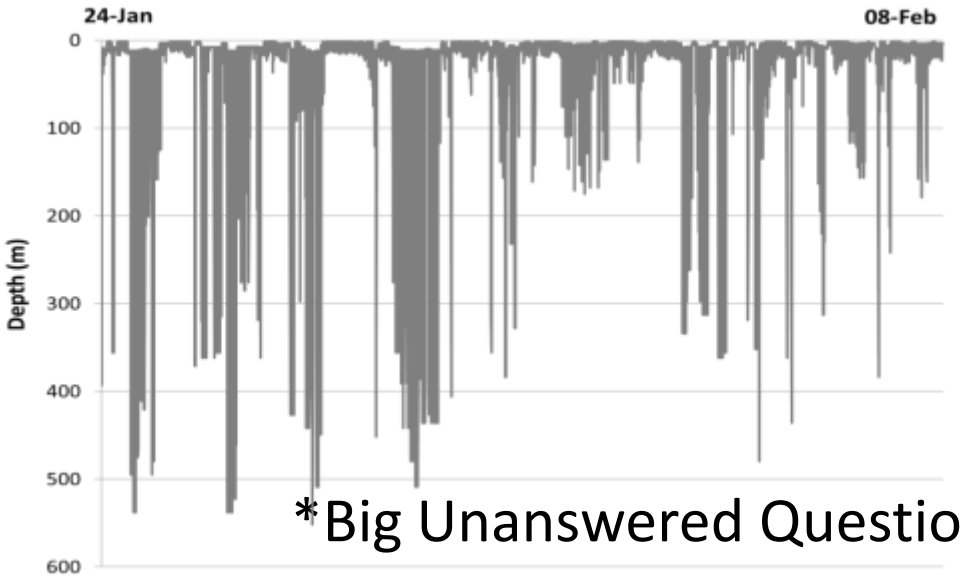
Squid

- Sperm whales
  - 10,000 males *(Brownell, pers. comm.)*
- Beaked whales
  - 599,300 Ziphiid whales (almost all *H. planifrons*) in the Southern Ocean *(Kasamatsu & Joyce 1995)*
  - *H. planifrons* – the most abundant cetacean in the Southern Ocean?
- Killer whales? (Type B)

- How much squid is consumed?*
- How does this consumption impact the ecosystem?*



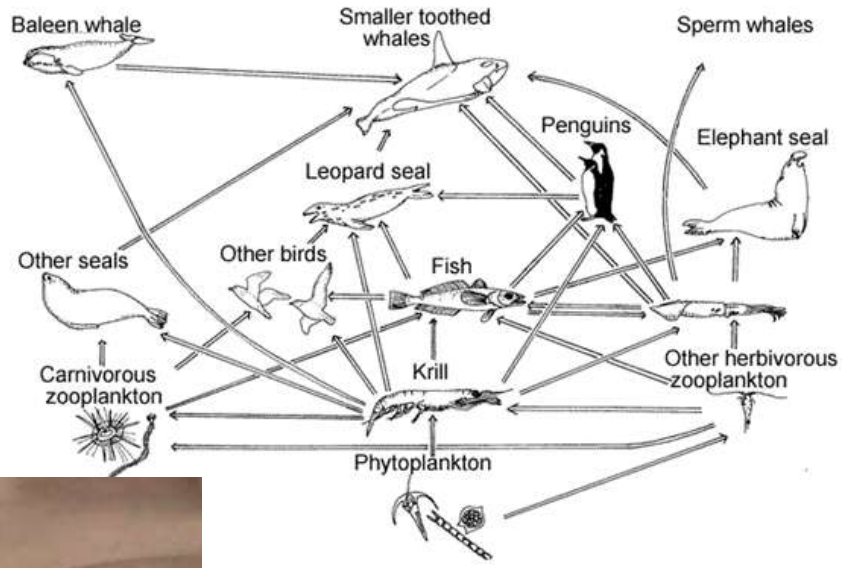
Durban & Pitman, unpublished data

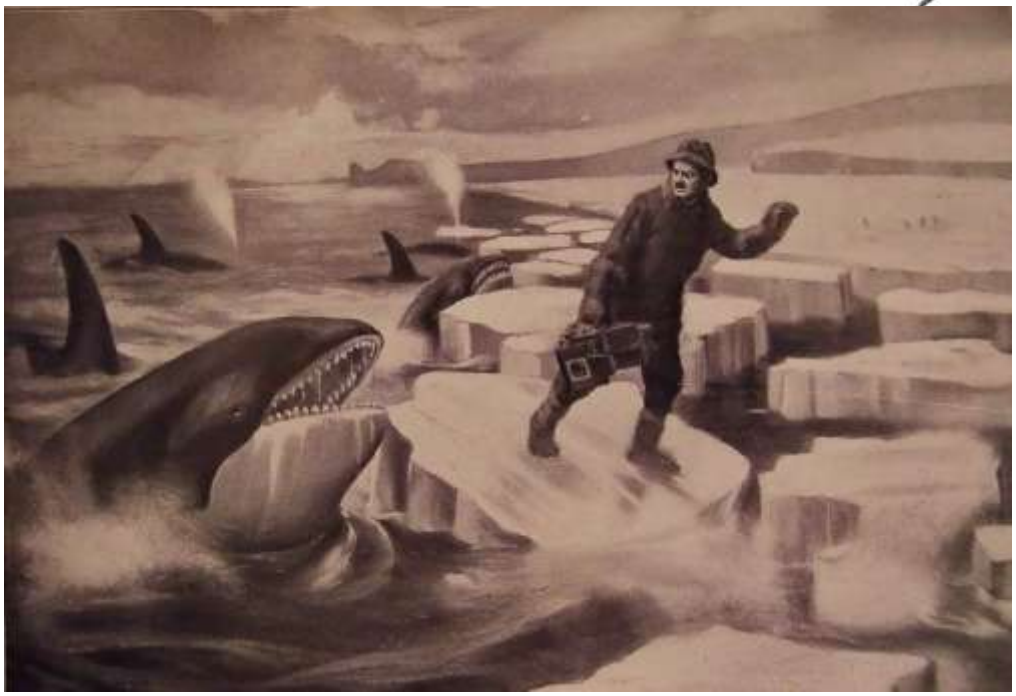


*Big Unanswered Questions

Other Species

- Killer whales as consumers of:





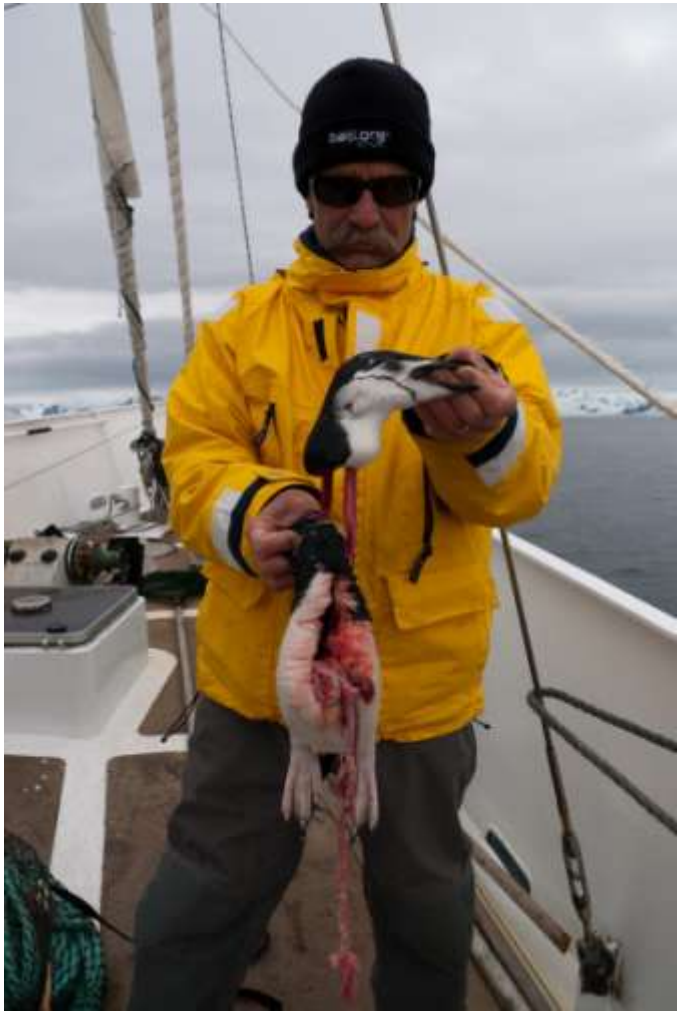
Fish, penguins, seals, whales

Fish - Ross Sea KWs *"Type C"*

Krahn et al. 2008

Penguins – Gerlache KWs "*Mini Type B*"

Pitman & Durban 2010



Seals - Pack Ice KW *"Big Type B"*

Pitman & Durban 2011

Whales – "*Type A*"

Pitman & Ensor 2003

How much of these species do killer whales consume?

- ~ 25,000 killer whales in the Southern Ocean *(Branch & Butterworth 2001)*
- ➢ Prey specialization (?)

- What is the distribution and abundance of KW ecotypes?*
- How does this consumption impact the ecosystem?*

*Big Unanswered Questions

Whales as Competitors

"…competition from any one species may profoundly affect the population dynamics and carrying capacity of another, either through its effect on their mutual resources or by direct interference." (Rickleffs 1990)

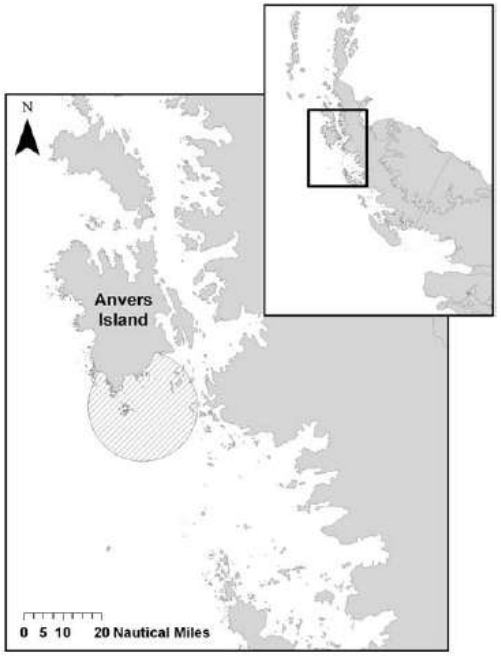
Competitive Release: The "Krill Surplus" Hypothesis

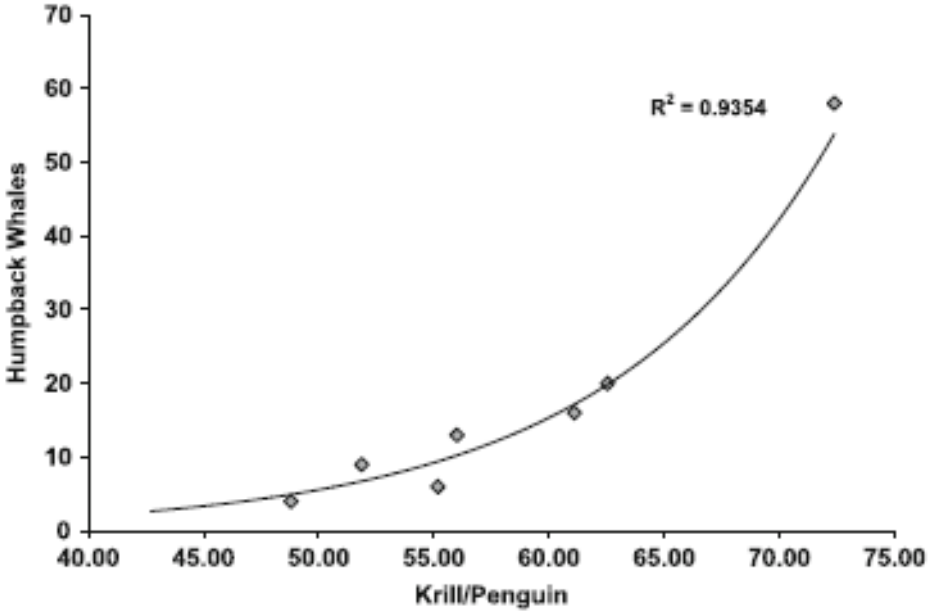
- > 2 million whales removed from Southern Hemisphere *(Clapham and Baker 2006)*
- Up to 150 million tons krill/yr unconsumed *(Laws 1977)*
- Theoretically could support addition of 200-300 million penguins per year (Sladen 1964; Emison 1968)
- Growth in penguin populations attributed to "krill surplus" *(Sladen 1964; Emison 1968; Conroy 1975; Croxall and Kirkwood 1979; Croxall et al. 1981; Laws 1985; Rootes 1988)*

Competition for krill is occurring.

- At Anvers Island, there are significant relationships between humpback whale abundance, the size-frequency distribution of krill targeted by Adélie Penguins, and penguin foraging success (1993-2001).

➢ Humpback whales and Adélie Penguins appear to target and share similar spatio-temporal prey resources.

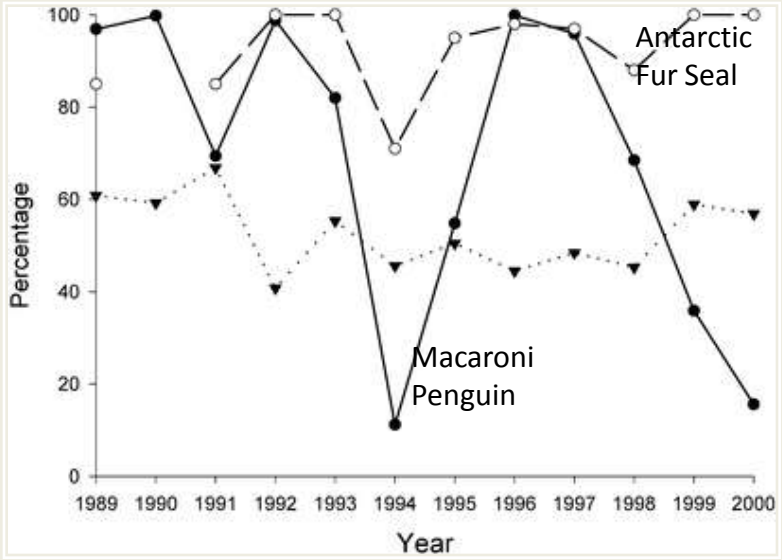




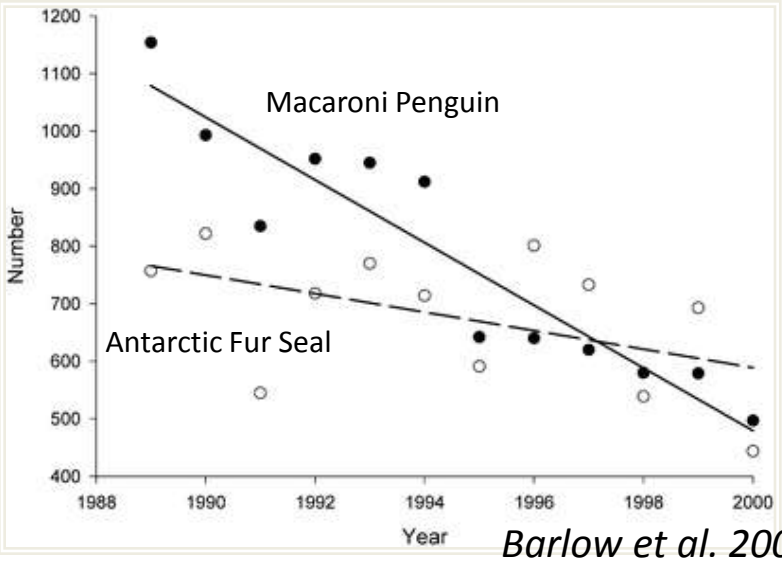
Friedlander et al. 2008

This competition can result in changes in abundance (of predators and prey).

- At Bird Island, South Georgia, Antarctic fur seals and Macaroni Penguins exploit the same size and population of krill
- % krill in fur seal diet > in penguin diet

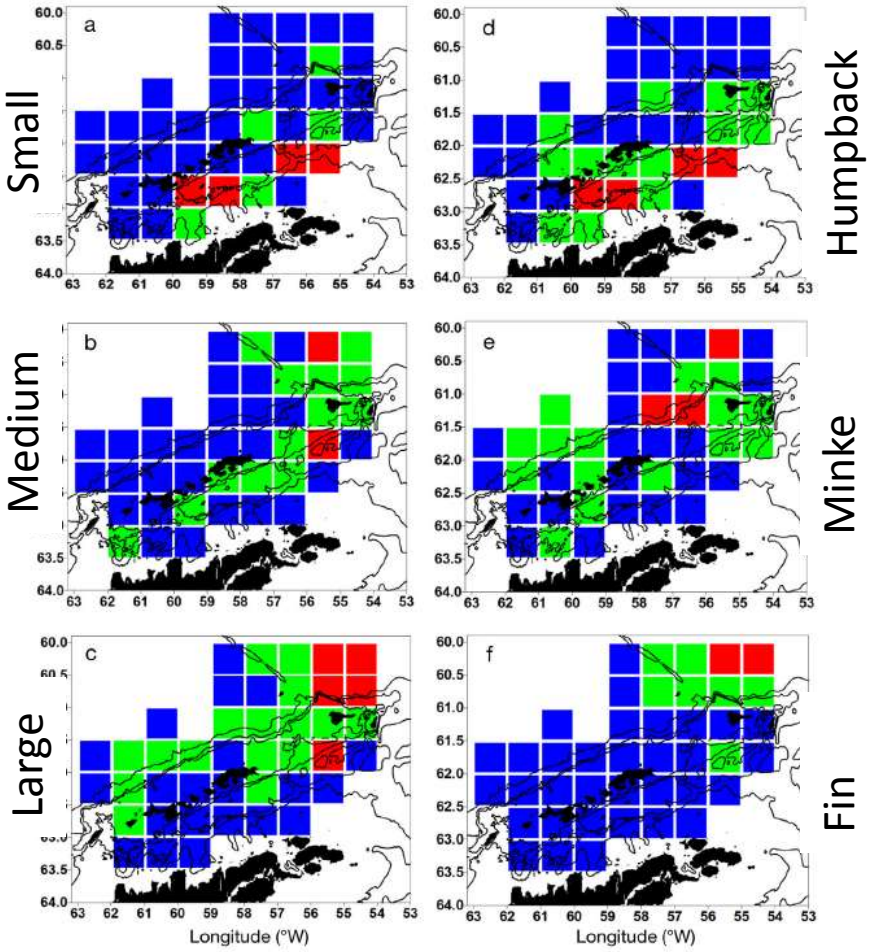


- Penguin population declining
- Interpretation
  - Predators reaching K
  - Competition for krill is occurring
  - Fur seals are outcompeting penguins



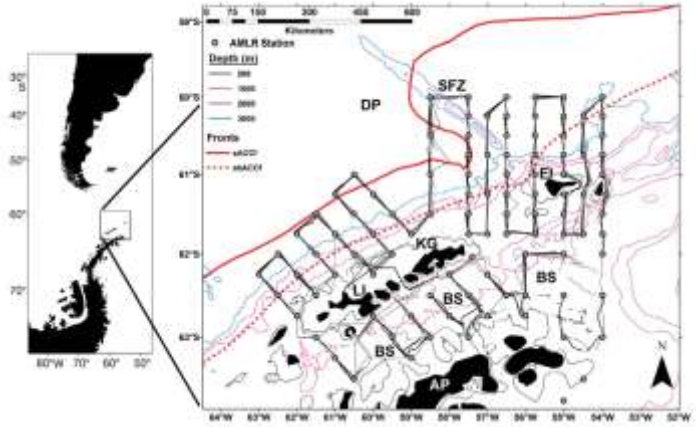
Barlow et al. 2002

Competition can result in niche partitioning.



Krill Hotspots

Whale Hotspots



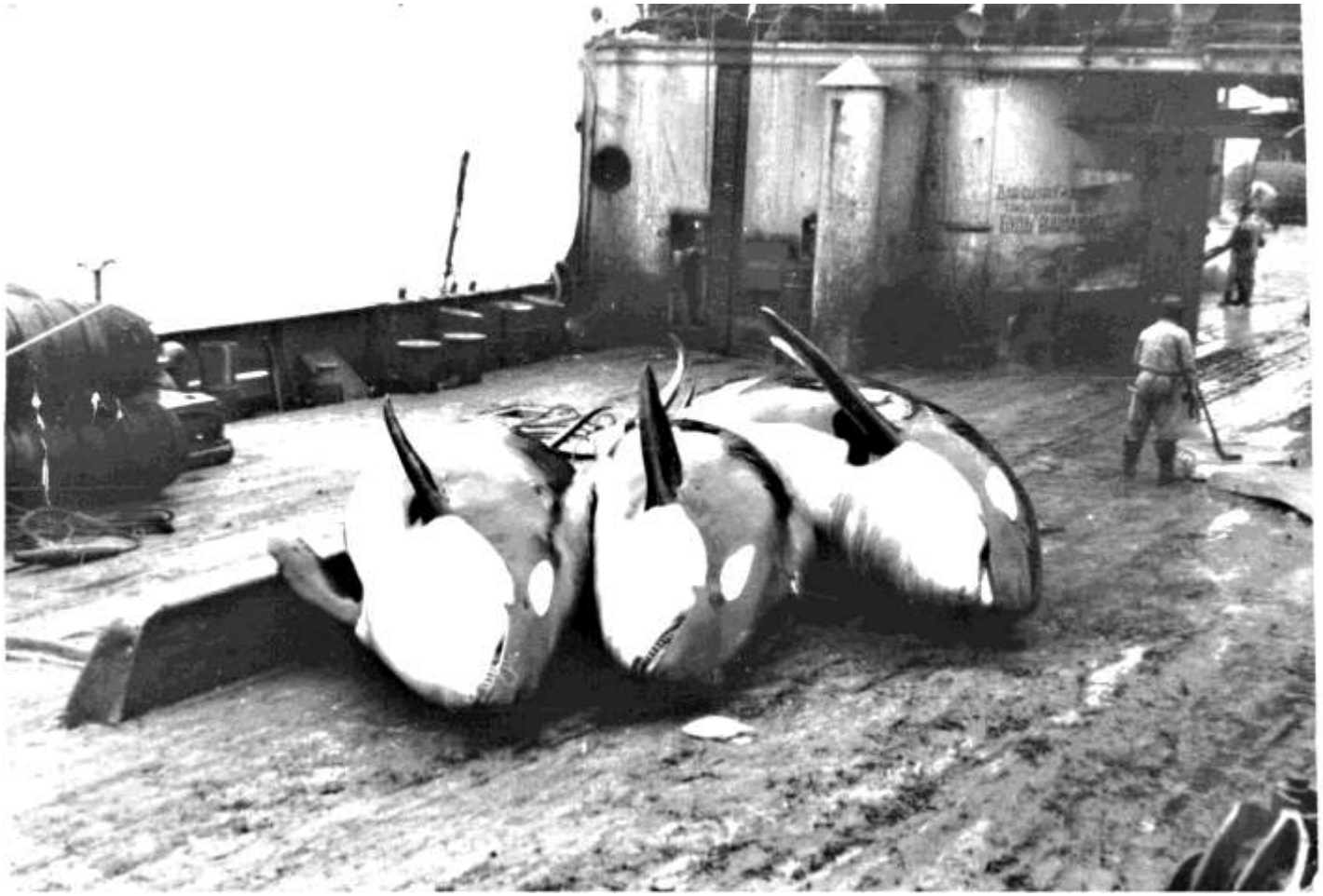
- Near the South Shetland Islands baleen whales show a krill size-dependent relationship with krill abundance hotspots

Santora et al. 2010

Whales as Prey

"The ecological role of large whales as prey is the most controversial of the three potential food web pathways …" (Estes et al. 2006)

Whales are prey for killer whales ….

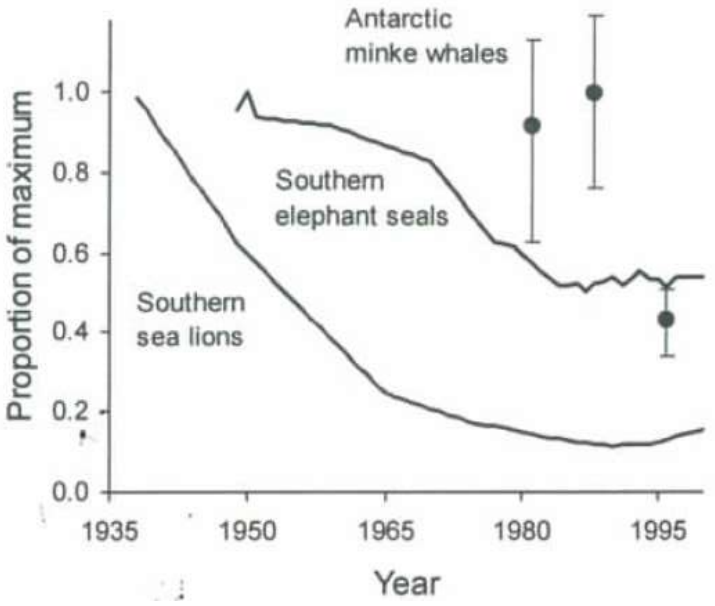


…. or humans.

Killer whale predation may drive:

- Baleen whale migration
  (Corkeron & Connor 1999)

- Trophic cascades: prey switching due to loss of large whales *(Branch & Williams 2006)*



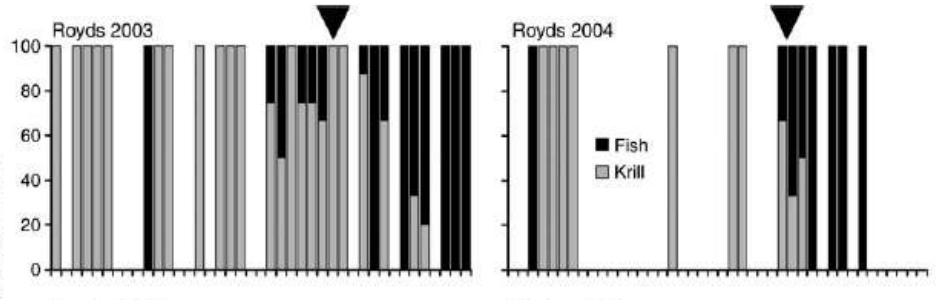
The Ecosystem Consequences of Consuming, Competing, and Predation: Whales as Drivers of Food Web Restructuring ("Top-Down Forcing")

"Despite its popularity among Southern Ocean ecologists 25 years ago, [the] top-down hypothesis (consumer effects on resources) has been largely replaced by an emphasis on bottom-up explanations …" (Ainley et al. 2009)

Trophic cascades in the western Ross Sea

- ~Nov
  - Adelie penguins (incubating eggs) feed on crystal krill
  - A. silverfish feed on c. krill
- ~Dec
  - Penguin chicks hatch; adults feed themselves and chicks on krill
  - minke whales arrive and feed on krill
- ~Jan
  - Krill abundance declines
  - Penguins and minke whales shift to silverfish
  - Older silverfish become cannibalistic

Ainley et al. 2006 and references therein



- ~Feb
  - Silverfish abundance declines
  - Penguin foraging duration and distance increases
  - Minke whales leave to forage elsewhere
  - Grazing pressure on phytoplakton relaxes

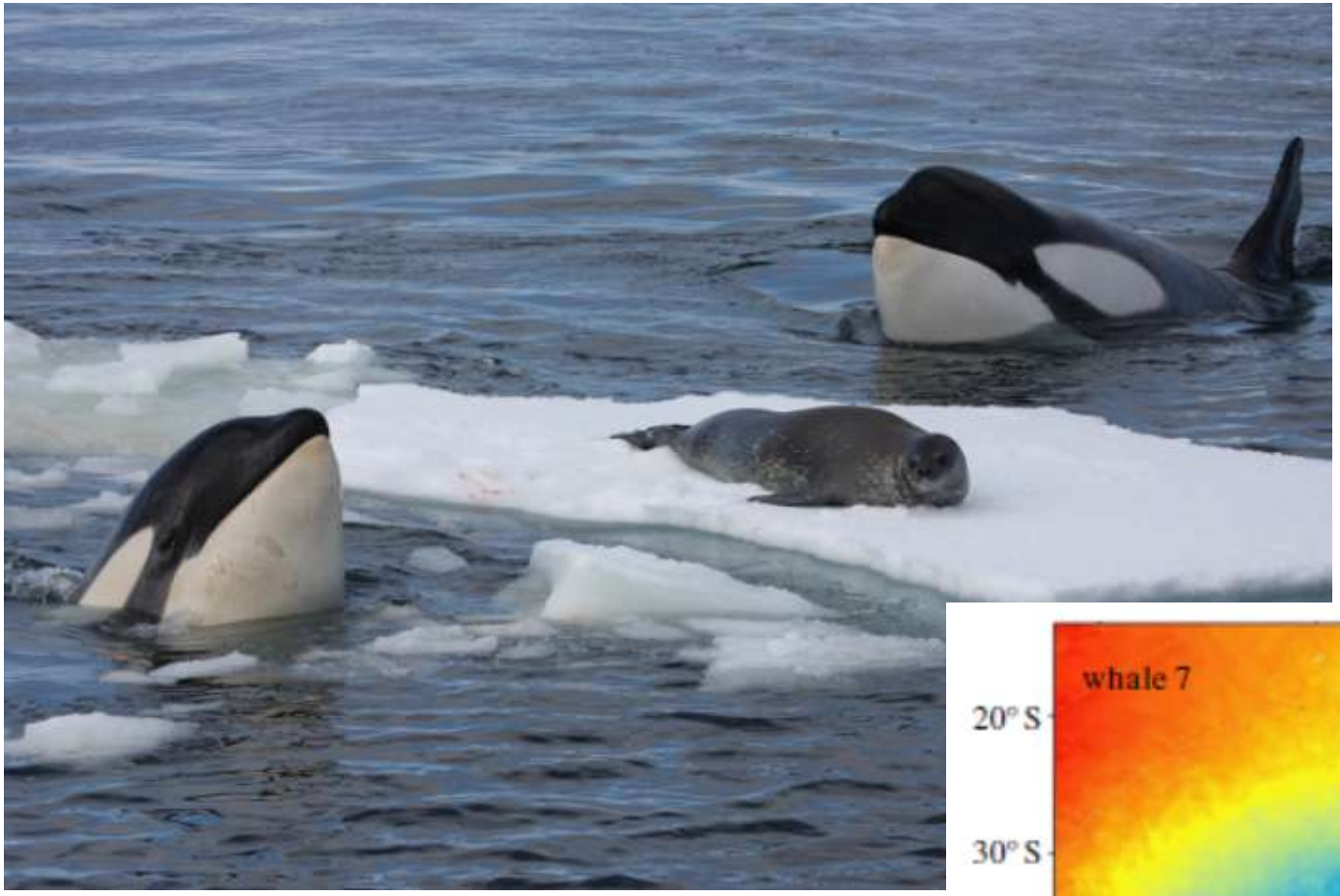
So, how do whales impact Southern Ocean ecosystems?

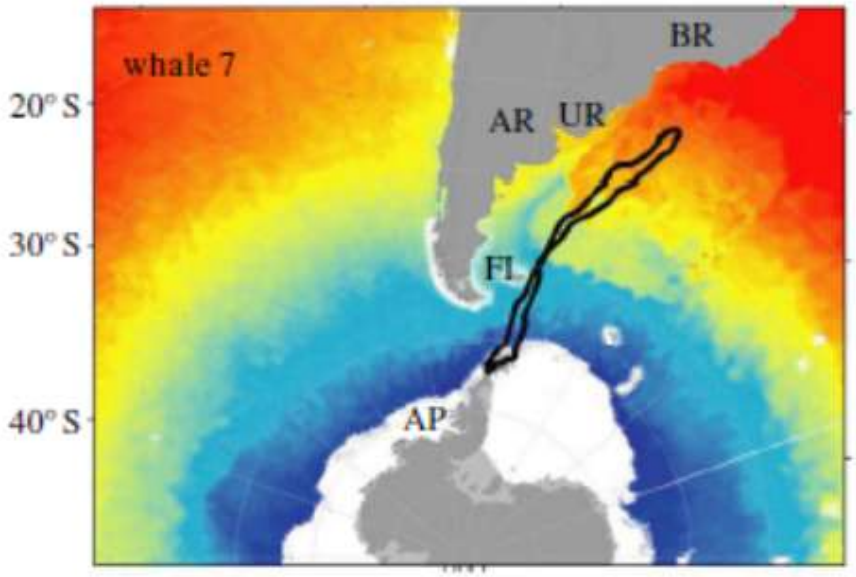
- They remove a huge amount of krill from the system (and maybe a huge amount of squid, penguins, seals, and whales)
- They impact other krill predators
- They may drive evolutionary responses of their prey
- They have the potential to restructure food webs

- Let us not forget, the Southern Ocean is a highly perturbed marine ecosystem
  - Whale populations are recovering
  - The planet is warming
  - Fisheries are removing krill and fish (and whales)

The Big Unanswered Questions

- Which is more important: top-down or bottom-up forcing
  - *Both* are important
  - As whales recover, top-down forcing deserves more attention
- Trophic linkages: which direction and how strong?
  - Squids: what are their trophic links with whales and their importance?
  - What is the distribution and abundance of killer whale ecotypes and to what extent do the specialize in (or switch) prey?
  - What are the indirect effects of food web restructuring?
- Are whales a year-round component of the ecosystem?





Satellite-tracked adult female Type B killer whale
13 Feb, 2010 for 109 days
30° S; 22.4° C
North of 60, swim velocity ≥ 5-10 km/hr
Returned 1 June, 2010

Durban and Pitman 2011