Marine Biology (2005) 147: 1435–1447
DOI 10.1007/s00227-005-0027-0

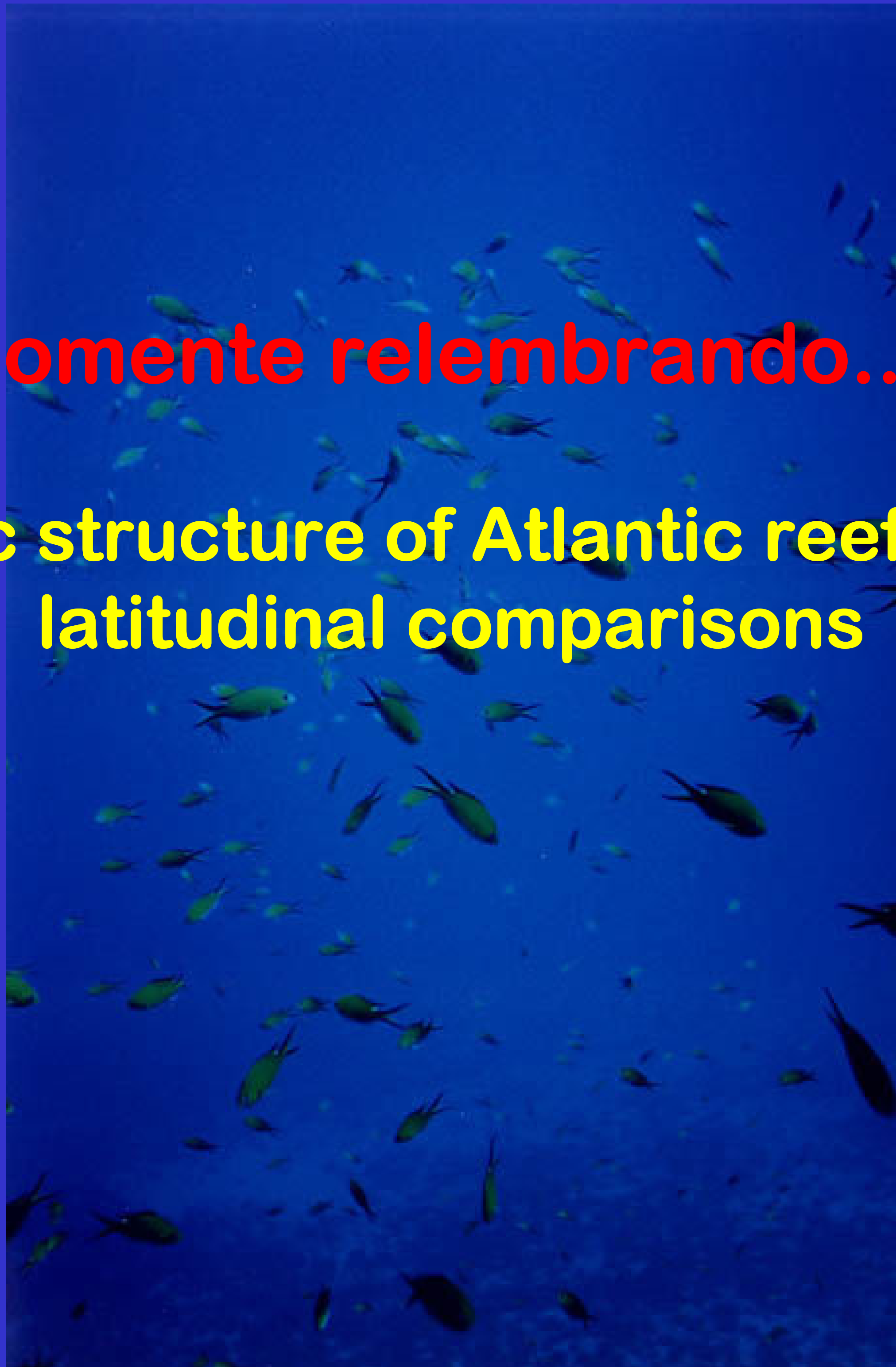
RESEARCH ARTICLE

S. R. Floeter · M. D. Behrens · C. E. L. Ferreira
M. J. Paddack · M. H. Horn

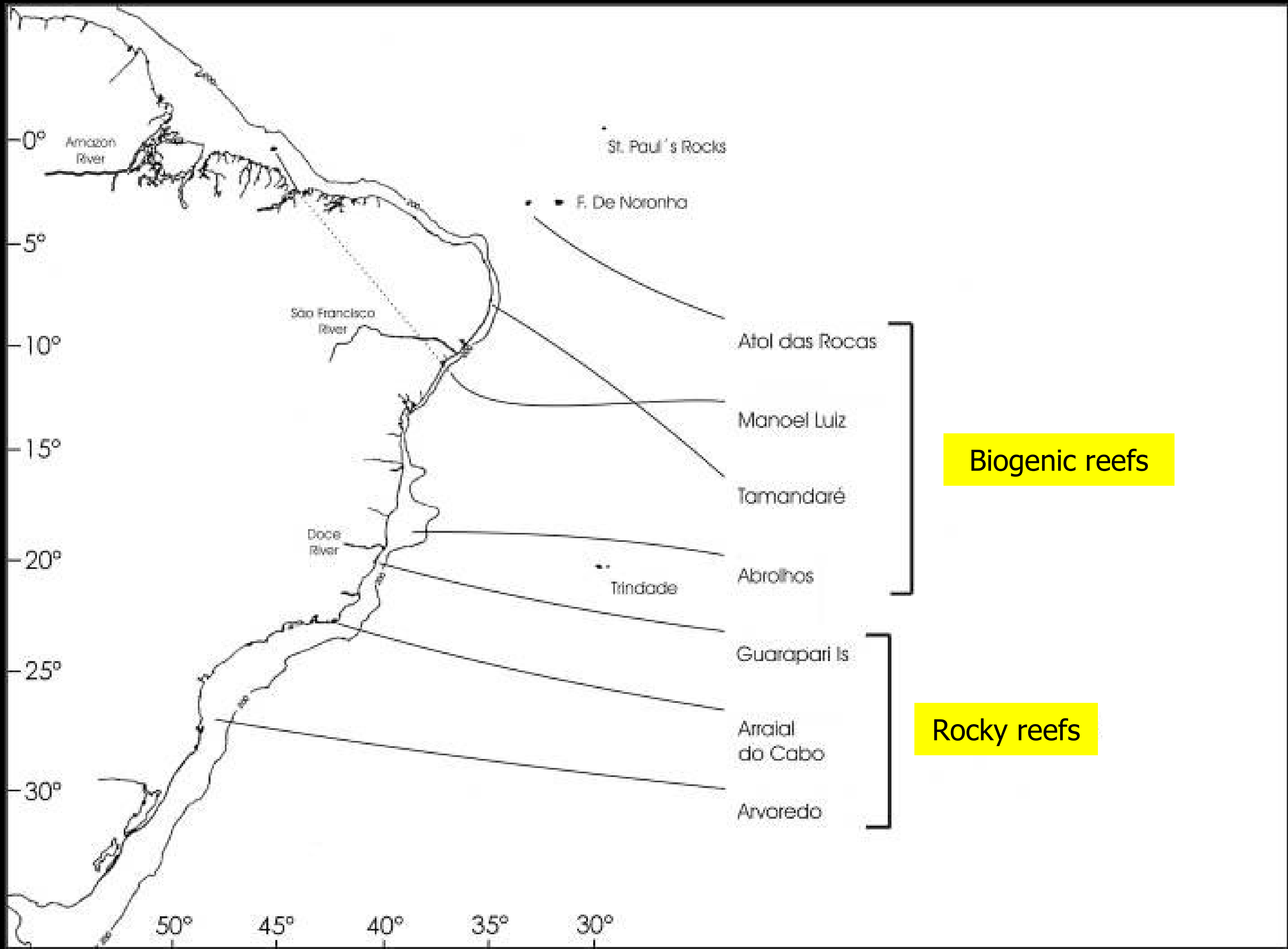
Geographical gradients of marine herbivorous fishes: patterns and processes

Somente relembrando....

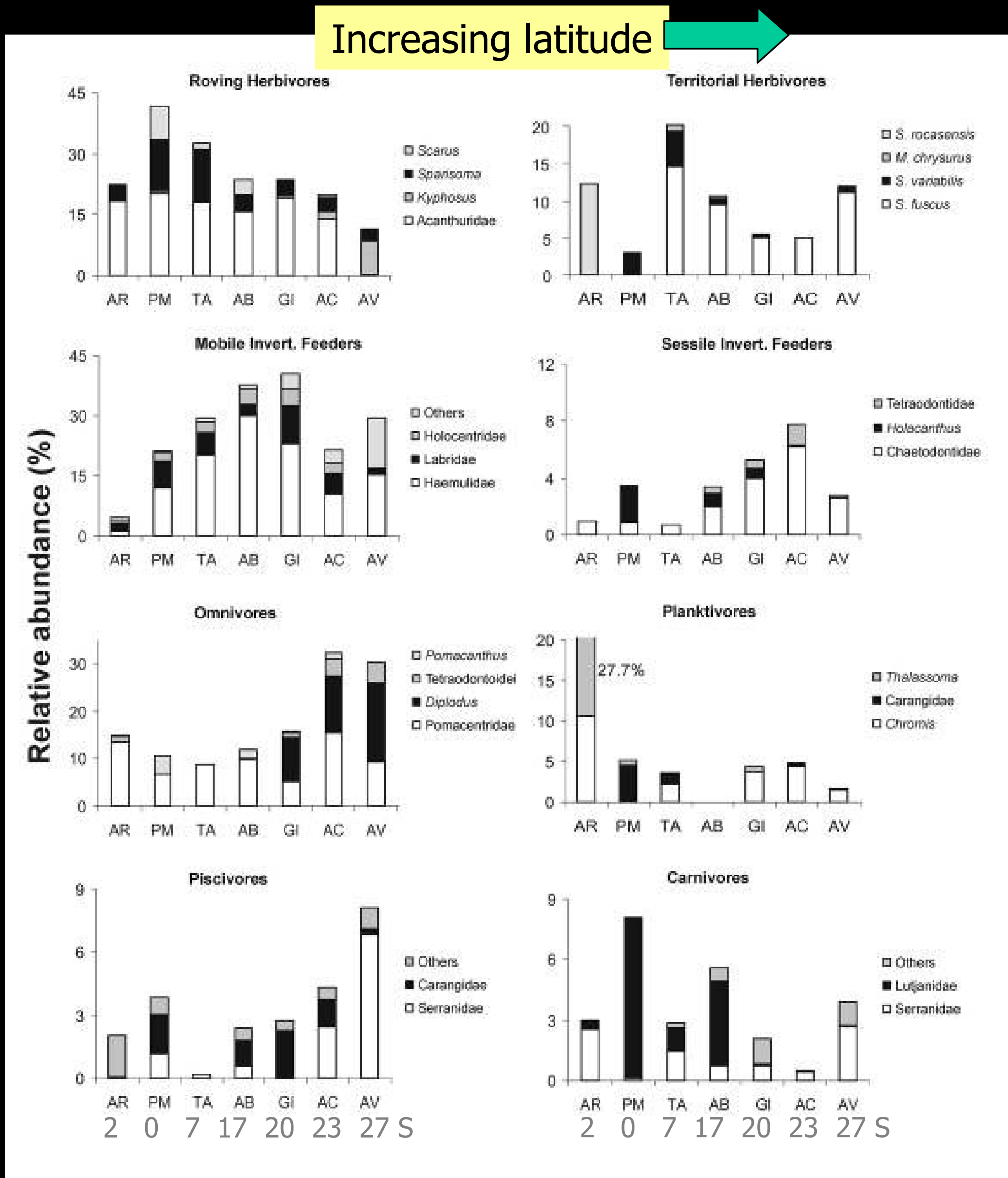
Trophic structure of Atlantic reef fishes: latitudinal comparisons



The Brazilian coast: quantitative patterns (visual census) of trophic groups

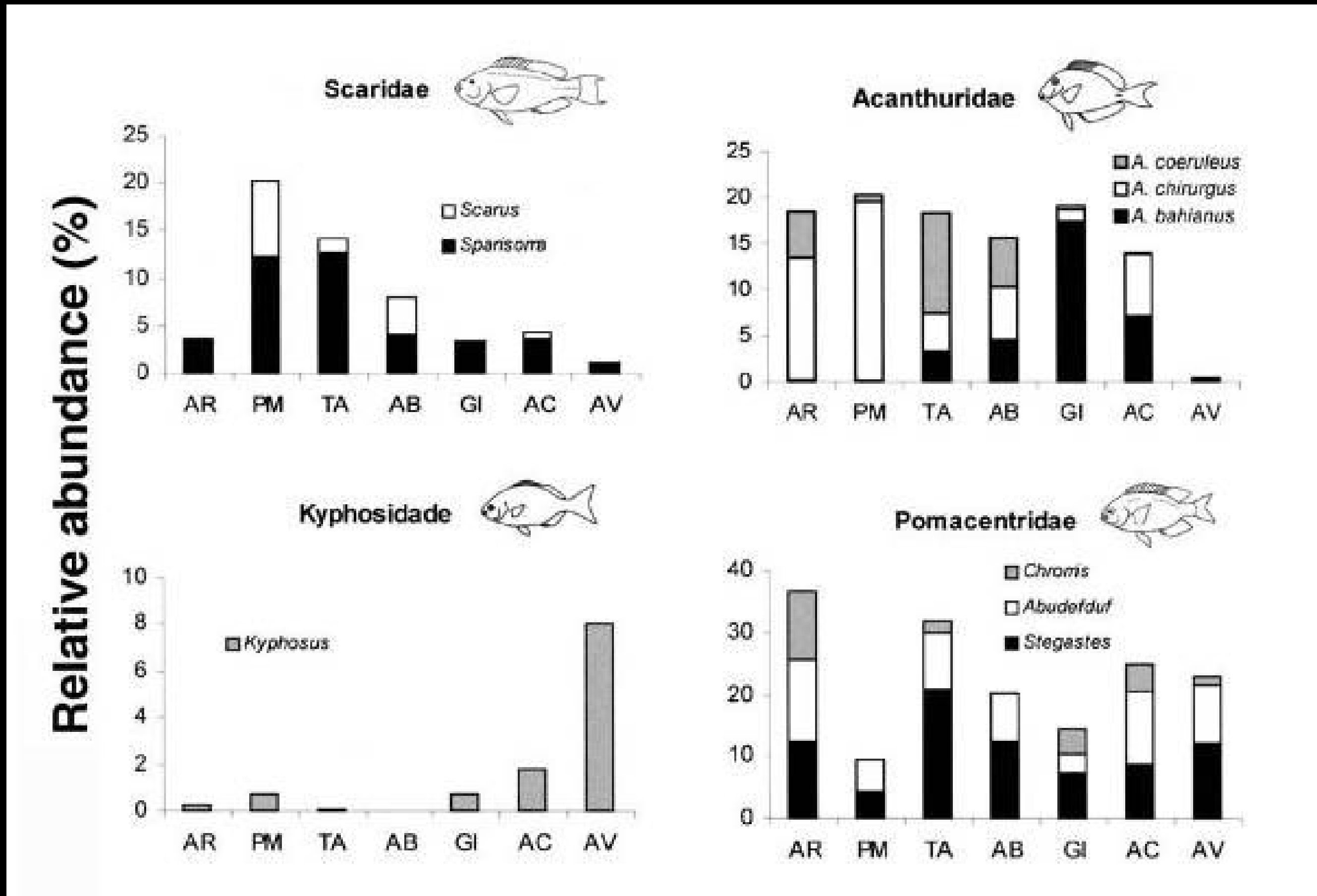


Trophic groups



Taxonomic groups

Increasing latitude



2 0 7 17 20 23 27 S

2 0 7 17 20 23 27 S

Ferreira et al. (2004) J Biogeogr 31: 1093-1106

Testing Harmelin-Vivien (2002) hypothesis with quantitative data…

Harmelin-Vivien, 2002

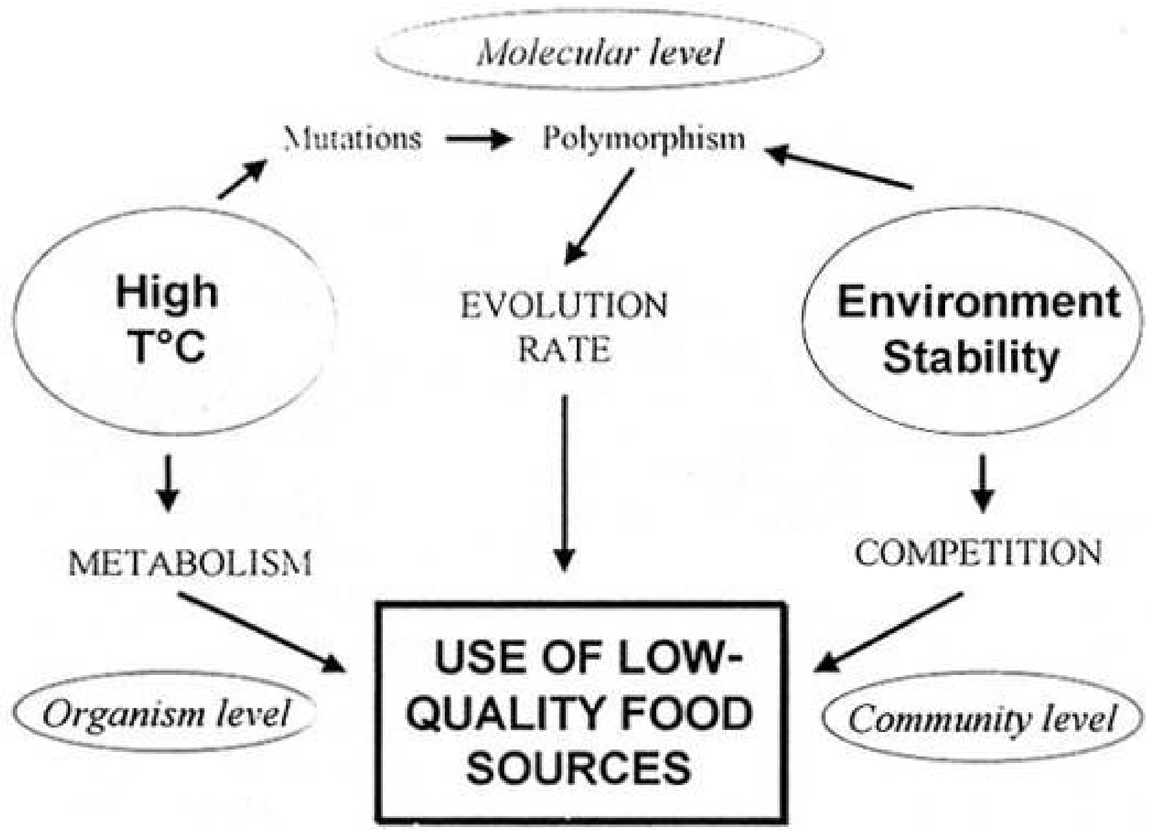


FIGURE 4 Schematic representation of the hypothetical effects of high temperature and environmental stability at different levels of biological organization to explain the higher consumption of low-quality food sources by fishes in the tropics compared to those in temperate zones.

Prediction

Is diversity and abundance of fishes that use relatively low-caloric food resources higher in the tropics?

FOOD QUALITY GROUPS

High-quality – **CARNIVORES, PISCIVORES, MOBILE INVERTEBRATE FEEDERS and PLANKTIVORES.** Highly energetic (with high protein content) and easily digestible food, e.g. zooplankton, mobile invertebrates and fishes.

Low-quality – **HERBIVORES, DETRITIVORES and SESSILE INVERTEBRATE FEEDERS.** Relatively low-energy content resources, generally with lower assimilation rates and indigestible components, and structural (e.g. calcium carbonate) and/or chemical defences against grazing.

Intermediate-quality – **OMNIVORES.** Algae plus some protein-rich animal food.

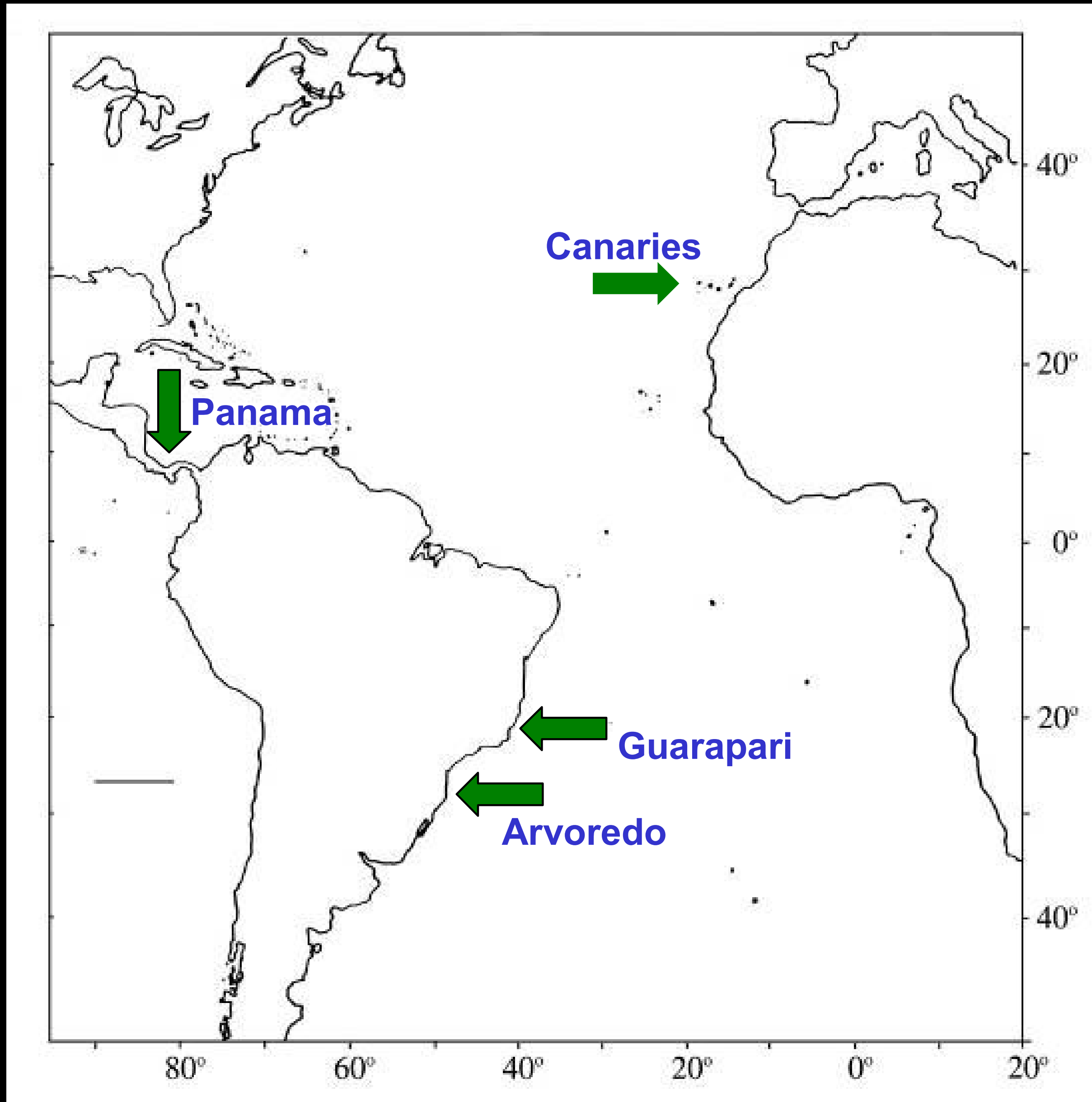
Journal of Fish Biology (2004) **64**, 1680–1699
doi:10.1111/j.1095-8649.2004.00428.x, available online at http://www.blackwell-synergy.com

Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns

S. R. Floeter*†, C. E. L. Ferreira‡,
A. Dominici-Arosemena§ and I. R. Zalmon*

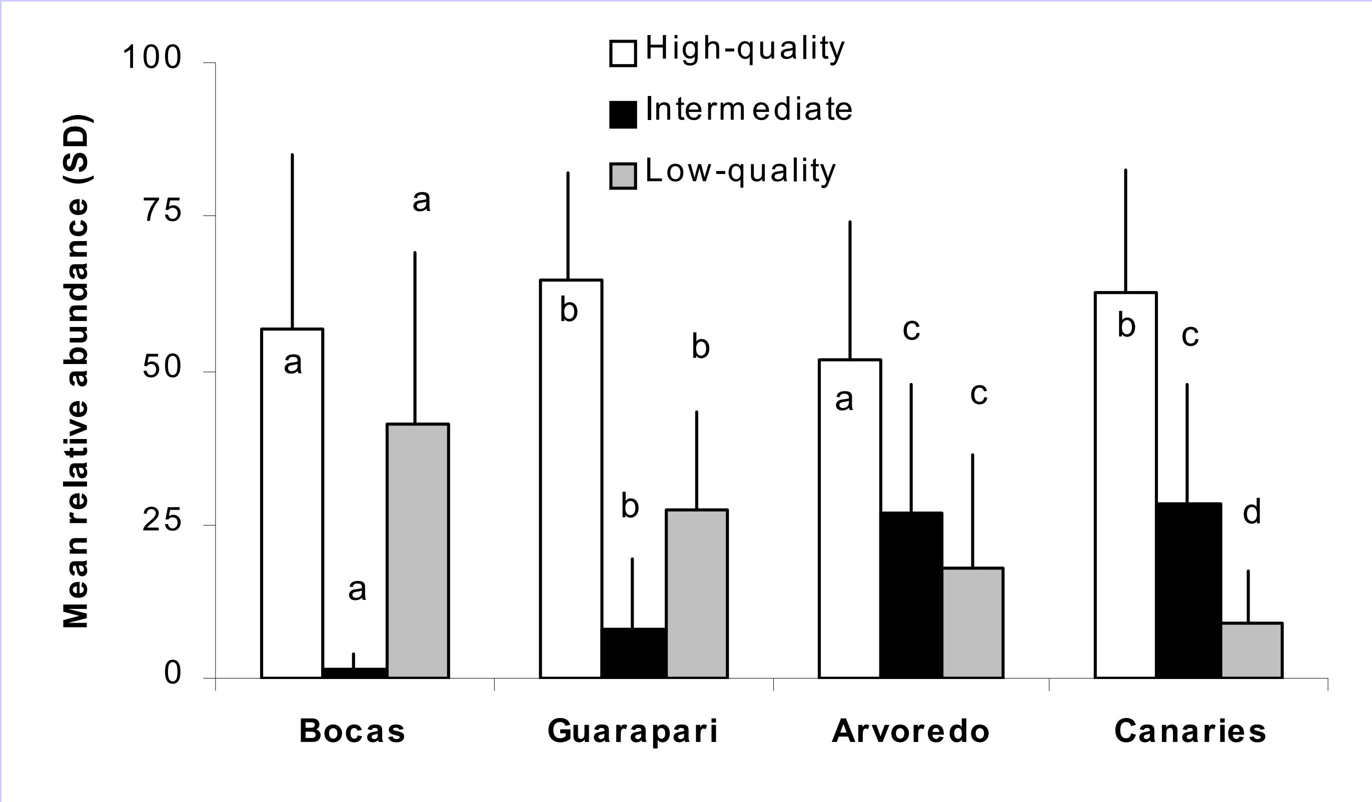
Floeter et al. (2004) J Fish Biol 64: 1680–1699

Quantitative data



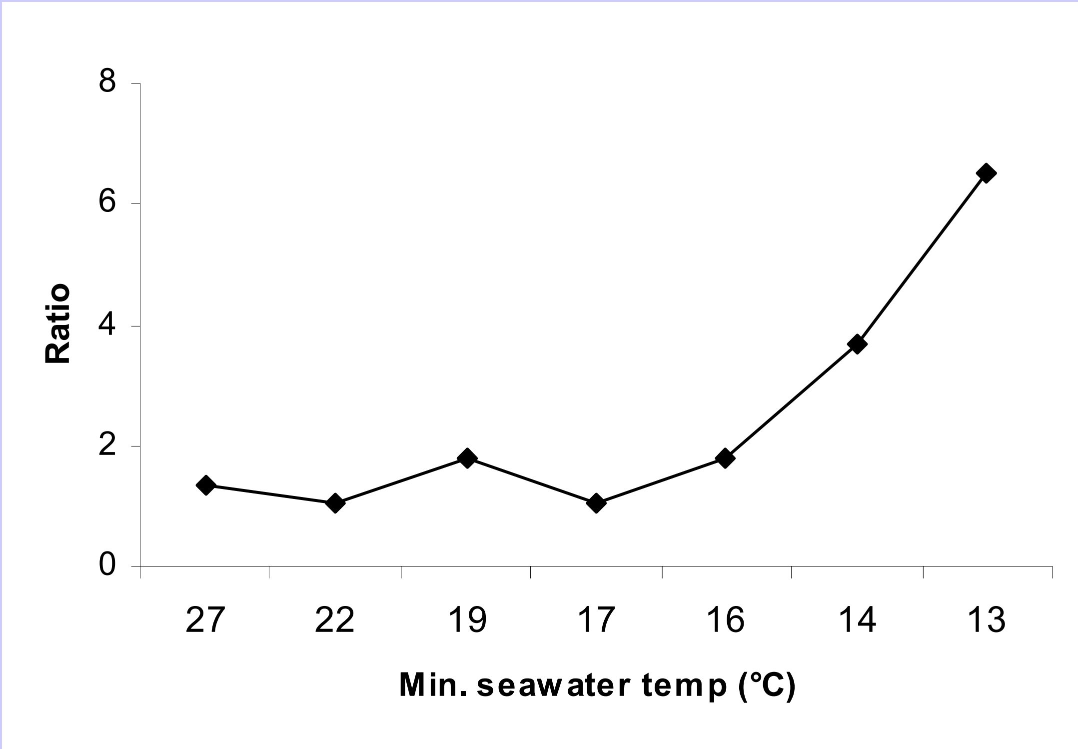
Floeter et al. (2004) J Fish Biol 64: 1680–1699

Relative abundance of food quality categories

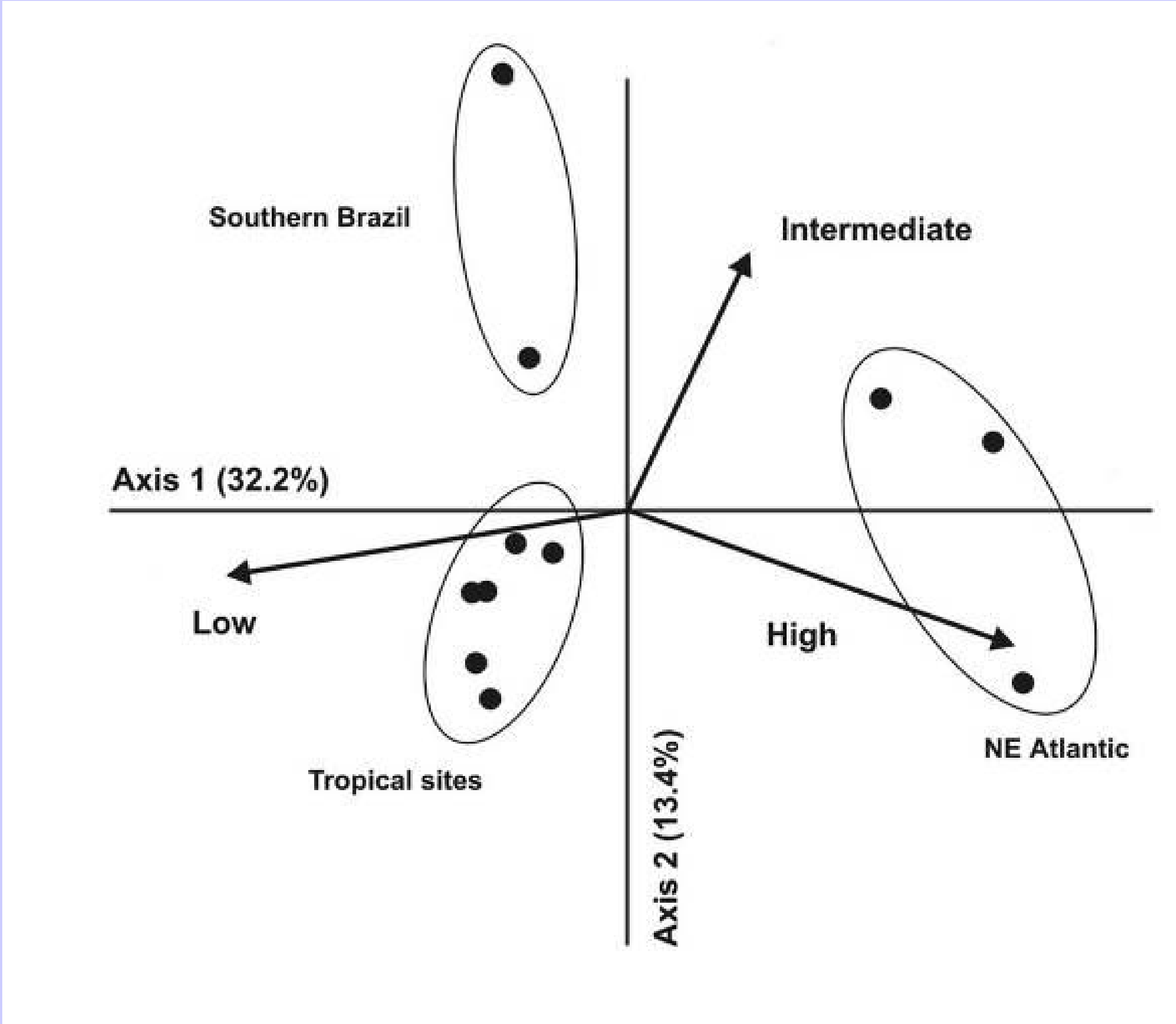


9 N 20 S 27 S 28 N

High-quality/intermediate + low quality food ratio in relation to minimum water temperature



Sites: Bocas del Toro, Panama, 9°N; Abrolhos Reefs, NE Brazil, 17°30’S; Guarapari Is., SE Brazil 20°S; Arvoredo, 27°30’S; Canaries, Macaronesia, 28°N; SE Mediterranean, Spain, 37°38’N; Santa Catalina Is., California, 33°30’N.



CCA: Tropical sites: Florida Keys; Cayos Cochinos, Honduras; Bocas del Toro, Panama; Manuel Luiz Reefs, NE Brazil; Tamandaré, NE Brazil; Abrolhos Reefs, NE Brazil; Guarapari Is., SE Brazil; **SE and Southern Brazil:** Arraial do Cabo, SE Brazil; Arvoredo, Southern Brazil; **NE Atlantic:** Canaries; SE Mediterranean, Spain; southern Italy.

Prediction

Is relative abundance of fishes that use relatively low-caloric food resources higher in the tropics?

YES,

at least from our data on the Atlantic

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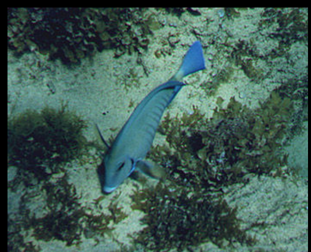
Geographical gradients of marine herbivorous fishes: patterns and processes

Importance of herbivorous fishes:

- They have profound impact on distribution, abundance and evolution of reef algae.

- They mediate competition between algae and coral (i.e. structuring force of reef communities).

- They are the major link for energy transfer to higher trophic levels.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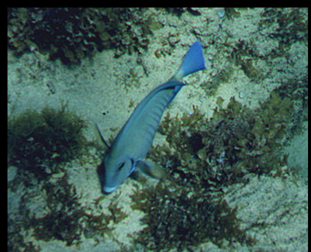


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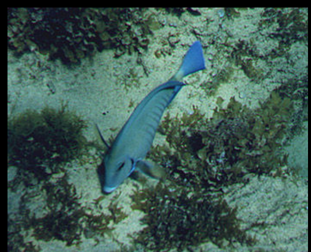
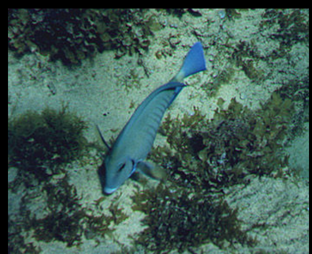



Big questions about geographical gradients of herbivorous fishes:

- Do herbivorous fishes decrease in importance (number of species, relative abundance, density, biomass) from tropical to temperate and polar waters?

- Does water temperature limit the distribution of herbivorous fishes?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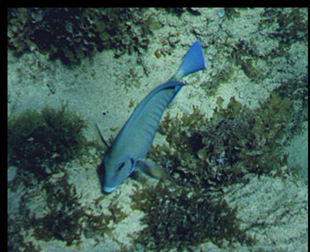
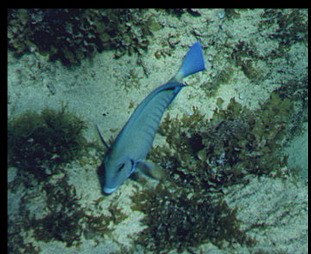
    

Aims:

- Present new data on latitudinal and thermal gradients of diversity, abundance and biomass of marine herbivorous fishes at different spatial scales.

- Examine the possible role of temperature limiting distribution of herbivorous fishes.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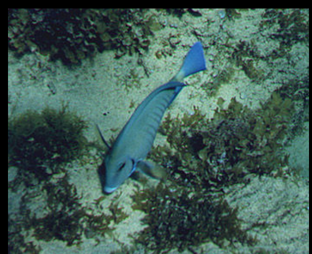


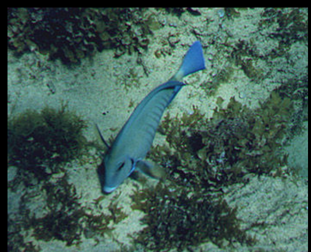

Methods:

- Global scale: relative abundance and relative richness: a database with 55 localities.

- Oceanic scale: Density and biomass patterns: standardized transects in 10 shallow and sheltered localities along the Western Atlantic.

- Local-scale (i.e. same latitude): relative abundance sampled at the Channel Islands, CA along a thermal gradient.

- Feeding rate: bite rate estimates of the surgeonfish *Acanthurus bahianus* at 3 locations.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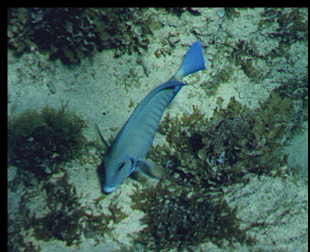

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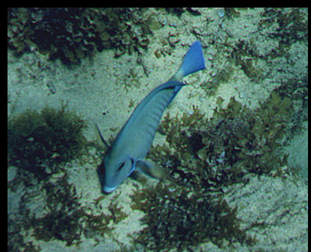


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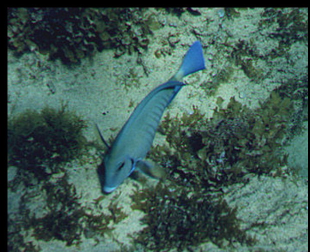
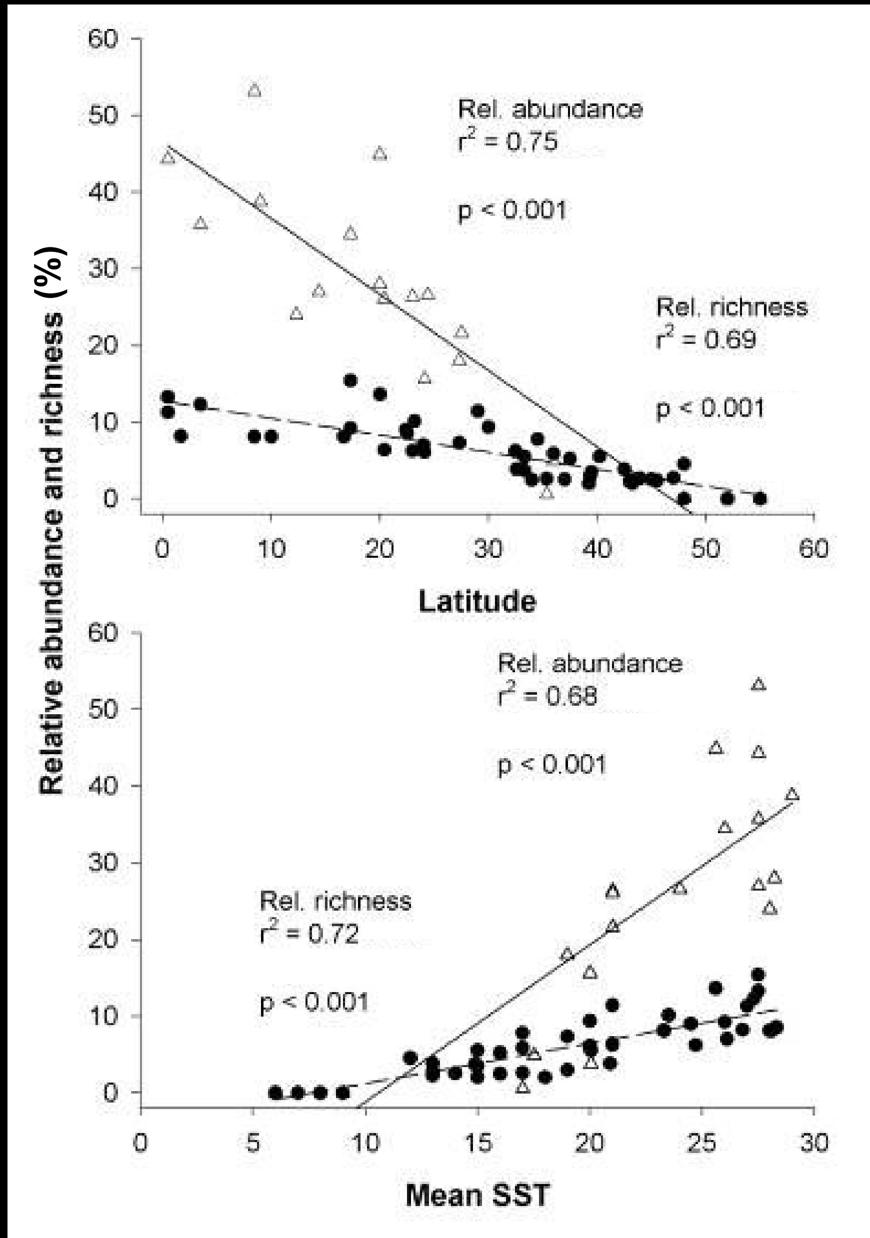
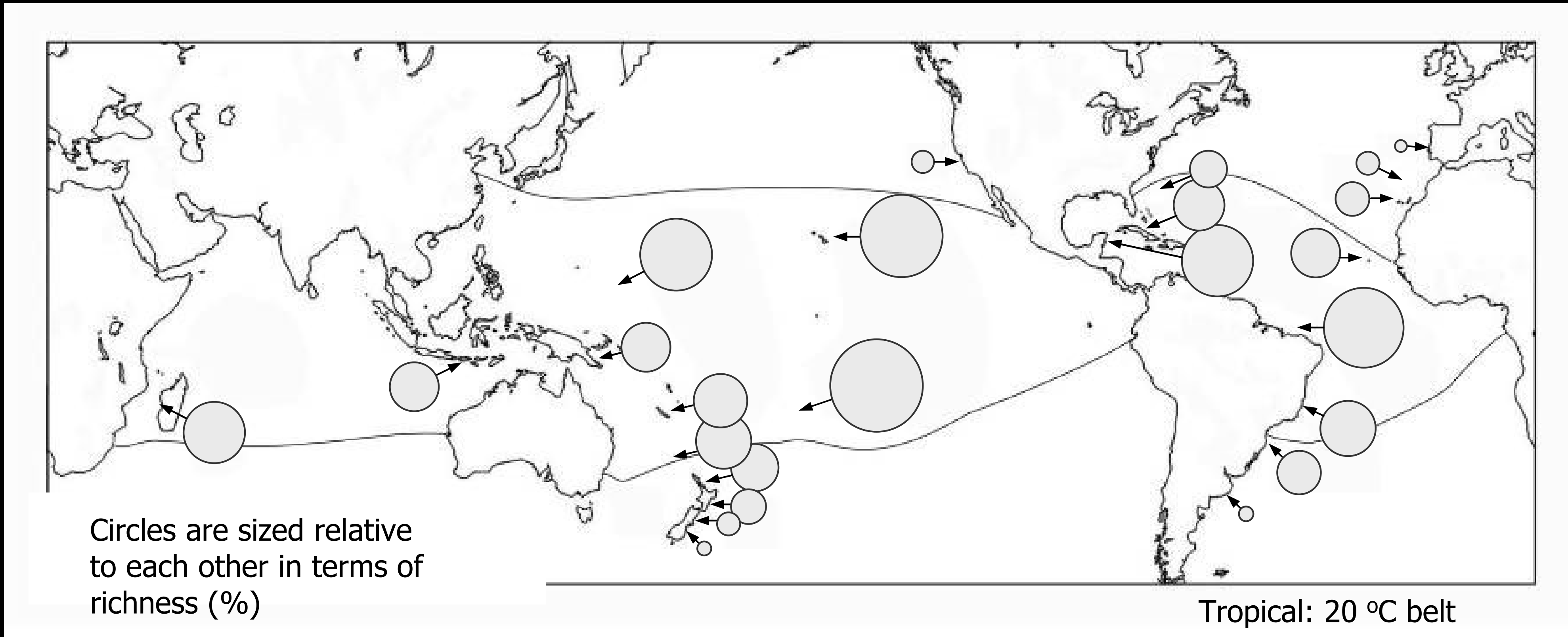



Global scale

Herbivorous fishes, latitude and sea surface temperature



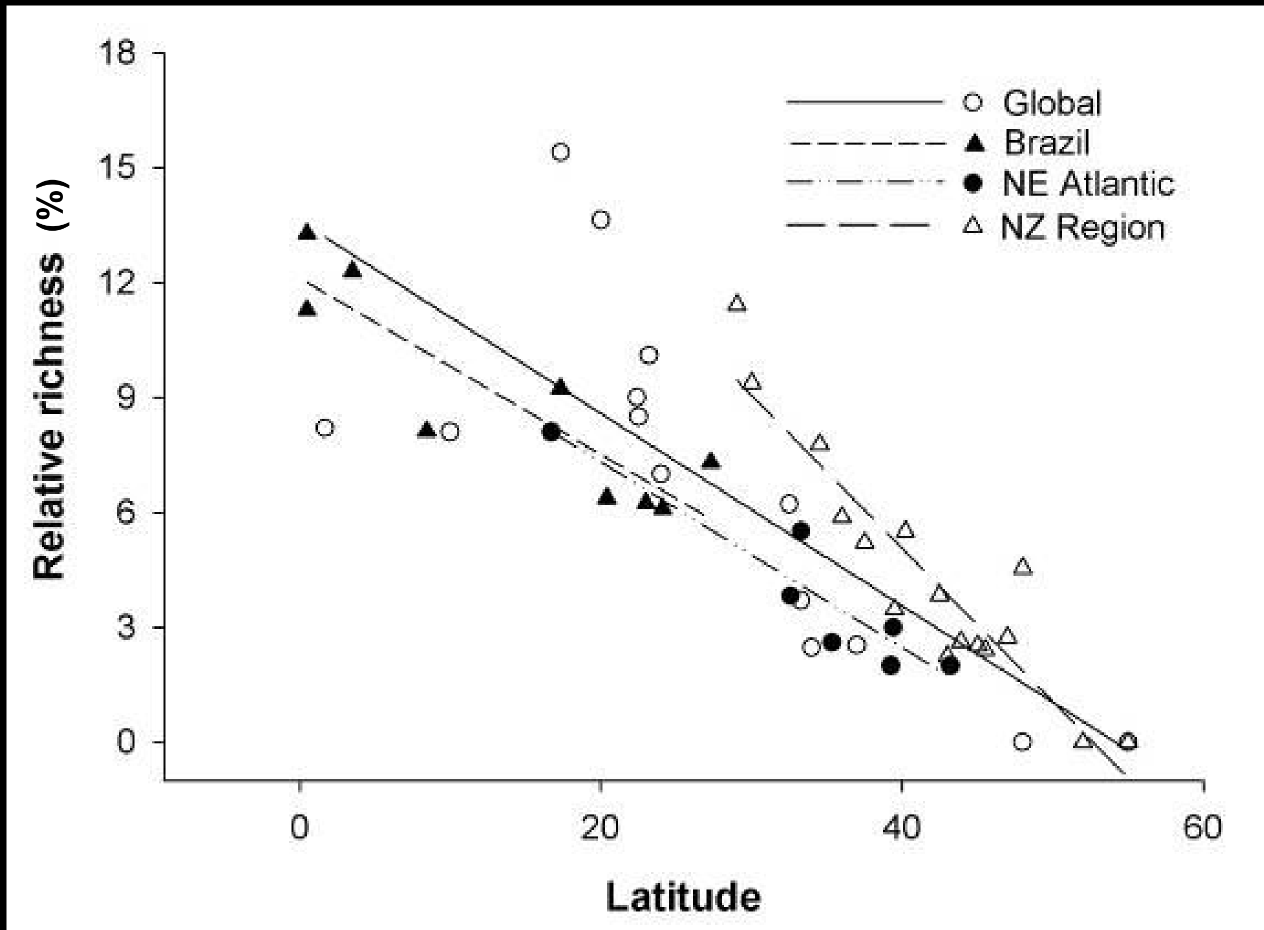
Percentage of herbivorous fish species richness worldwide



Tropical: 6-15% (mean of 9.8 ± 2.7 sd)
Extratropical: 0-9% (mean of 3.6 ± 2.4 sd)

Global scale

Proportion of herbivores and latitude among regions

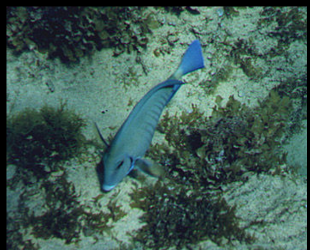


Brazil: $r^2 = 0.80$, $p = 0.001$; Northeastern Atlantic: $r^2 = 0.87$, $p = 0.002$; New Zealand: $r^2 = 0.86$, $p = 0.001$; Global: $r^2 = 0.58$, $p = 0.002$

Conclusions:

- Consistently negative relationships between latitude and relative richness and relative abundance were found worldwide, irrespective of the ocean or region considered.

- Consistently **positive** relationships between SST and relative richness and relative abundance were found worldwide, irrespective of ocean or region.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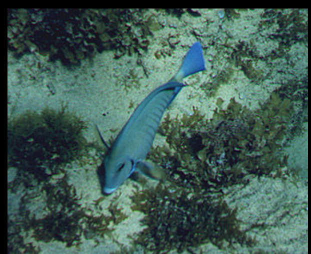
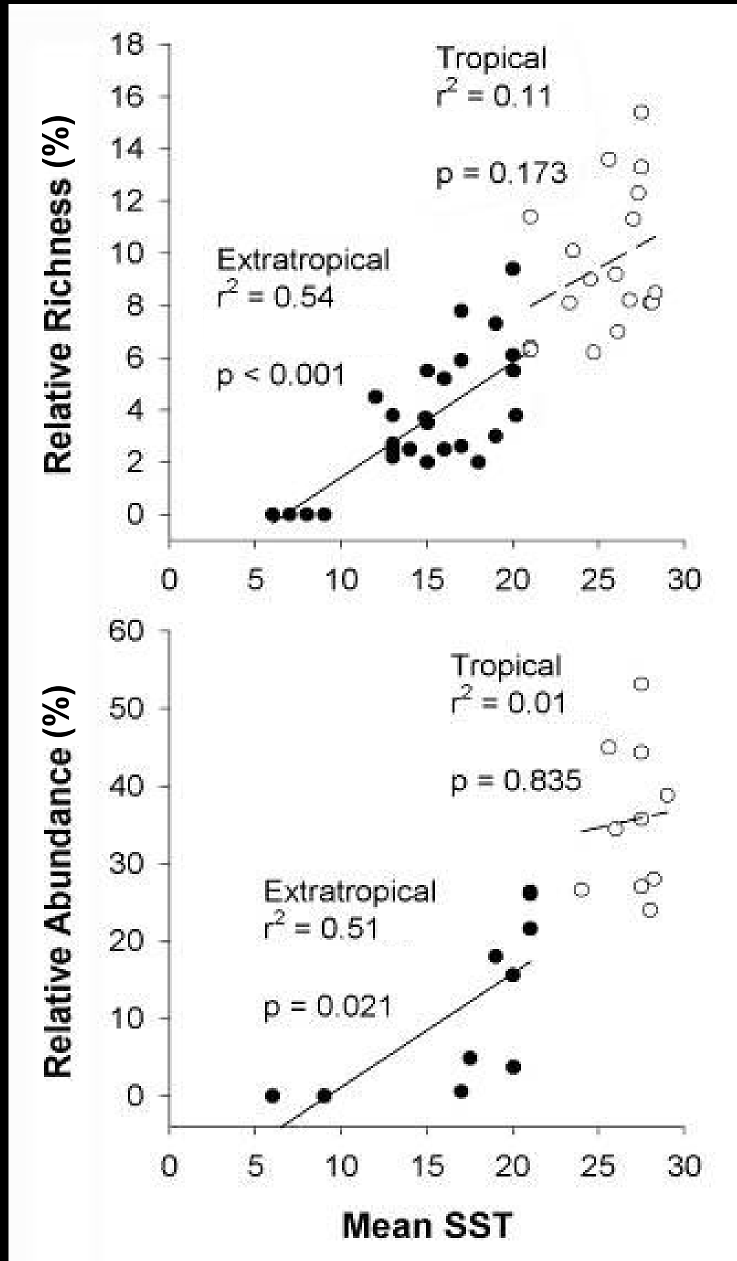


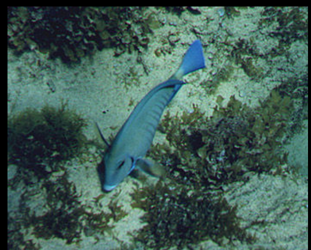

Global scale

Tropical vs. extratropical sites



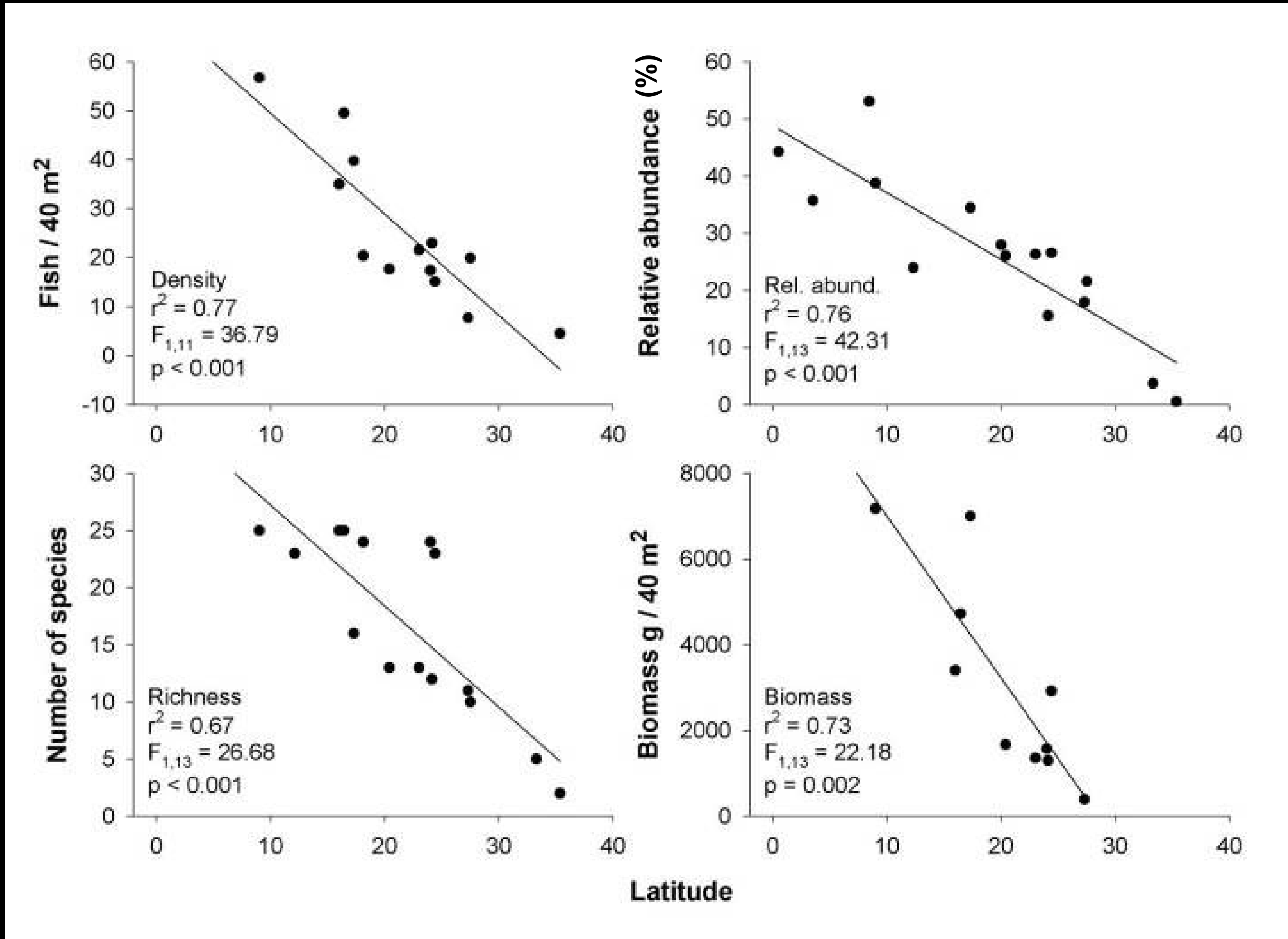
Conclusion:

- Relationships between SST and relative richness and relative abundance are <u>not significant in the tropics</u> but are <u>highly significant</u> in the <u>extratropical</u> zone.

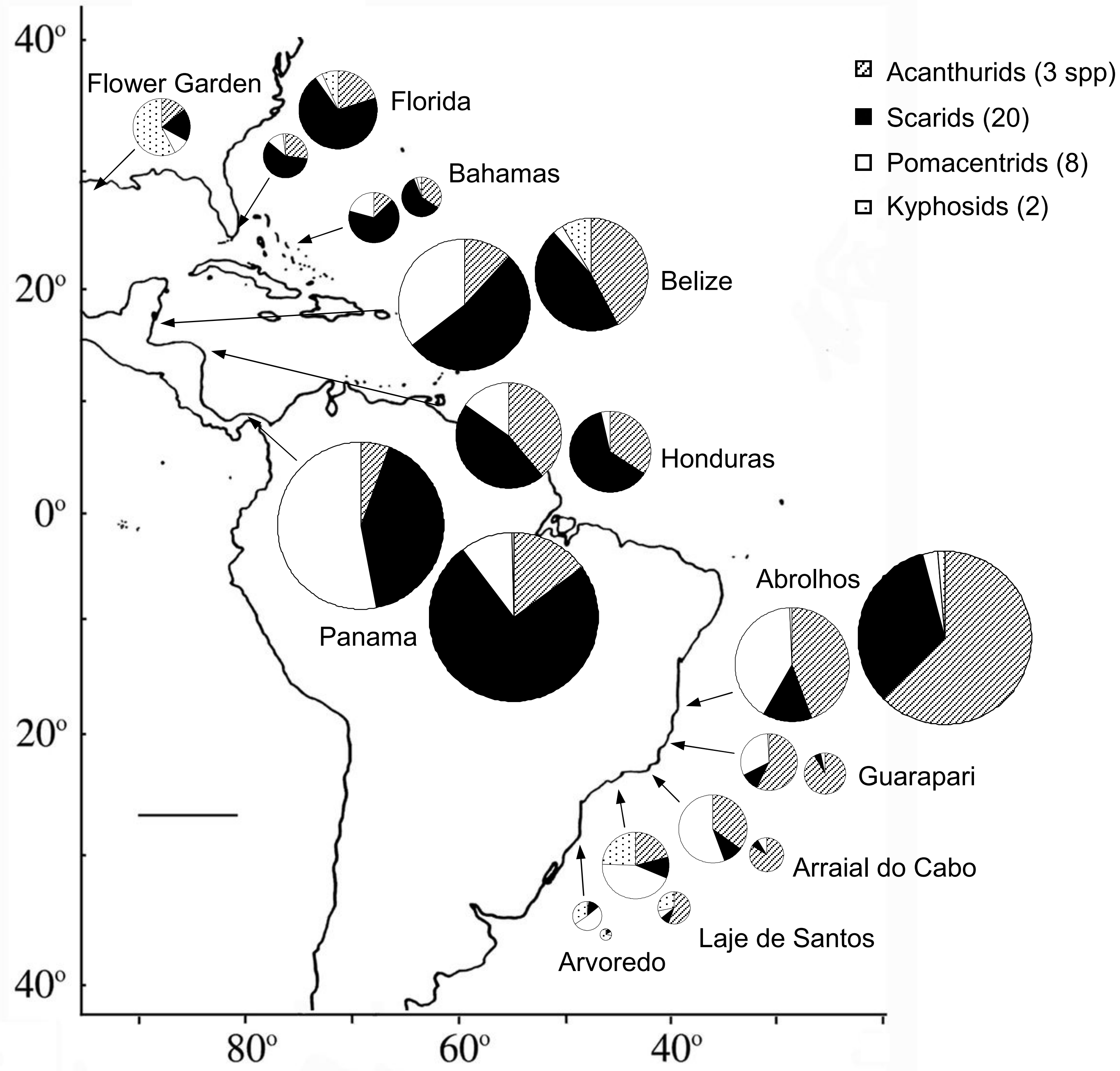

Oceanic scale

Western Atlantic

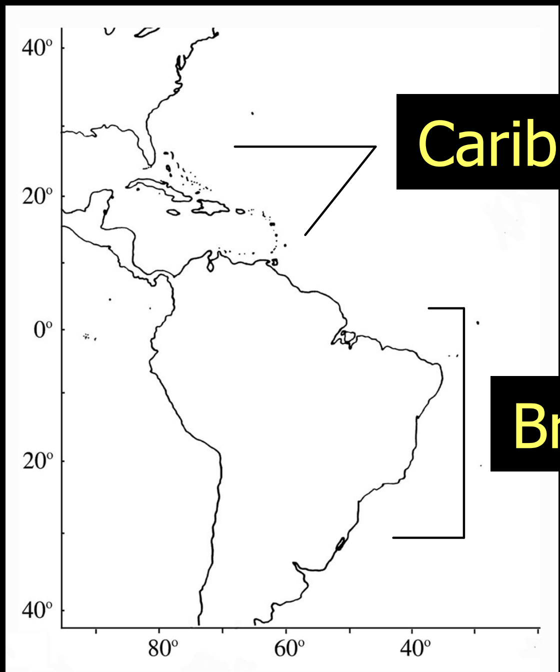


Herbivore fish density and biomass

Pies are sized relative to each other in terms of density (left) and biomass (right)



Acanthuridae : Scaridae ratio



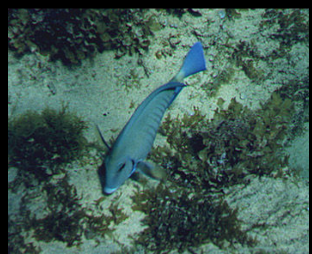
Caribbean ratio: 0.1 - 0.84

Brazil ratio: 3.2 - 5.7

Conclusions:

- Density, biomass, relative abundance and species richness significantly decrease with latitude in the Western Atlantic.

- Patterns in the Atlantic are driven by different families, i.e. scarids in the Caribbean and acanthurids in Brazil.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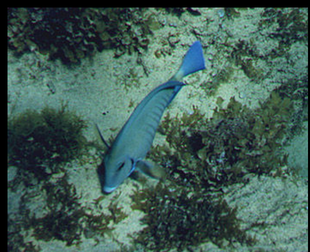


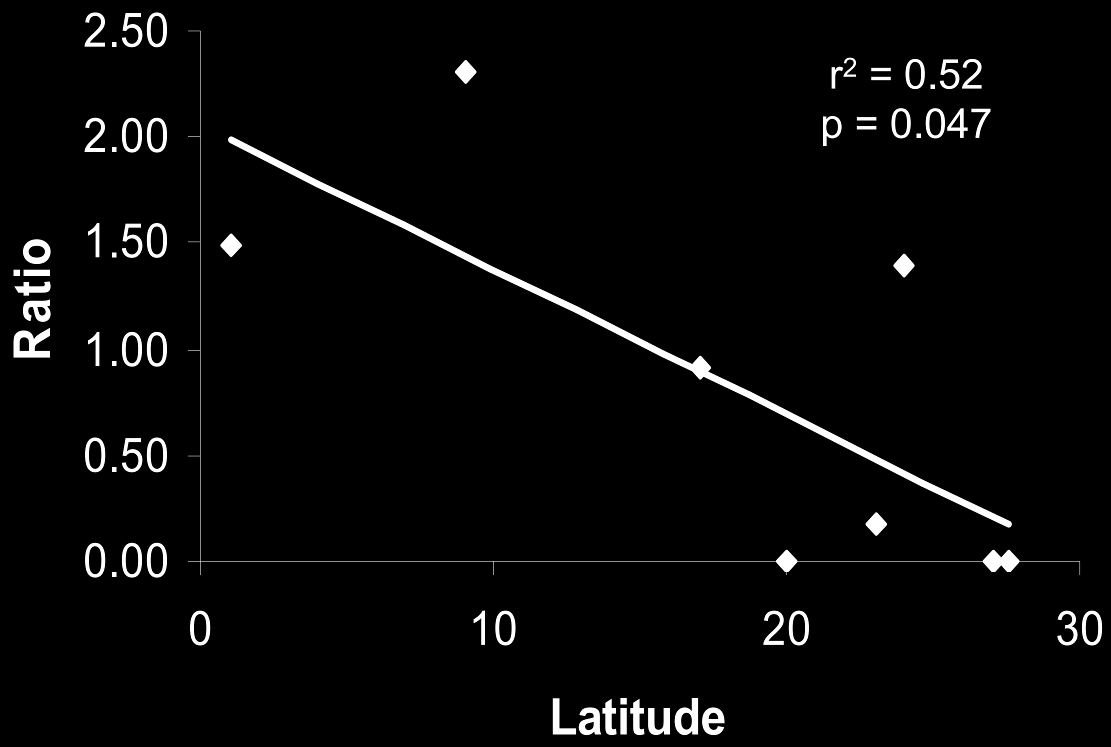

Scarus : *Sparisoma*

Parrotfishes

Given the wide range of feeding modes (browsing and biting) of the genus *Sparisoma* we predicted that they present wider distributions and are proportionally more important at higher latitudes, than *Scarus* (specialist scraping).

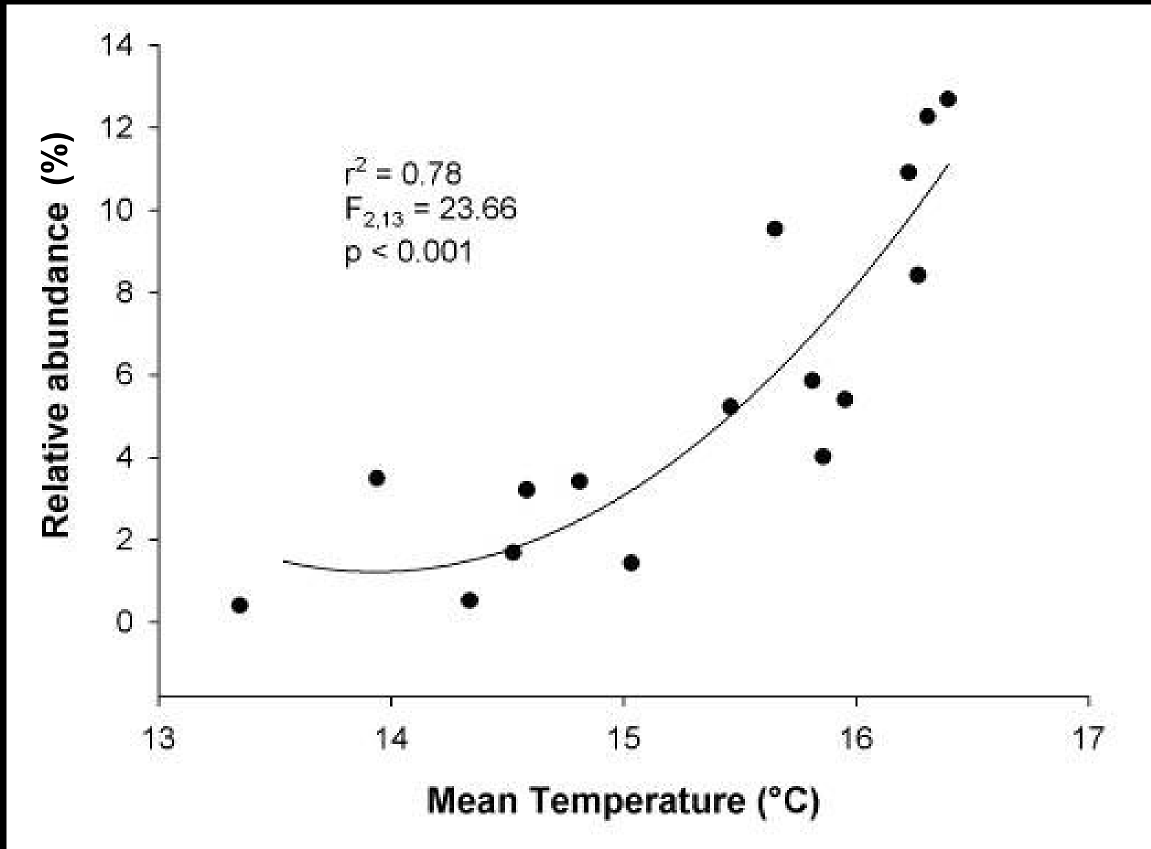
(Bernardi *et al.*, 2001, Streelman *et al*, 2002)

Scarus : *Sparisoma* ratio



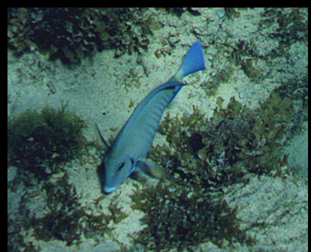
Local scale

Thermal gradient of herbivorous fishes at the Channel Islands, California (same latitude)



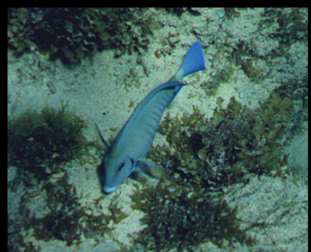
Conclusion:

- Thermal gradients associated with extensive latitudinal gradients also were found at the local scale.

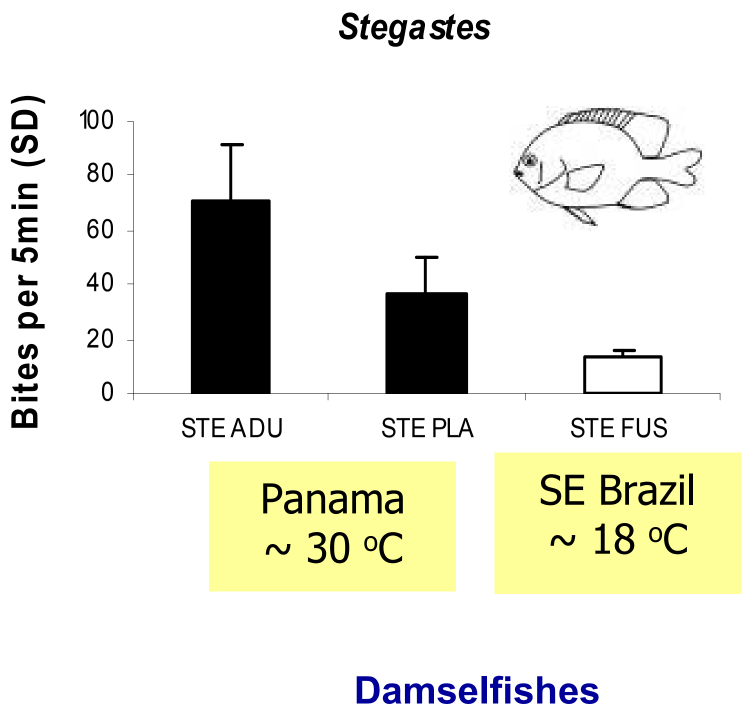



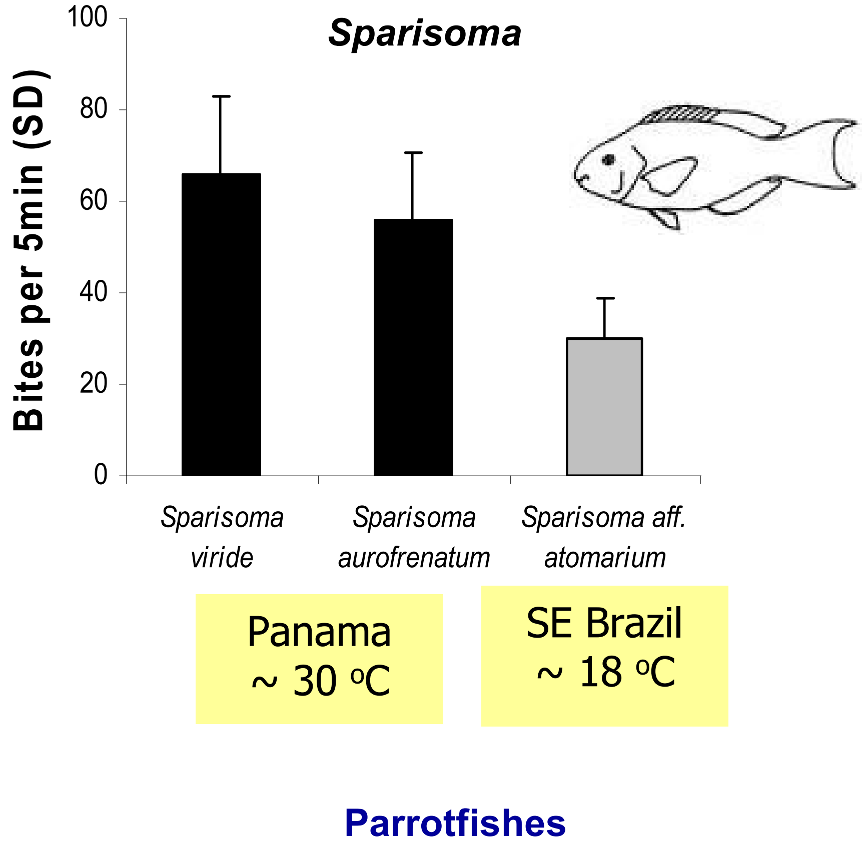

Feeding rate

- Is feeding rate related to temperature?

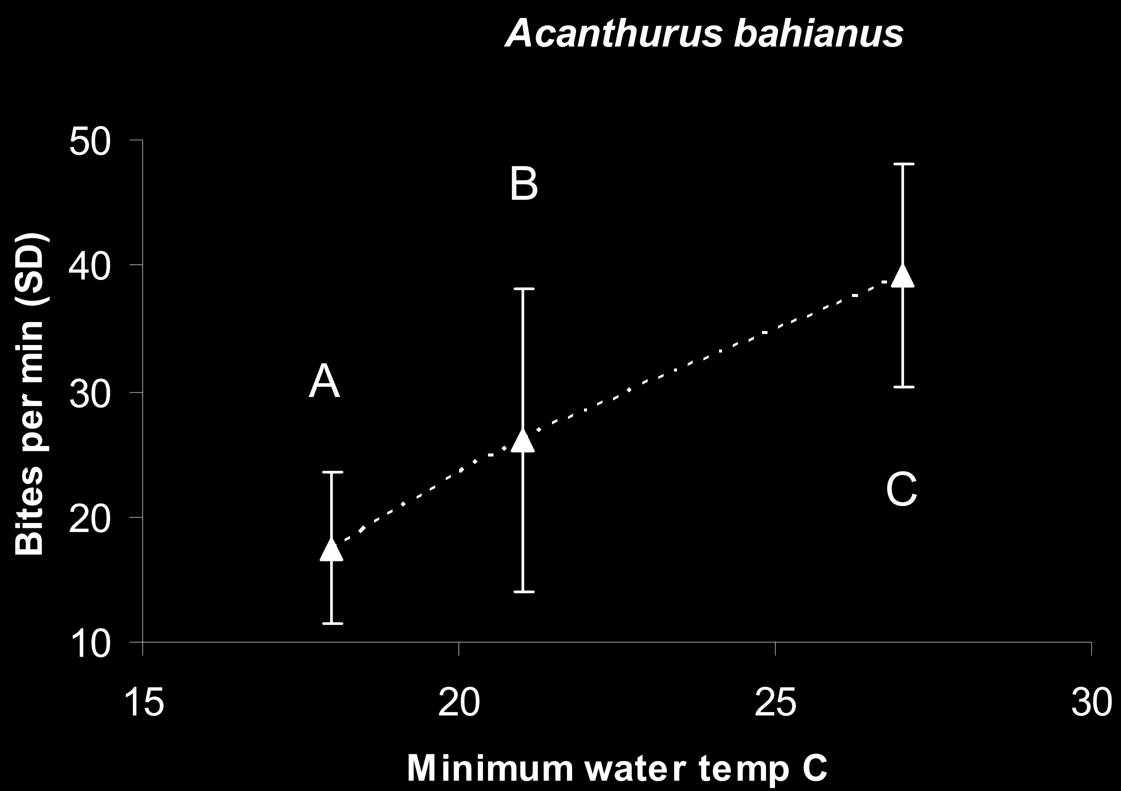




Feeding rates



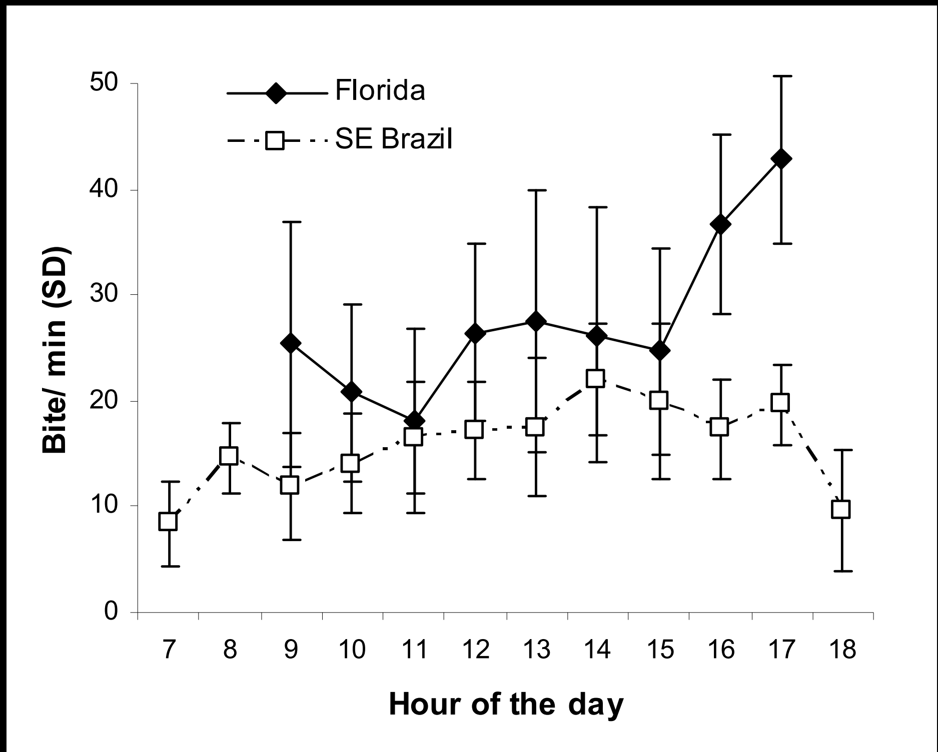


Average feeding rate of the ocean surgeonfish

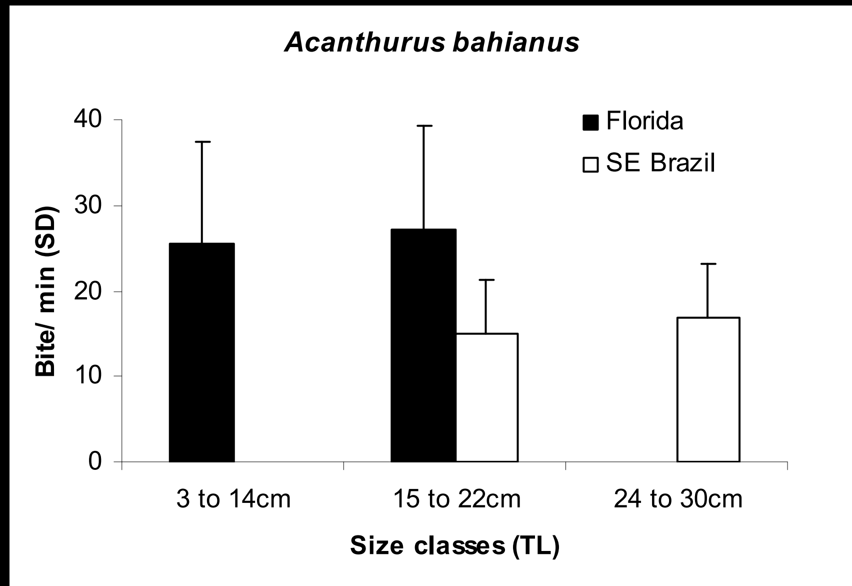


ANOVA $p < 0.001$; Tukey post-hoc test: Arraial do Cabo, SE Brazil ≠ Florida ≠ Bocas del toro, Panama. Data from 10 to 17h at all sites.

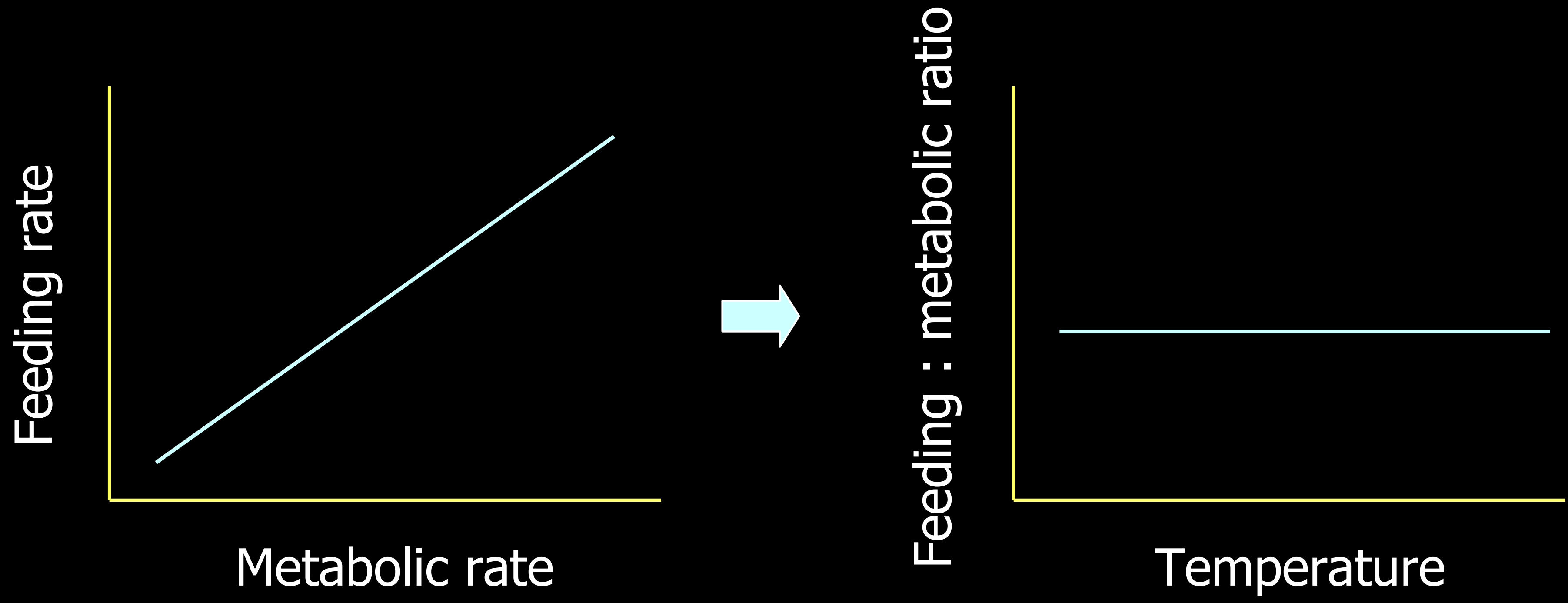
Average feeding rate of the ocean surgeonfish *Acanthurus bahianus*



Time

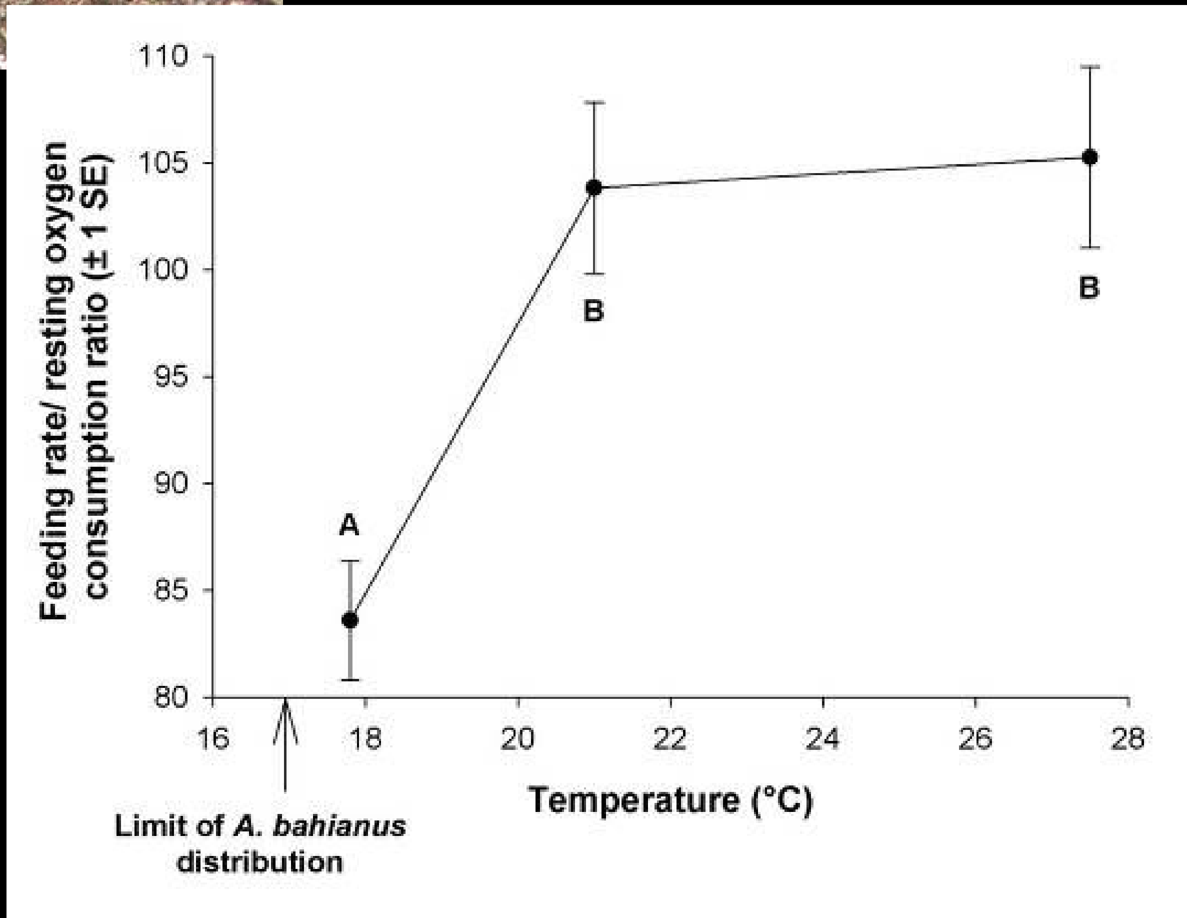


Size


Feeding rate
Metabolic rate
Feeding : metabolic ratio
Temperature

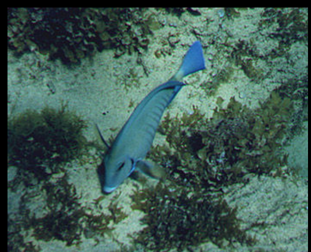
Acanthurus bahianus

Ratio between average feeding rate and metabolic rate for teleost fish



Conclusion:

- Feeding rate of the *A. bahianus* is proportionally lower in cool water than expected by metabolic rate of teleost fishes, suggesting a temperature-related physiological constraint.


Things to think about!

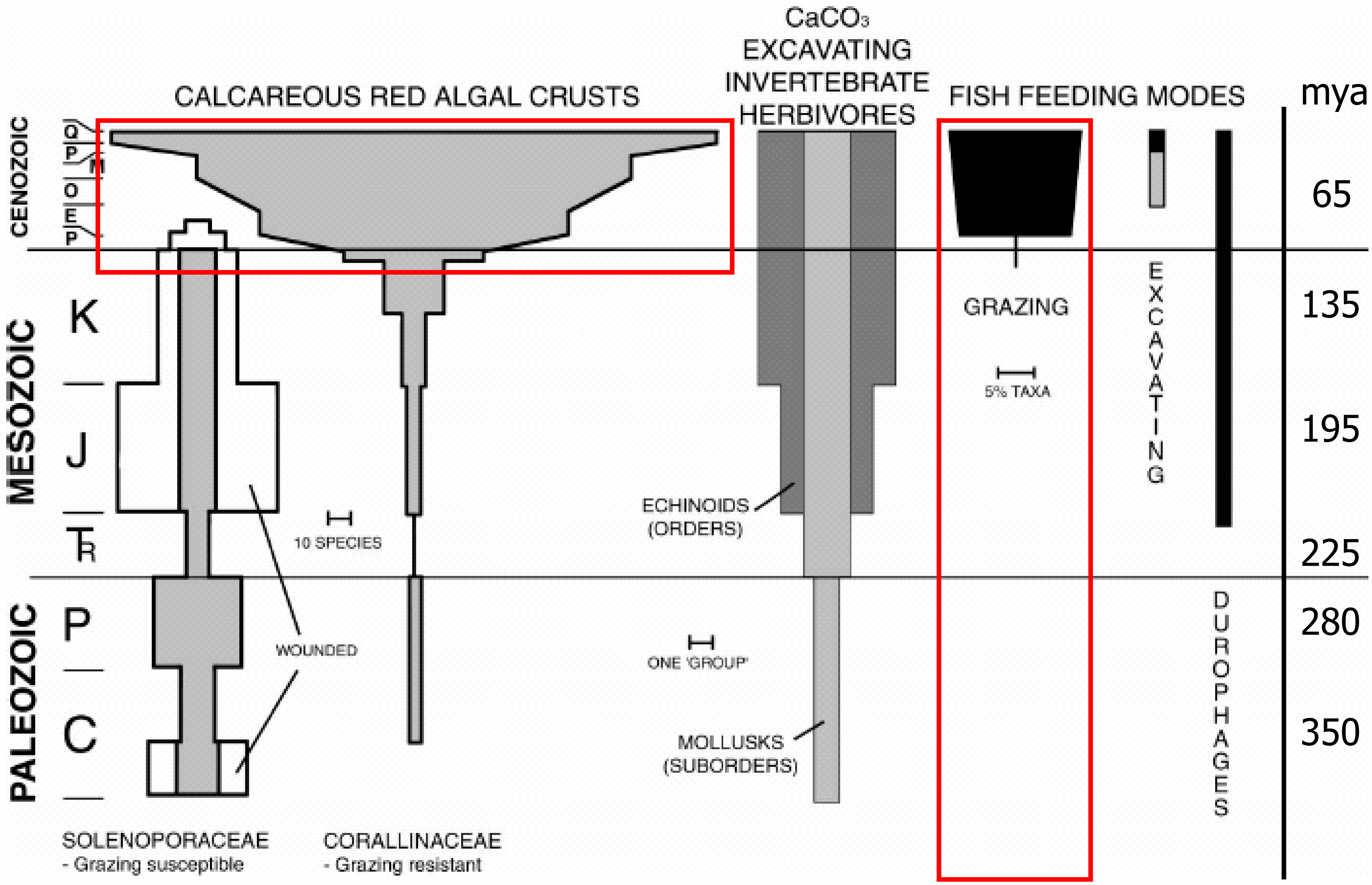
- Exclusive selective macroalgae feeders, which use special digestion by hind gut fermentation and symbionts [‘**true herbivores**’ *sensu* Choat & Clements (2002) such as kyphosids, odacids, aplodactylids, and stichaeids] are also found in **temperate** rocky reefs.

- **Detritivore-herbivore** groups like scarids and acanthurids do not penetrate colder waters [differences in the detritus web?], but…

- Why scarids dominate in the Caribbean while acanthurids are proportionally more abundant in Brazil?

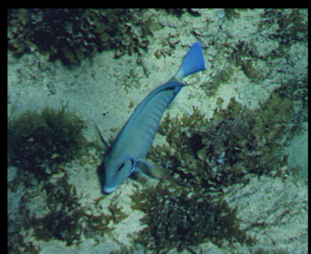
- What about patterns in **terrestrial herbivores**? Birds? Mammals? Reptiles? Any latitudinal trend?

Evolution of Herbivory in Fishes

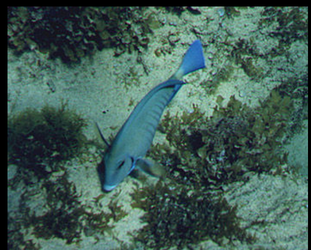


Evolutionary Requirements for Herbivory

- Jaw Structure
  - Ancestral condition
    - High velocity
  - Herbivory
    - High force
- Gut length
- Digestive enzymes


Why has the evolution of herbivory at temperate latitudes apparently been so difficult (or at least slow)?


Proposed Mechanisms

Food Quality

Latitudinal differences in algal quality

Algae is seasonably unavailable in temperate latitudes

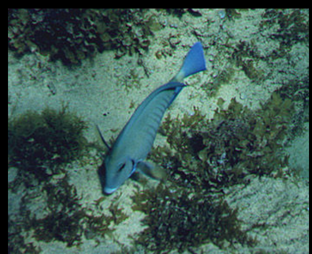
Evolution

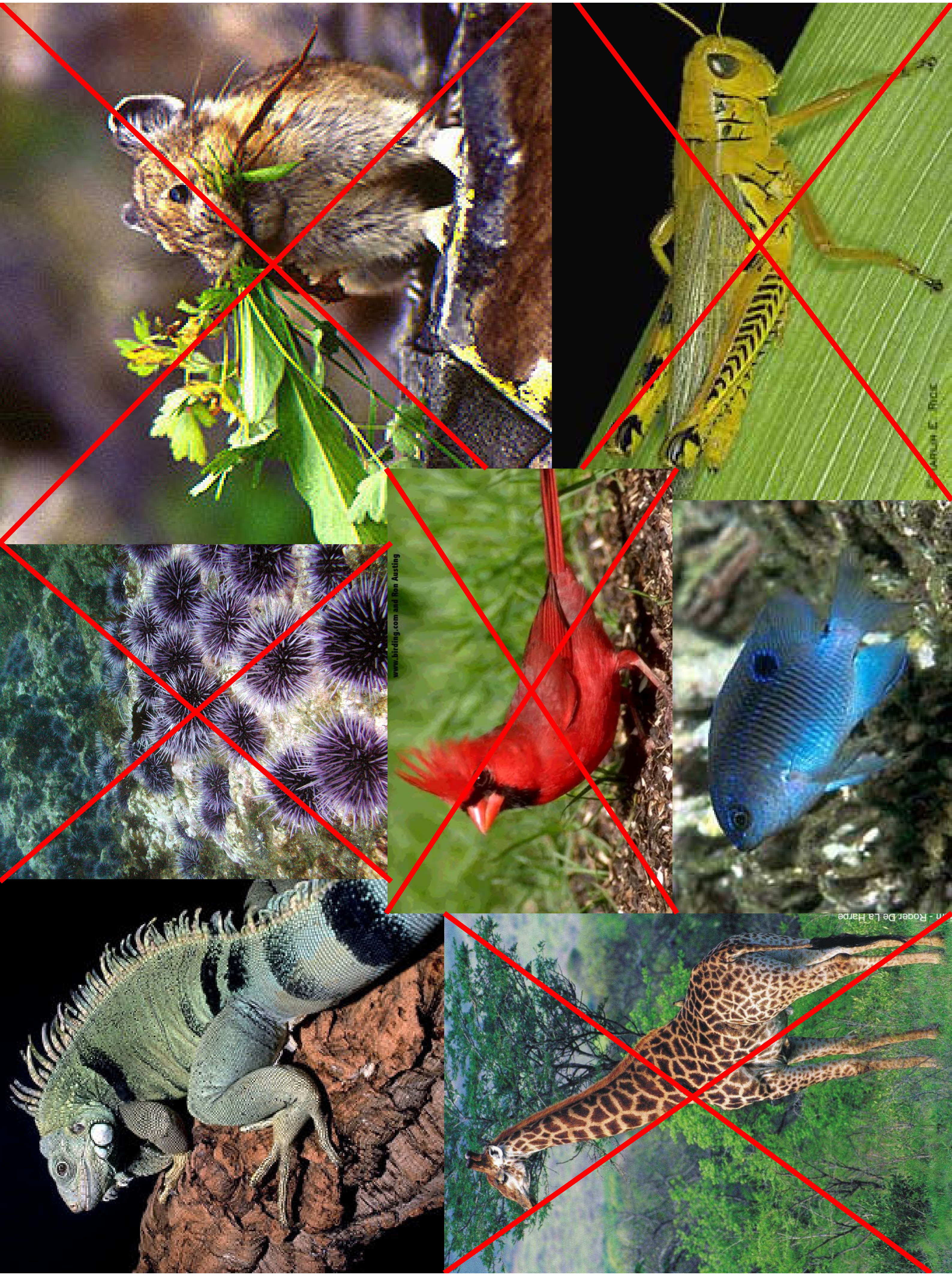
Insufficient time for evolution and expansion

Tropical evolution towards use of energy-deficient foods

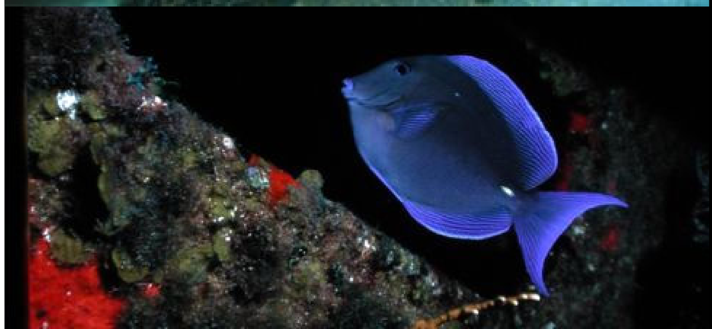
Physiology

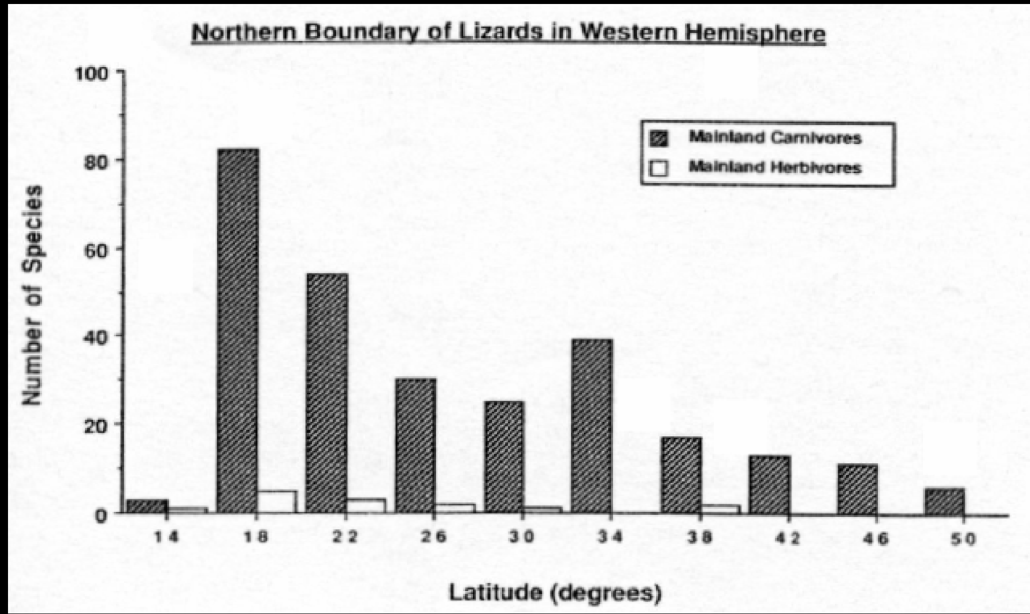
Thermal constraints on digestive physiology

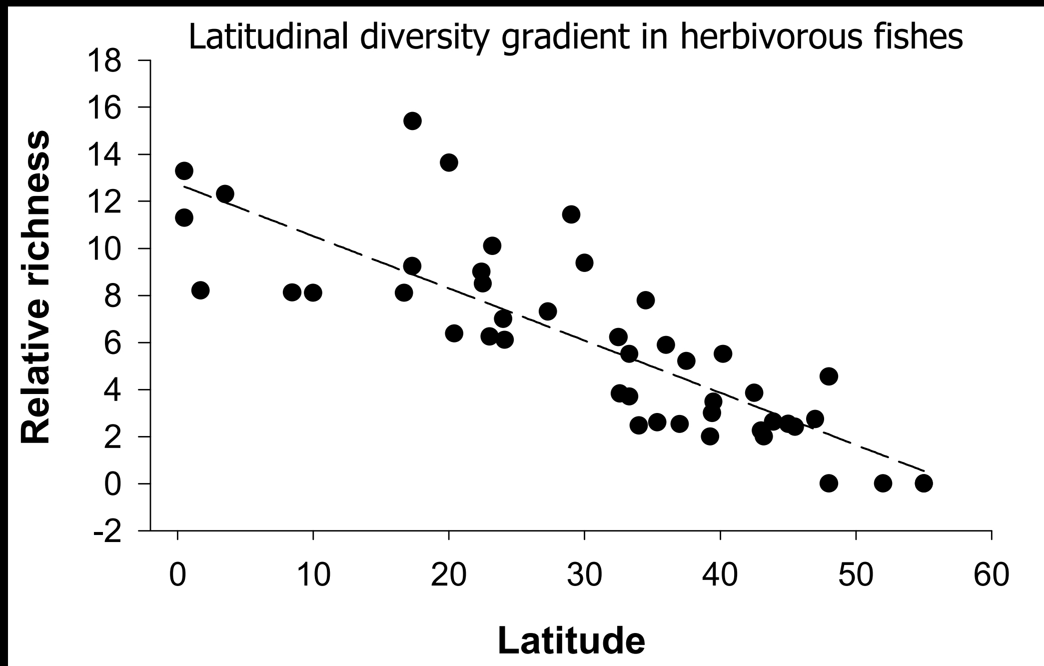





www.birding.com and Ron Austing

Distribution of Herbivorous Ectothermic Vertebrates







Why Might Temperature Be Important?

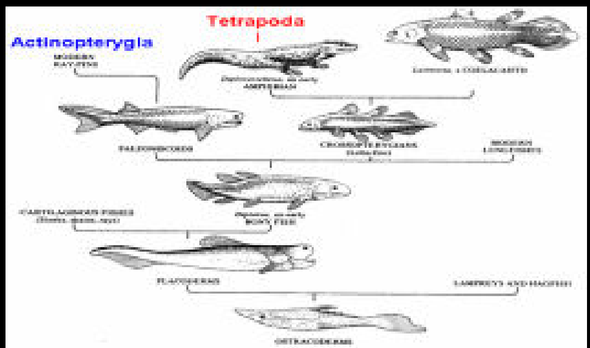
Temperature Dependent	Energy Loss/Gain
Metabolic rate	-
Consumption rate	+
Gut passage rate	+
Microbial fermentation rate	+

Temperature Independent	Energy Loss/Gain
Assimilation efficiency	+

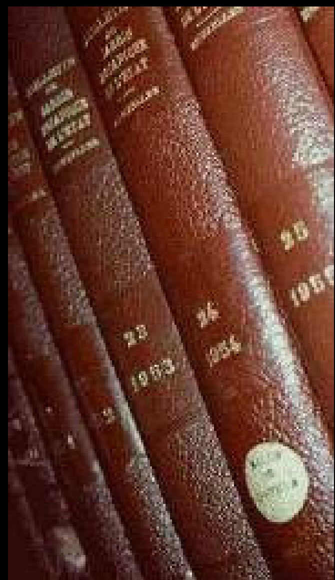
45 Years and No Definitive Answers!

Large scale problems often require multidimensional approaches.

Phylogenetic analysis



Macroecology/
Metaanalyses

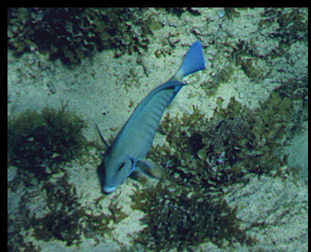


Field Studies

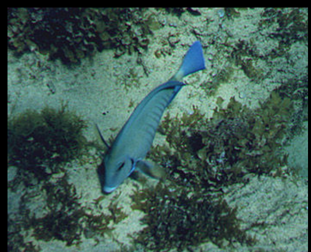
Lab Studies

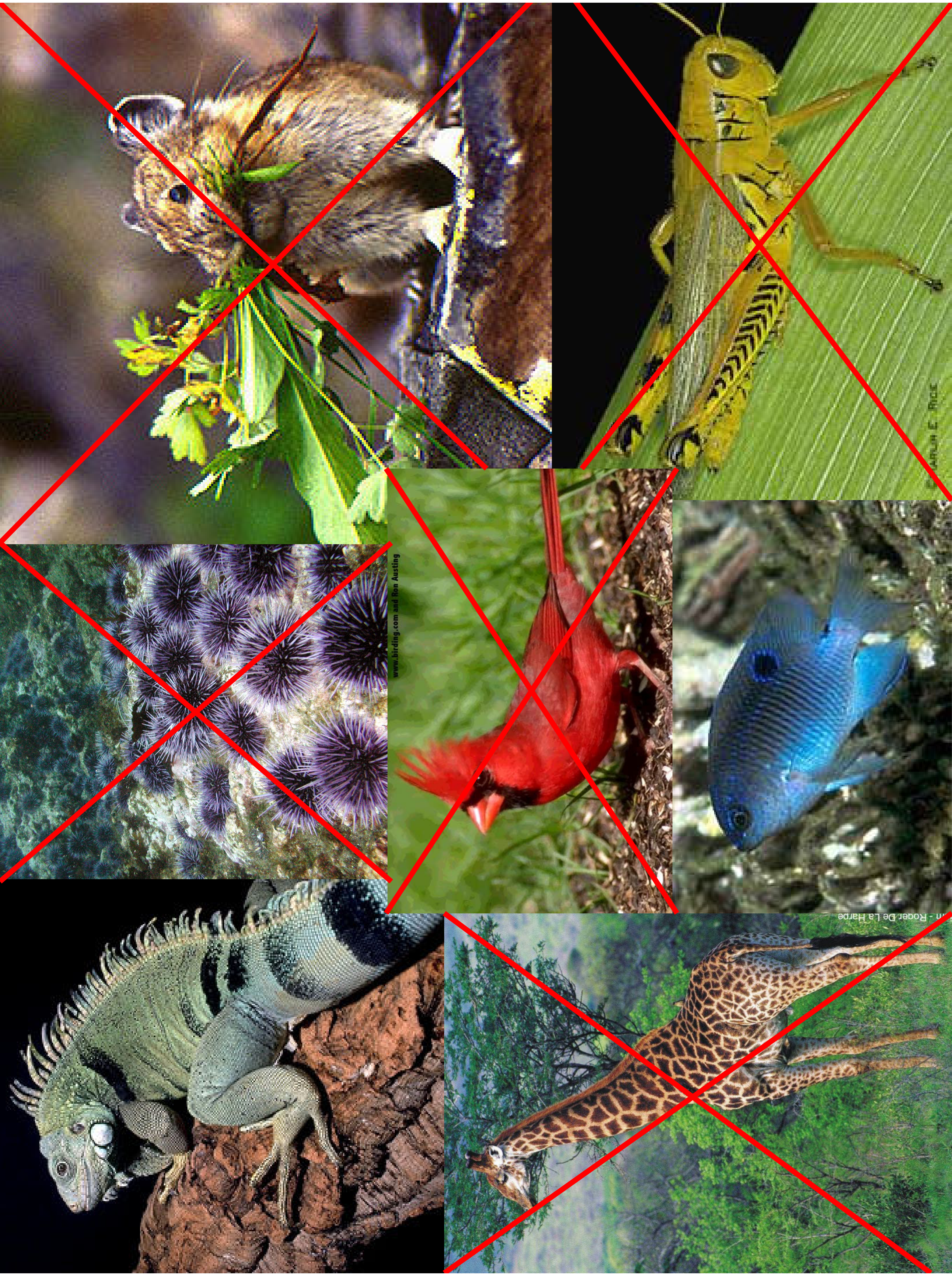
Evolutionary constraints on herbivorous fish distributions

- Macroecological approach
- Feeding ecology of herbivorous fish
- Temperature and diet effects on condition
- Temperature effects on fermentation
- Conclusions


By looking at fish community data over a range of spatial scales, can we reject any mechanisms as important factors related to herbivorous fish distributions?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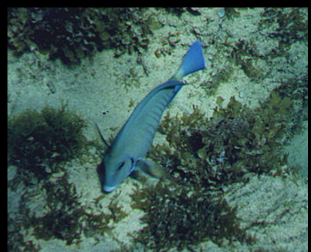
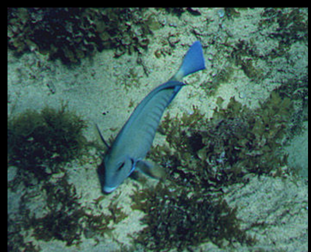
Implications to Herbivorous Fish Evolution

If a physiological constraint due to temperature does exist in herbivorous fishes, then opaleye may be shifting their diet to more energy rich animal material at colder temperatures to combat this constraint.

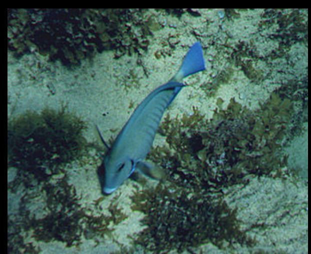

Outline

- Macroecological approach
- Feeding ecology of herbivorous fish
- Temperature and diet effects on condition
- Temperature effects on fermentation
- Conclusions


Is the effect of temperature on growth and nutritional condition dependent on diet?

Can this invoke temperature-dependent selection against certain diets?

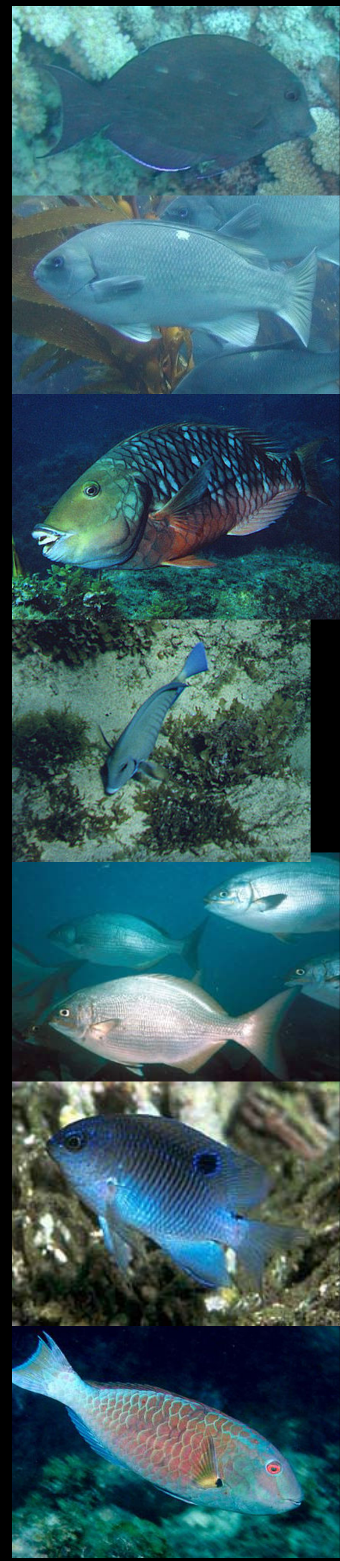

Diet and temperature effects on dietary condition

If a physiological constraint due to temperature exists:

- Assuming competition and evolutionary constraints on morphology impact food choice

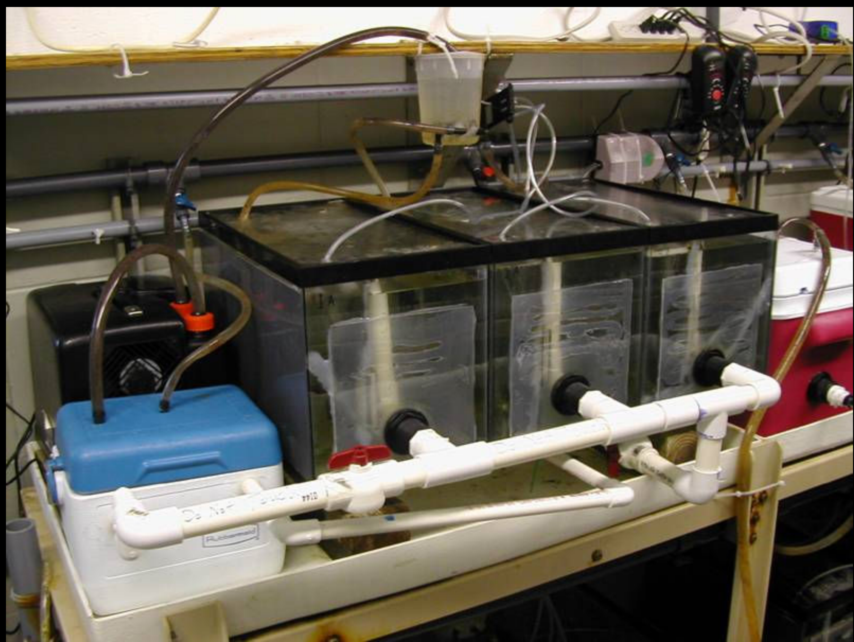
Corollary:

- If a species could shift to a higher quality diet, then they should be able to increase performance.
- Most important in cold waters



Experimental Design

- *Girella nigricans*
- 12°, 17°, 22°, and 27° C
- Diets
  - Algae (*ad lib.*)
  - Algae (*ad lib.*) + 1% BM Squid

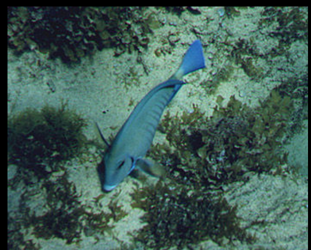


- 28 day duration

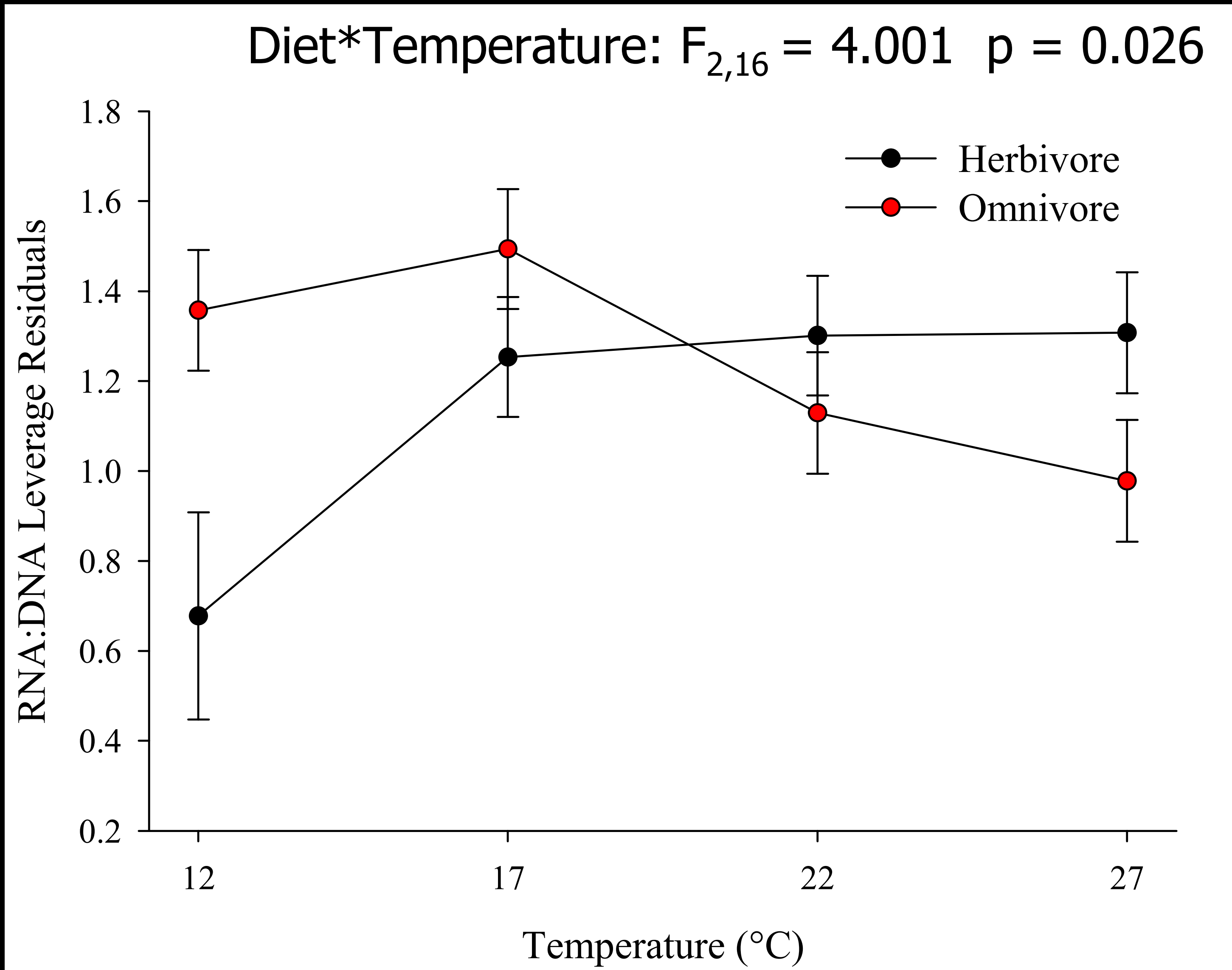
Data Analysis

- RNA:DNA analysis of white muscle
  - Potential for protein synthesis
  - Proxy for growth and nutritional condition

- Diet x Temperature interaction

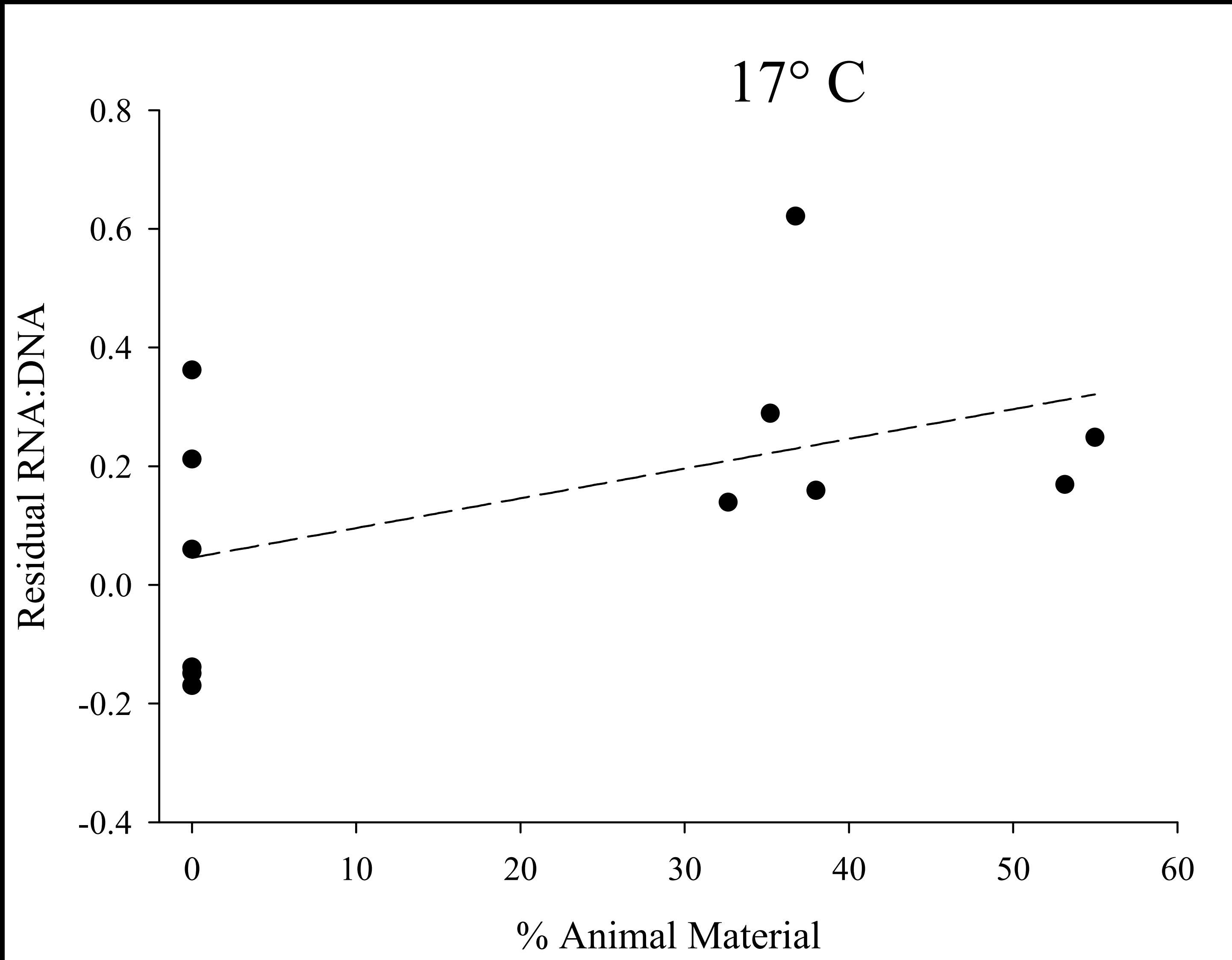




Temperature – Diet Interactions

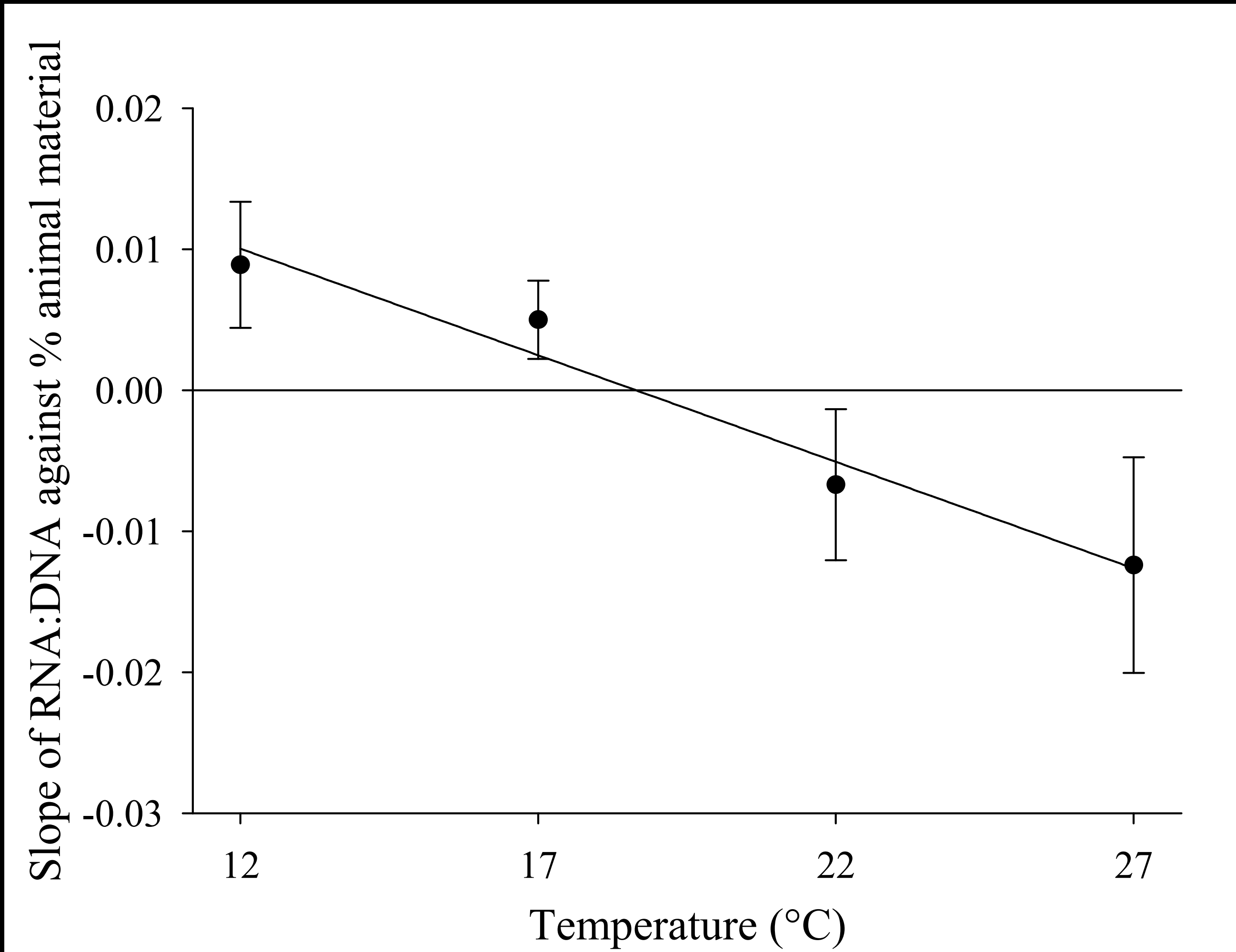


- Omnivores perform better at low temperatures
- Herbivores perform better at high temperatures

RNA:DNA Changes with Diet



Temperature Dependent RNA:DNA Changes



Temperature * % Animal material:

$F_{3,40} = 3.421$ $p = 0.026$

Temperature and Diet Effects on Gut Passage Rate

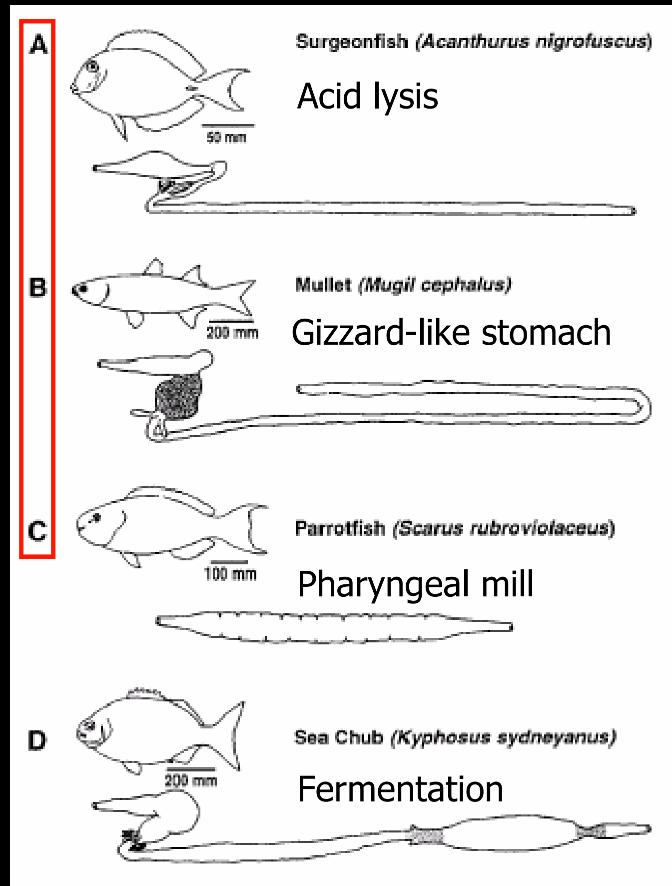
Gut Passage Rate (GPR)

- Non-fermenters – high
- Fermenters – low

GPR increases with temperature

Diet changes can lead to changes in GPR

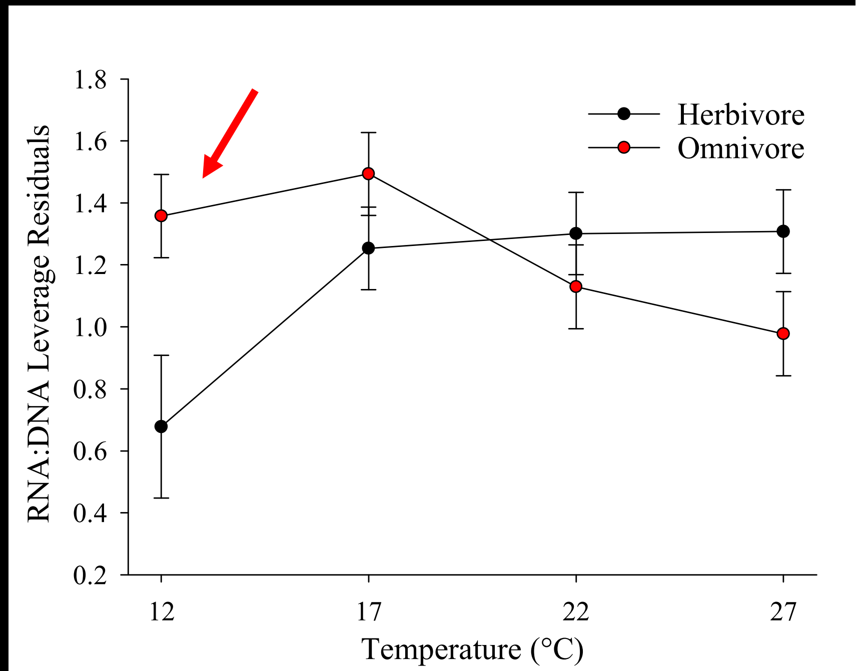
- Carnivores 10-158 hours
- Herbivores < 10 hours



- *Hyporhamphus melanochir* –diel diet shifts accompanied by GPR changes

Conceptual Model

	Low Temp	High Temp
Omni.	GPR low Metabolism Low Diet Quality High	GPR low Metabolism High Diet Quality High
Herb.	GPR low Metabolism Low Diet Quality Low	GPR High Metabolism High Diet Quality Low



Conceptual Model

	Low Temp	High Temp
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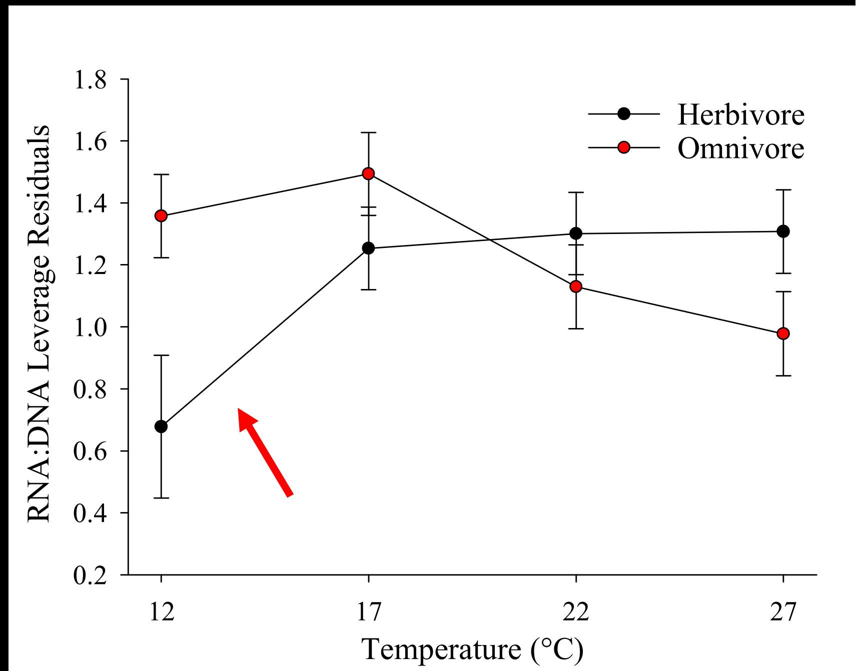

Conceptual Model

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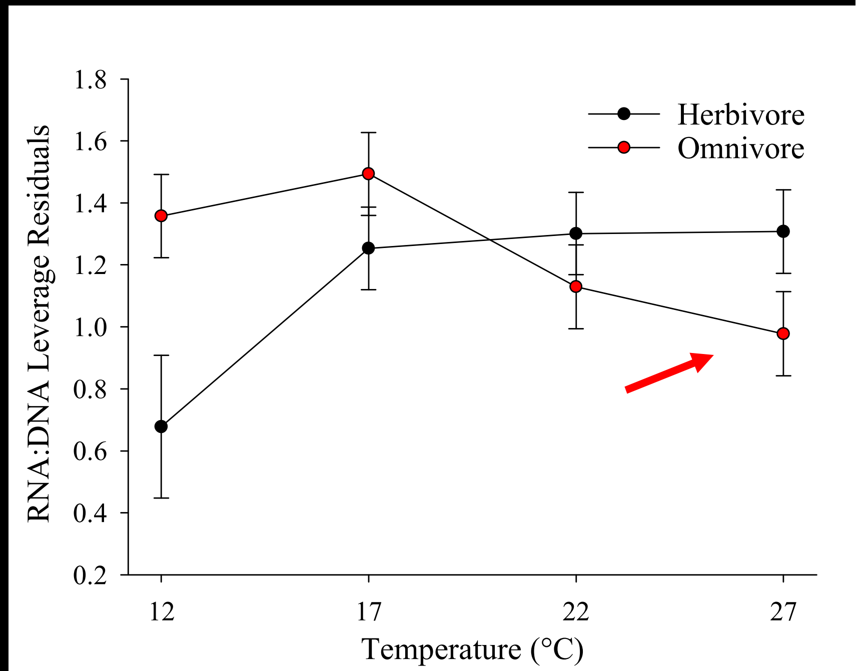

Conceptual Model

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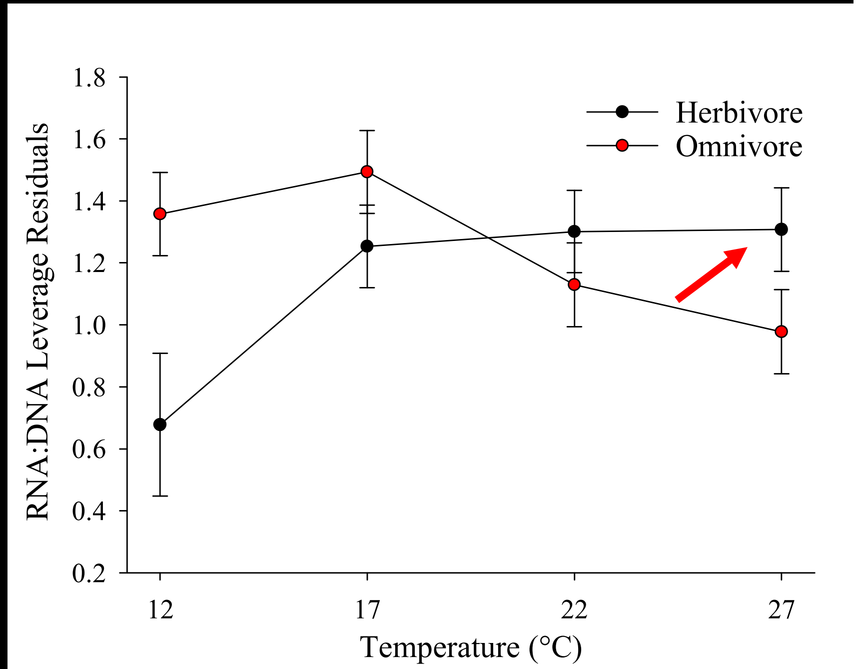
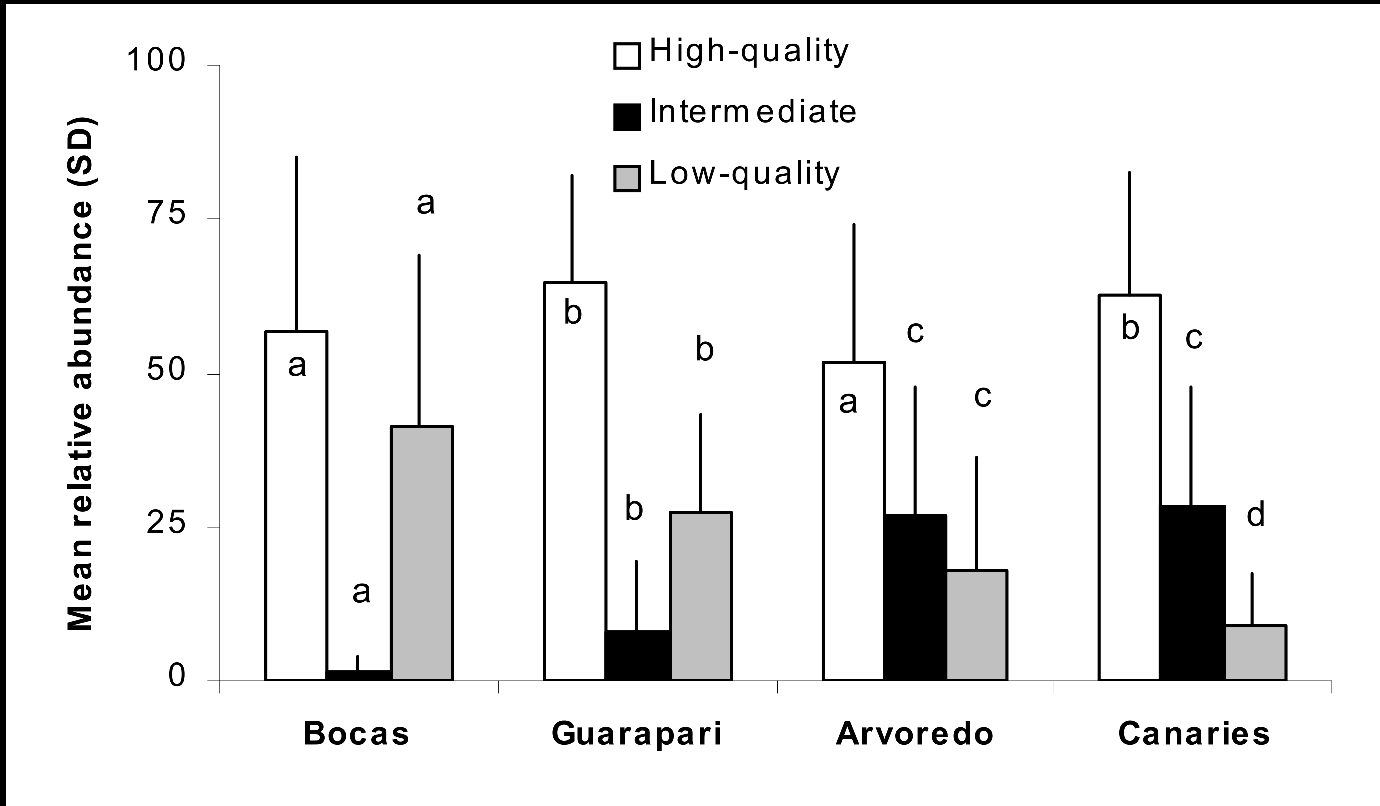


Relative abundance of food quality categories



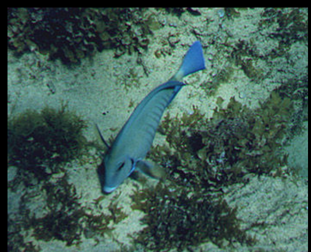
9 N 20 S 27 S 28 N

Conclusions

- Diet quality and temperature affect nutritional condition

- Scaling of physiological rates may explain relative fish performance on different diets

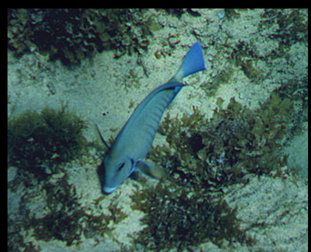
- Data support the existence of a physiological constraint due to temperature


Implications to Herbivorous Fish Evolution

Based on changes in nutritional condition with temperature, there should be temperature-dependent selection.

This may explain low-temperature diet shifts in the species.



Acknowledgements

NCEAS

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