Predator Nonconsumptive Effects, Trait-Mediated Indirect Interactions and Influences of Seaweed Canopies in Intertidal Systems

- An Introduction to Manipulative Field and Lab Experiments -

Dr. Julius A. Ellrich, Postdoctoral Researcher

Predator Nonconsumptive Effects (NCEs), Trait-Mediated Indirect Interactions (TMIIs) and Influences of Seaweed Canopies in Intertidal Systems

Outline:

I. Predator NCEs on Prey Behavior

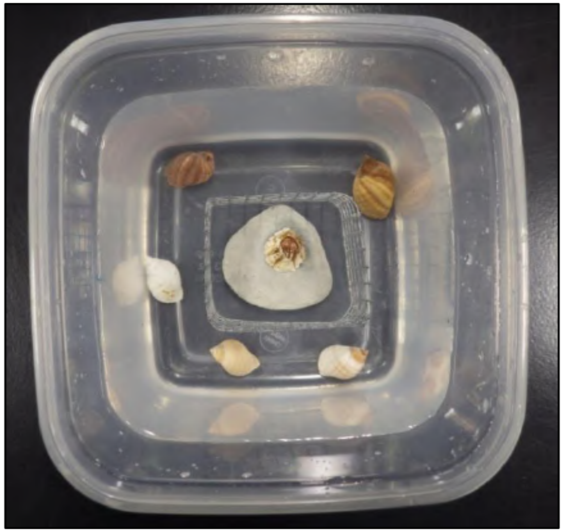
II. Predator NCEs on Prey Demography

III. Predator NCEs on Prey Morphology

IV. TMIIs in Benthic Food Chains

V. Seaweed Canopies: The Interplay of Positive and Negative Influences on Barnacle Recruitment

Manipulative Field & Lab Experiments



I. Predator NCEs on Prey Behavior: Predator chemical cues affect prey feeding activity differently in juveniles and adults

Johnston, Molis & Scrosati 2012, *Canadian Journal of Zoology*

Predator Consumptive Effects & Nonconsumptive Effects (NCEs)

Predation

Predator cues

Killing

Predator

Chemical, tactile,
audible & visual cues

Prey

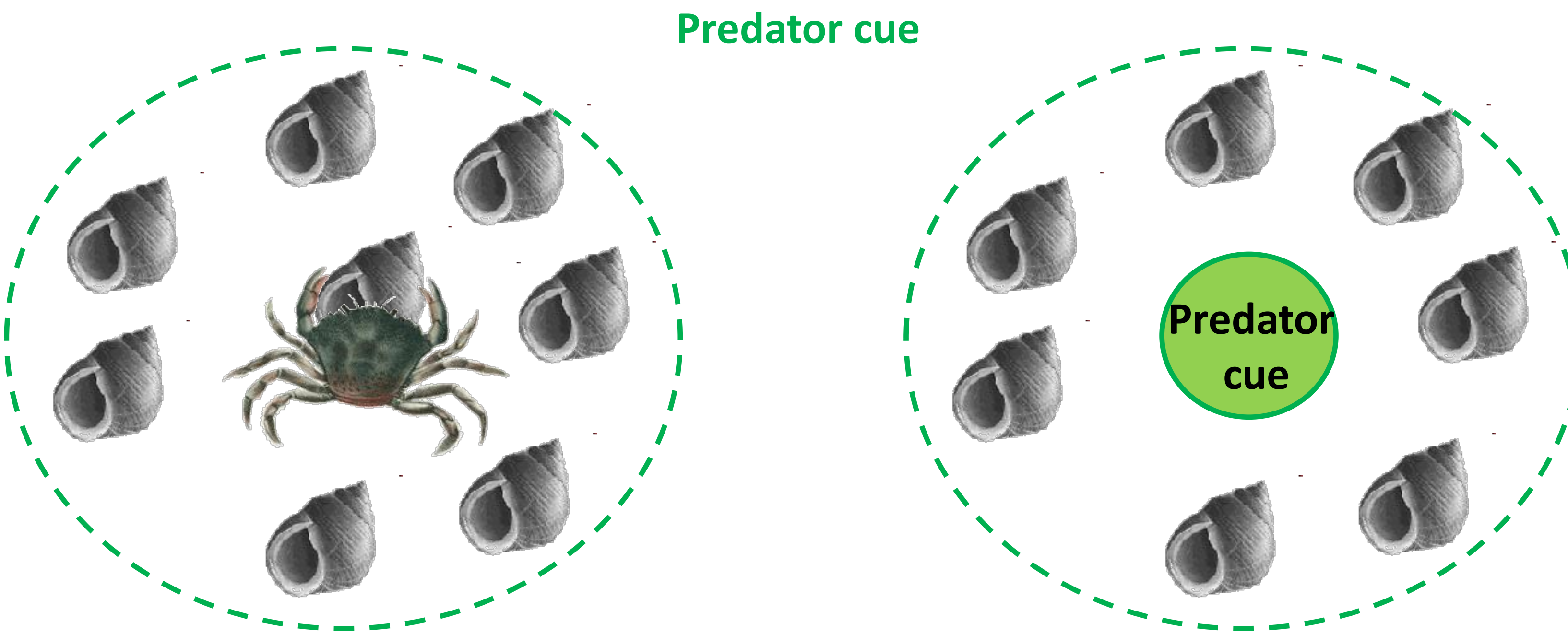
Prey density changes

Prey responses / trait changes

- Morphology
- Behavior

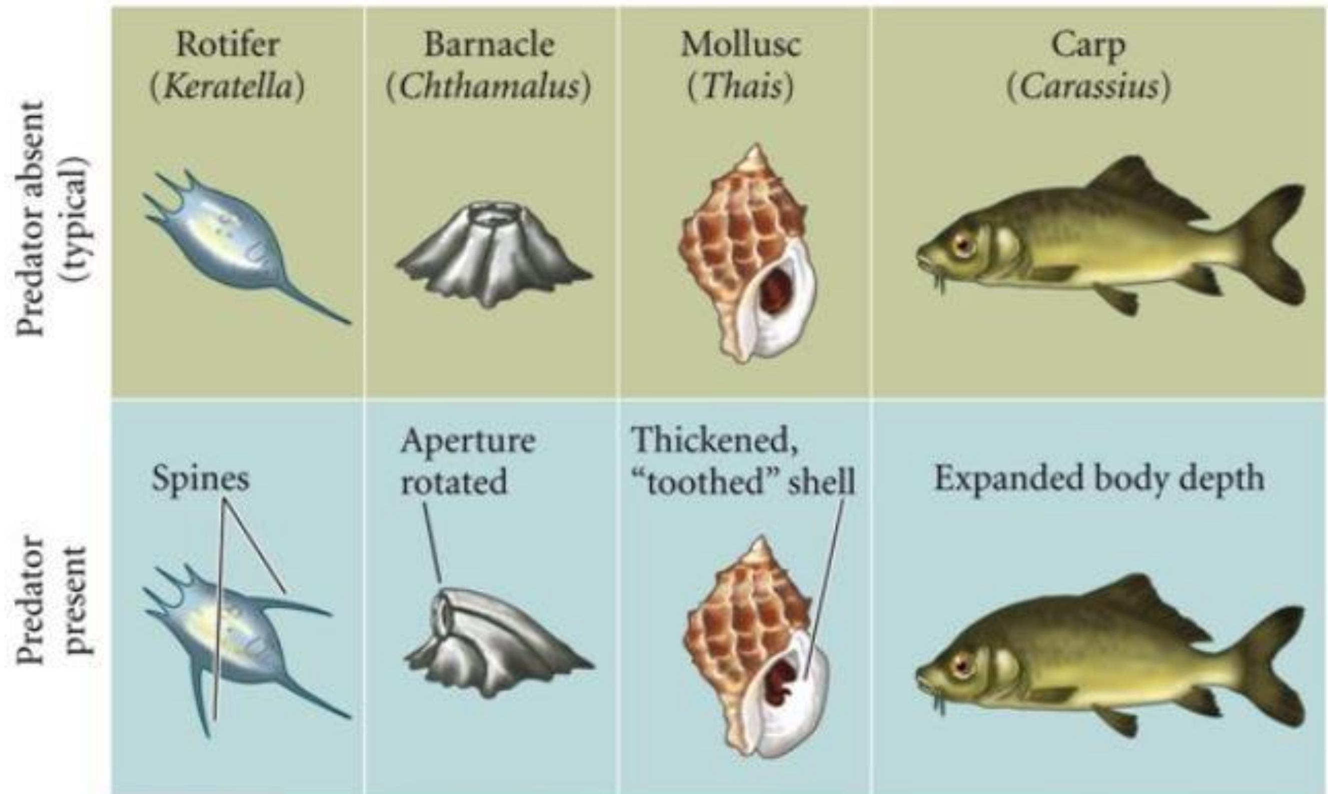
that may limit predation risk

Nonconsumptive Effects on Prey Populations are Often Stronger than Consumptive Effects



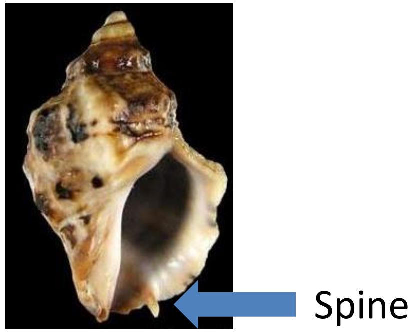
Preisser et al. 2005, Trussell et al. 2006

Prey Morphological Responses to Predator Cues

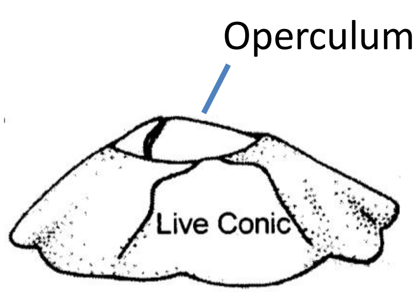


Scott F. Gilbert, Developmental Biology

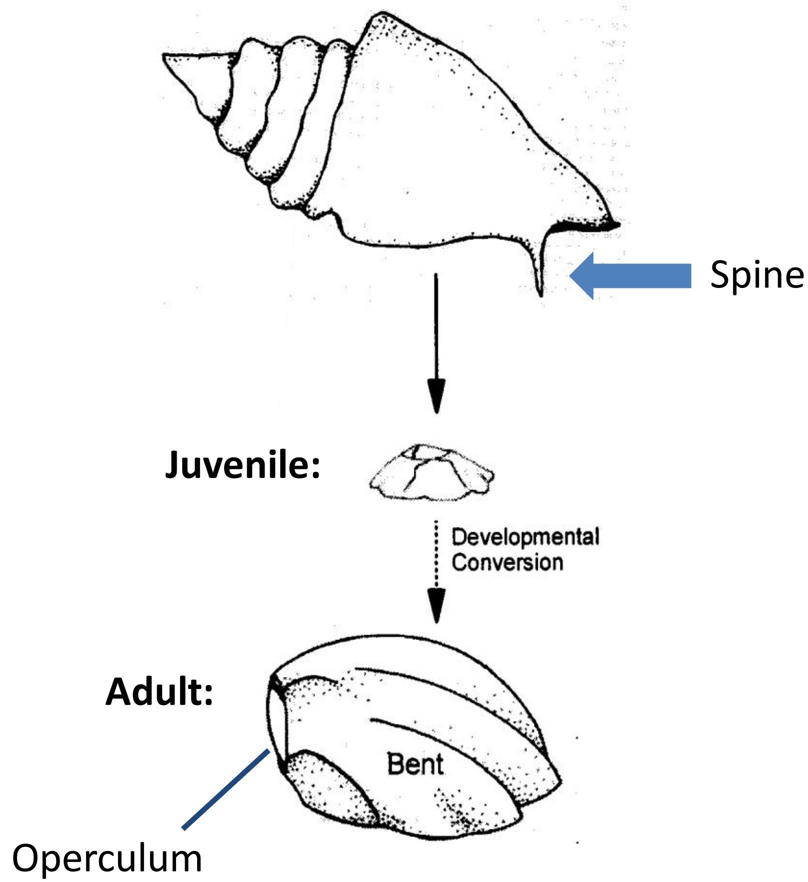
Prey Morphological Responses to Predator Cues



Predator: dogwhelk,
Acanthina angelica



Prey: barnacle,
Chthamalus anisopoma



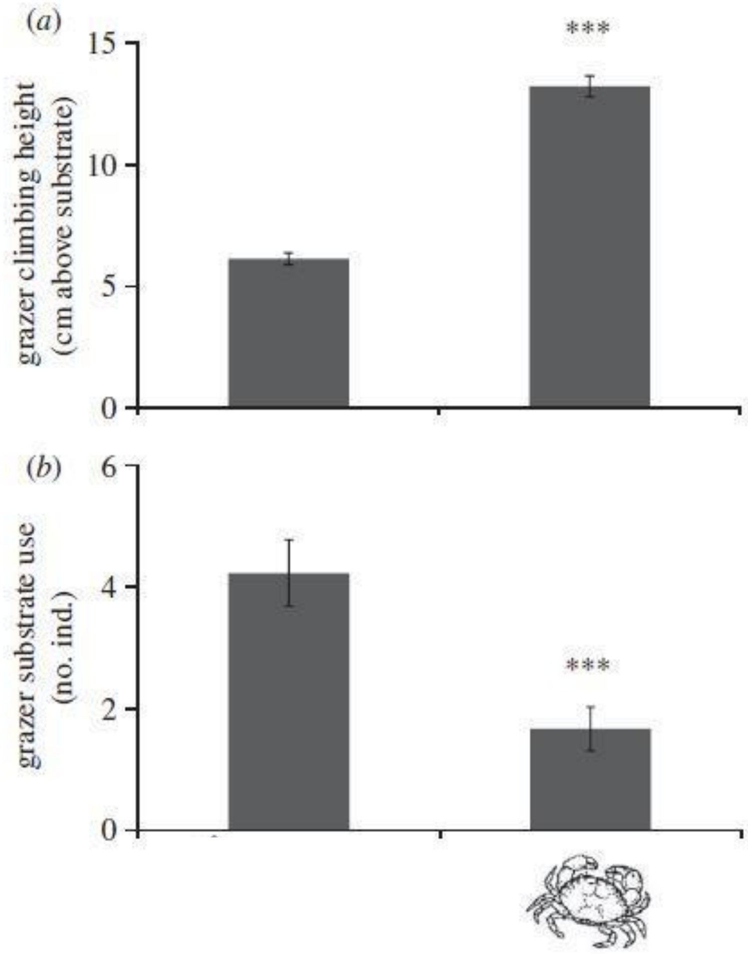
Barnacles develop bent morphology when exposed to predator cues.

Lively 2000, Jarrett 2008

Prey Behavioral Responses to Predator Cues

Prey: Periwinkles, *Littoraria irrorata,* on marsh grass

A predatory crab, *Panopeus obesus,* on the substrate



Periwinkles reduce substrate use & increase climbing height when exposed to predator cues.

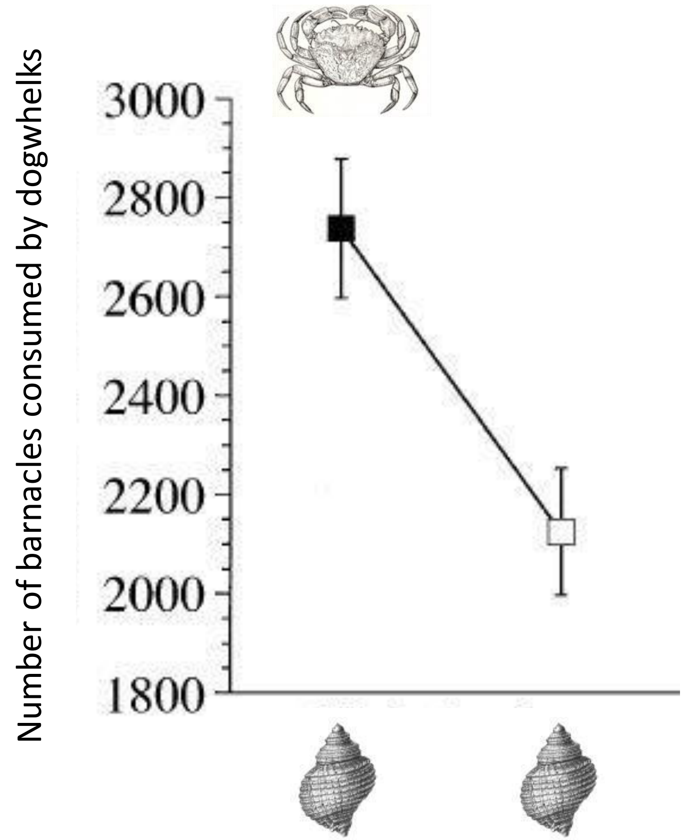
Griffin et al. 2011

Prey Behavioral Responses to Predator Cues

Predator: green crab,
Carcinus maenas

Crab prey: dogwhelk,
Nucella lapillus

Dogwhelk prey: barnacle,
Semibalanus balanoides



Dogwhelks reduce feeding activity when exposed to predator cues.

Trussell et al. 2003

Prey Behavioral Responses to Predator Cues May Vary With Prey Life-History Stage

Predatory dogwhelk feeding on an adult barnacle

if different probabilities of predator induced mortality exist for different prey life-history stages.

Dogwhelks prefer adult barnacles over juvenile barnacles.
(Dunkin & Hughes 1984)

→ ***Adult barnacles may show a stronger behavioral response to dogwhelk cues than juvenile barnacles.***

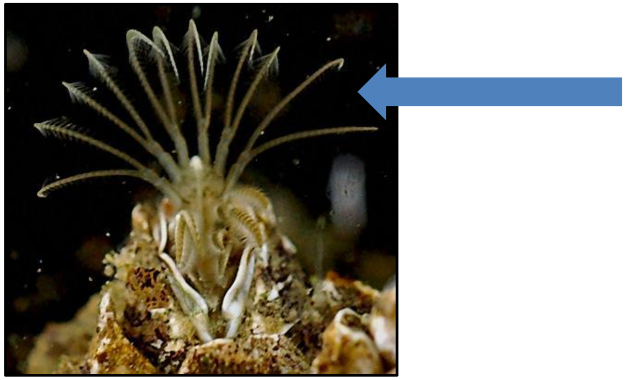
Predator-Prey Model System

Dogwhelks *Nucella lapillus* (L. 1753) & barnacles *Semibalanus balanoides* (L. 1767)

Barnacles



Facilitation



Filter feeding barnacle[1]

[1]zottoli.wordpress.com/saltmarshes/mud-flats-zone-1/

Ecological Relevance

- Facilitators of seaweeds, mussels & periwinkles
  (van Tamelen 1987, Petraitis 1987, Harley 2006)
- Bentho-pelagic coupling
  (Menge et al. 2003, Cole et al. 2011)
- Food for predators
  (Largen 1967, Palmer 1983)

Barnacles are sessile filter feeders

Barnacle legs (= cirri)

- filter feeding & dissemination of barnacle cues

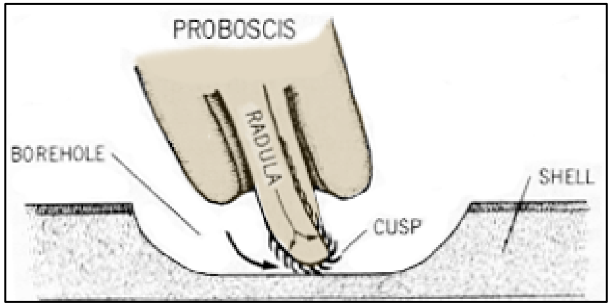
Barnacle active filter feeding video

https://youtu.be/oq0vvJD9jNs

Dogwhelks

- common intertidal snails
- active: April – November
- slow moving
- easy to collect in high amounts
- easy to manipulate dogwhelk occurrence
- barnacle & mussel predators
- drilling or prising attack
- prefer adult over juvenile barnacle prey

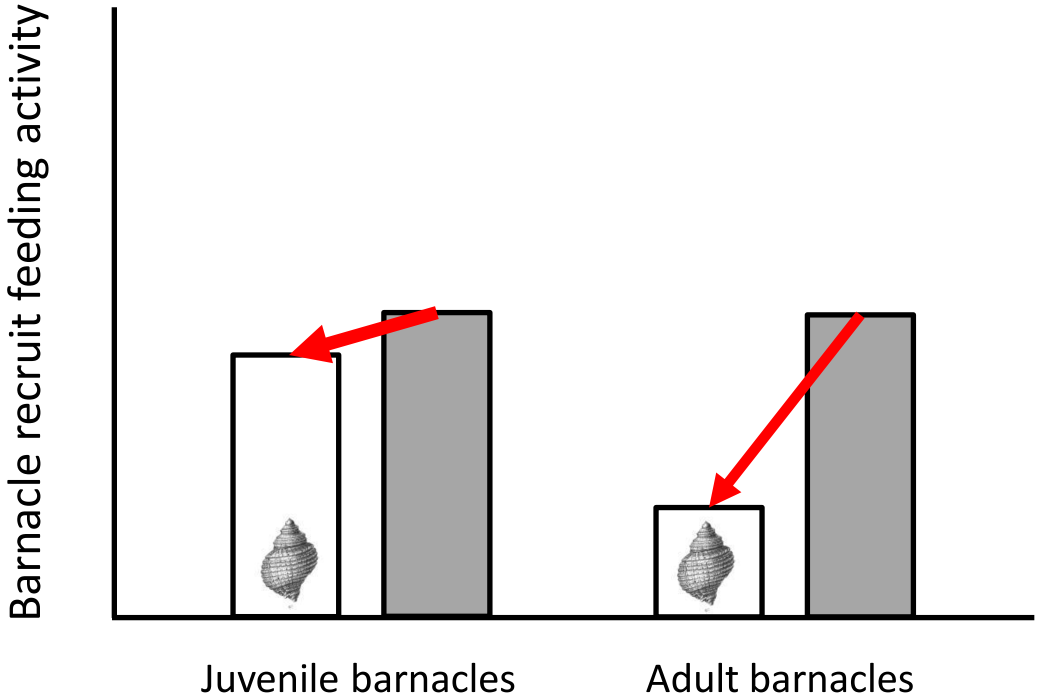
Dogwhelk,
Nucella lapillus



Dogwhelk radula drilling[1]

Crothers 1985 (dogwhelk biology review), [1]www.asnailsodyssey.co

Hypothesis



Adult barnacles show a stronger feeding activity reduction in response to dogwhelk cues than juvenile barnacles.

Study System

North East Atlantic

Helgoland, North Sea

Picture: https://en.wikipedia.org/wiki/Heligoland#/media/File:Helgoland_Vogelperspektive_sx.jpg

Kringel Shore, Helgoland

Pictures: M. Lohmeyer; www.duene1.de/homepage/weiss08/weiss4.htm

Field Collection of Dogwhelks & Barnacles at Kringel Shore, Helgoland

Manipulative Lab Experiment

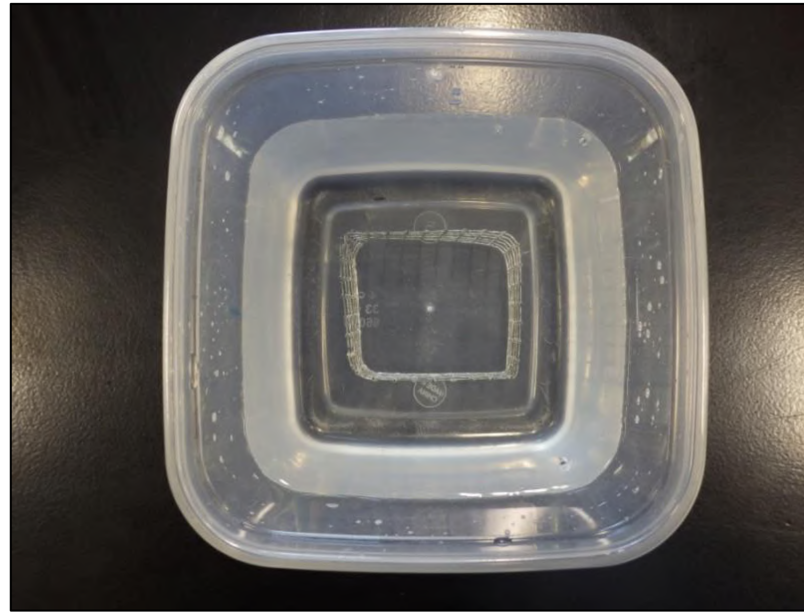
Biological Institute Helgoland

BIOLOGISCHE ANSTALT HELGOLAND · BIOLOGISCHE ANSTALT HELGOLAND ·

Picture: https://de.wikipedia.org/wiki/Biologische_Anstalt_Helgoland#/media/File:BAH_Helgoland.jpg

Experimental Unit

Side view



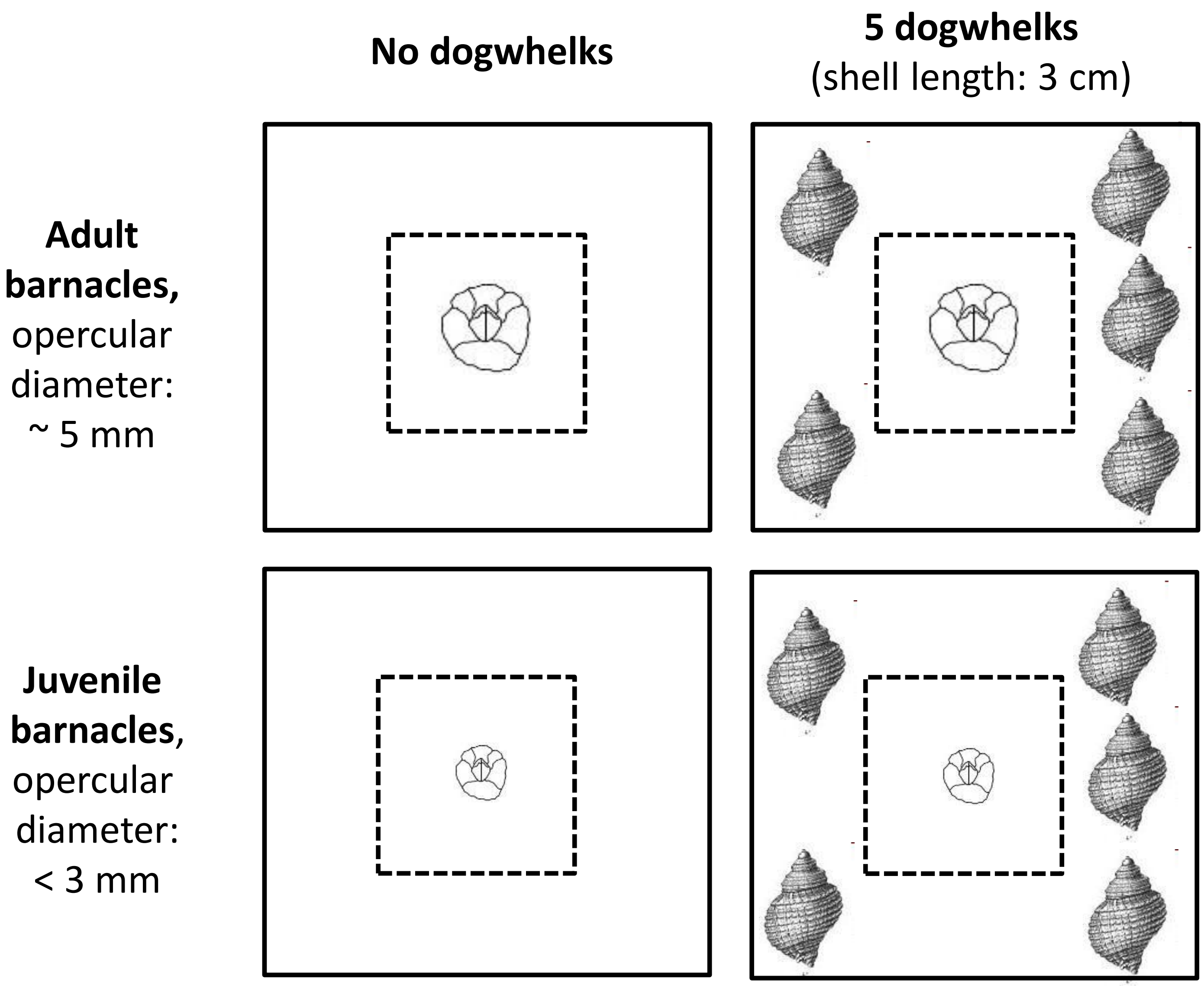
Top view

Plastic tub

500 ml seawater, 16 °C

Mesh, window size: 0.5 mm X 0.5 mm

Predator Presence & Prey Life-History Stage Manipulation



Predator Presence Manipulation

No dogwhelks

Adult barnacle

5 dogwhelks

Adult barnacle & dogwhelks

Sample size: 20 replicates of both predator treatments

Experimental Procedure

No dogwhelks

Add barnacle,
10 min acclimation

Count barnacle leg
swipes for 10 sec

5 dogwhelks

Add dogwhelks,
30 min acclimation

Add barnacle,
10 min acclimation

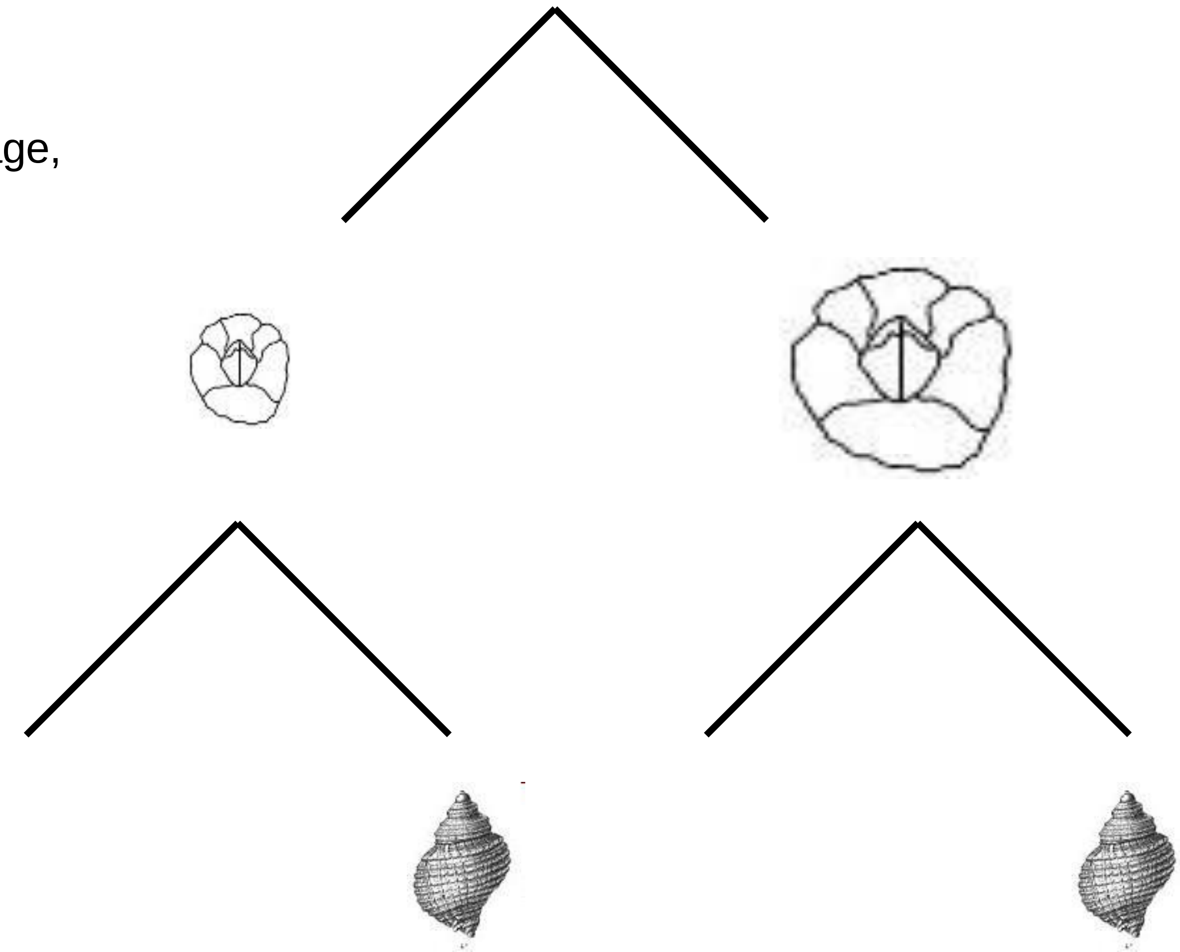
Count barnacle leg
swipes for 10 sec

Statistical Analysis

Barnacle life-history stage,

fixed factor

with 2 levels



Predator presence,

fixed factor

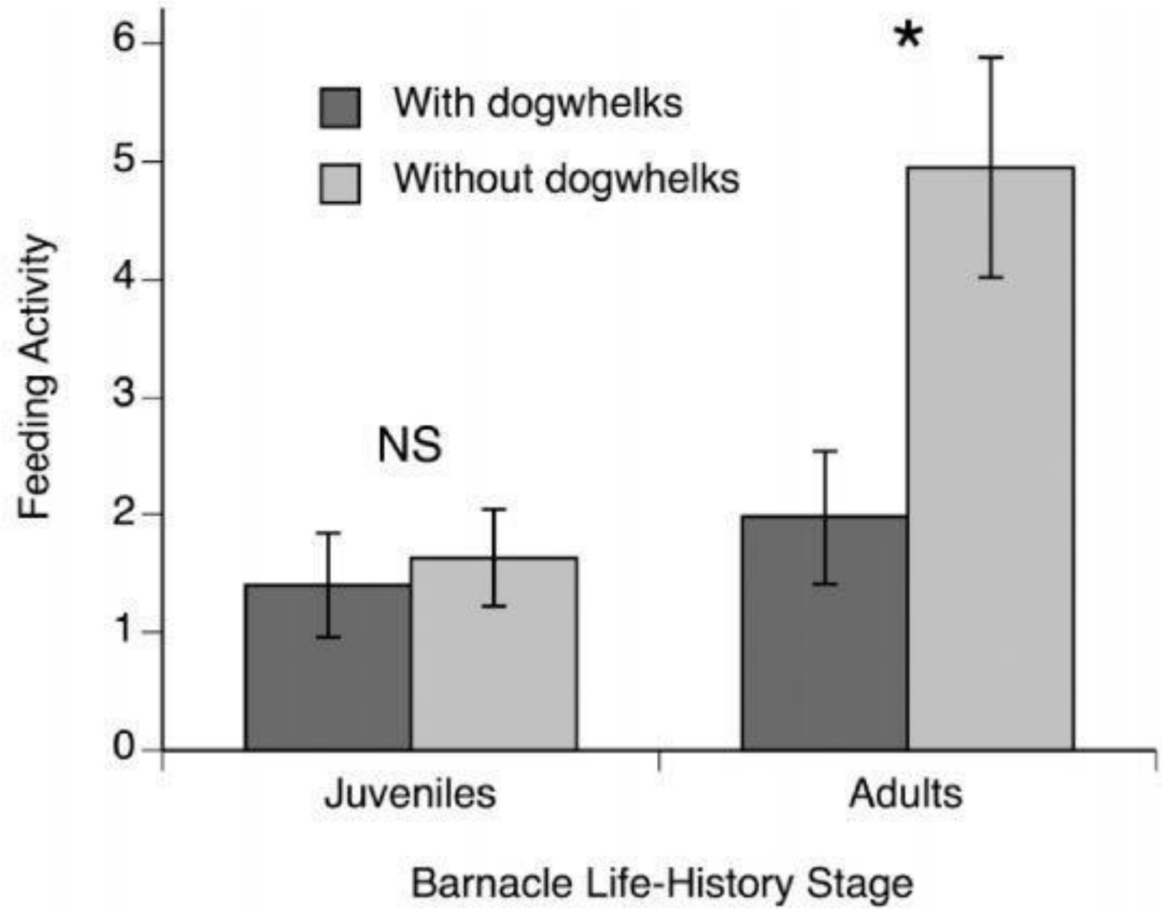
with 2 levels

Dependent variable: barnacle leg swipe frequency

Analysis of Variance, Simple Effects Test

Results & Discussion

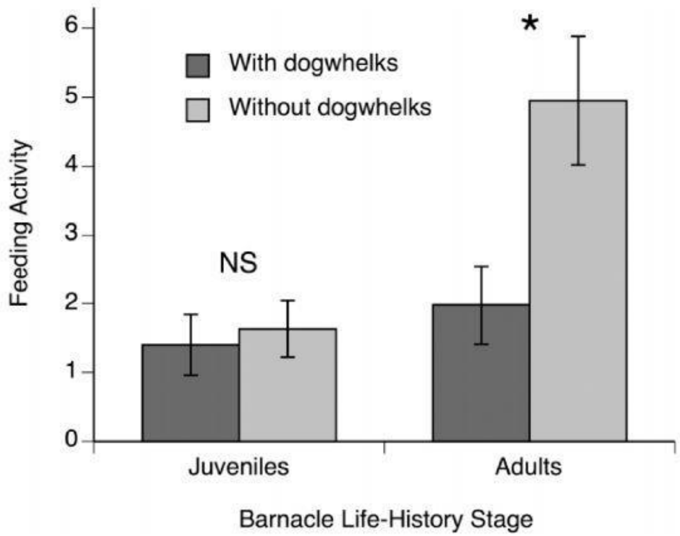
Results: Dogwhelk cues limit feeding activity in adult barnacles but not juvenile barnacles



→ *Reduced feeding activity may limit dissemination of barnacle cues attracting predators.*

Johnston, Molis & Scrosati 2012, *Canadian Journal of Zoology*

Discussion



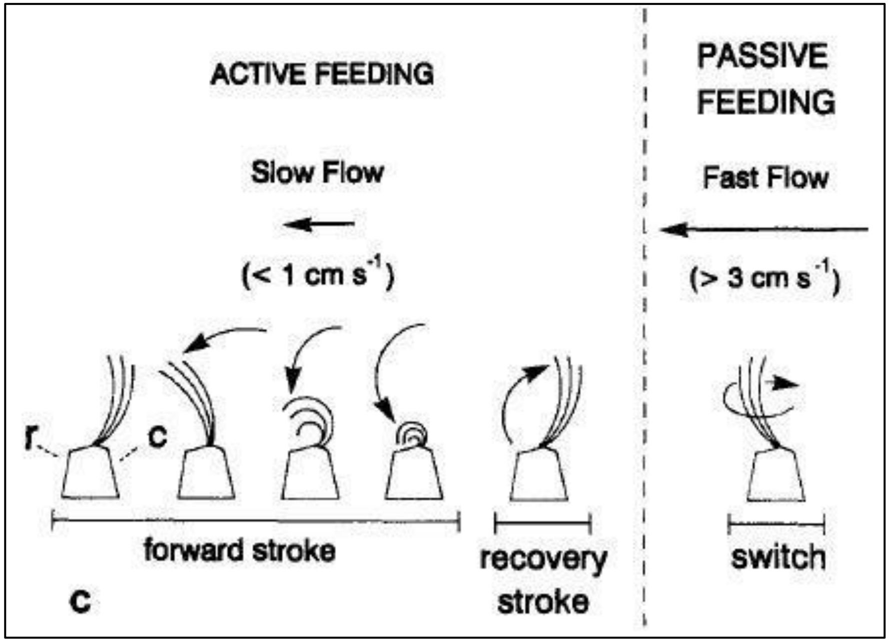
Reduced feeding activity in adult barnacles exposed to dogwhelk cues may

(1) be a result of selection through dogwhelk predation, or

(2) result from juveniles being able to learn recognizing dogwhelk cues.

Johnston, Molis & Scrosati 2012, *Canadian Journal of Zoology*

Discussion



Graph: Trager et al. 1990

Future research conducted under flow conditions could examine the hypothesis that barnacles shorten cirri extension periods during passive feeding when exposed to dogwhelk cues.

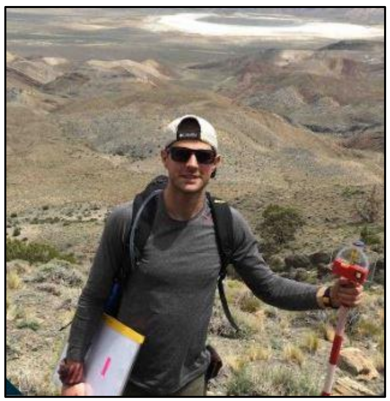
Johnston, Molis & Scrosati 2012, *Canadian Journal of Zoology*

Summary: NCEs…

- … are induced by predator cues (i.e. chemical, tactile, audible & visual cues).
- … alter prey responses / traits (e.g. prey morphology, behavior, habitat use).
- … were shown to be stronger than consumptive effects.
- … affect prey (multiple individuals!) even without a physical encounter.
- … are common in predator-prey systems.
- … can affect prey feeding activity differently in juveniles and adults.

Predator chemical cues affect prey feeding activity differently in juveniles and adults

Bradley R. Johnston, Markus Molis, and Ricardo A. Scrosati



Brad Johnston

Markus Molis

Ricardo Scrosati

Johnston, B. R., M. Molis & R. A. Scrosati. 2012. Predator chemical cues affect prey feeding activity differently in juveniles and adults. Canadian Journal of Zoology 90: 128-132. doi: 10.1139/Z11-113

Kringel Shore Panorama, Helgoland

Picture: http://www.welkoam-iip-lunn.de/grafiken/schlagworte/kringel-1.jpg

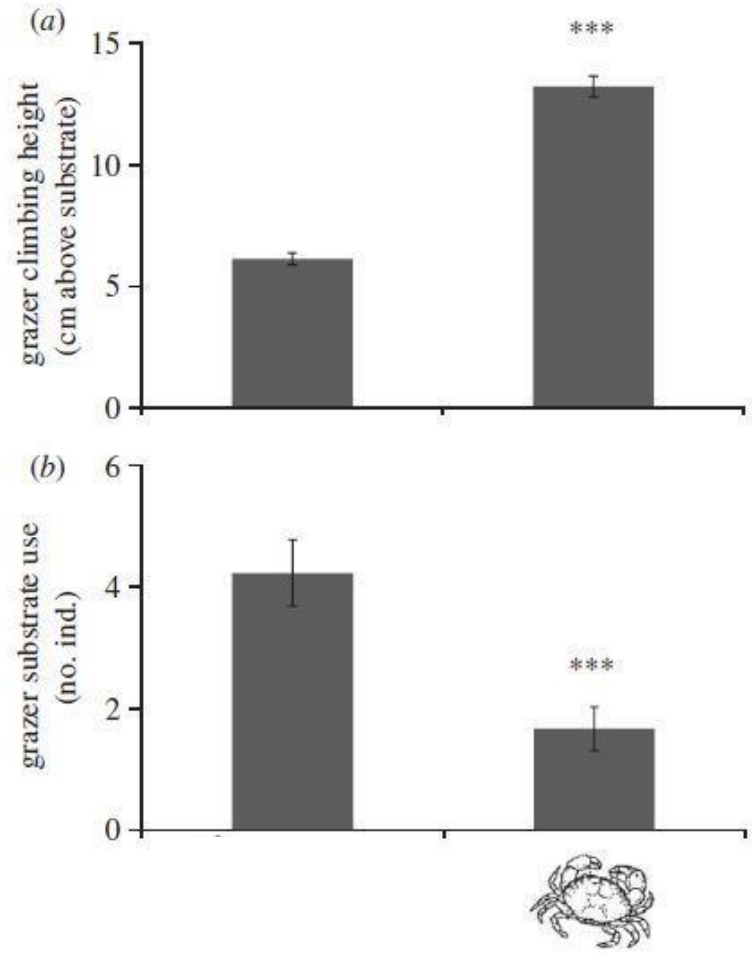
II. Predator NCEs on Prey Demography: Predator Nonconsumptive Limitation of Prey Recruitment

Ellrich, Scrosati & Molis 2015, *Ecology*
Ellrich, Scrosati & Petzold 2015, *Journal of Experimental Marine Biology and Ecology*

Behavioral Responses to Predator Cues in Adult Prey

Prey: Periwinkles,
Littoraria irrorata,
on marsh grass

A predatory crab, *Panopeus obesus,*
on the substrate



Periwinkles reduce substrate use & increase climbing height when exposed to predator cues.

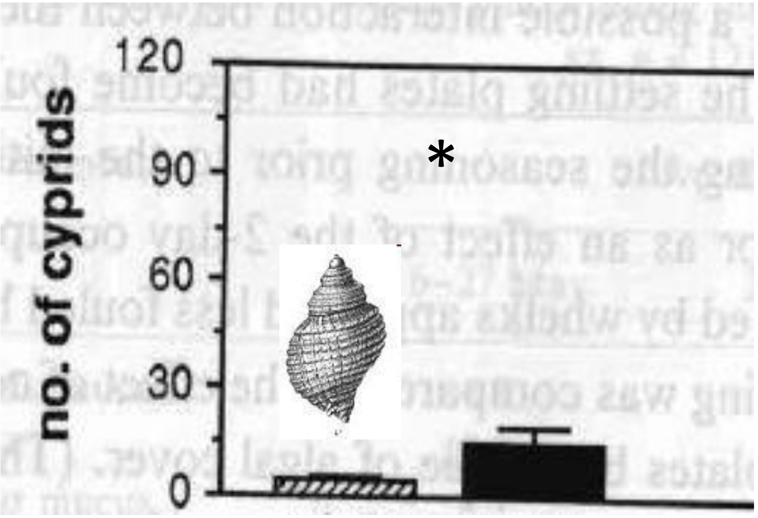
Griffin et al. 2011

Prey Larvae Settlement Responses to Predator Cues

Barnacle cyprid larva[1]

Balanus glandula[2]

Nucella lamellosa[3]



Nucella lamellosa **chemical cues limit *Balanus glandula* settlement.**

(Johnson & Strathmann 1989)

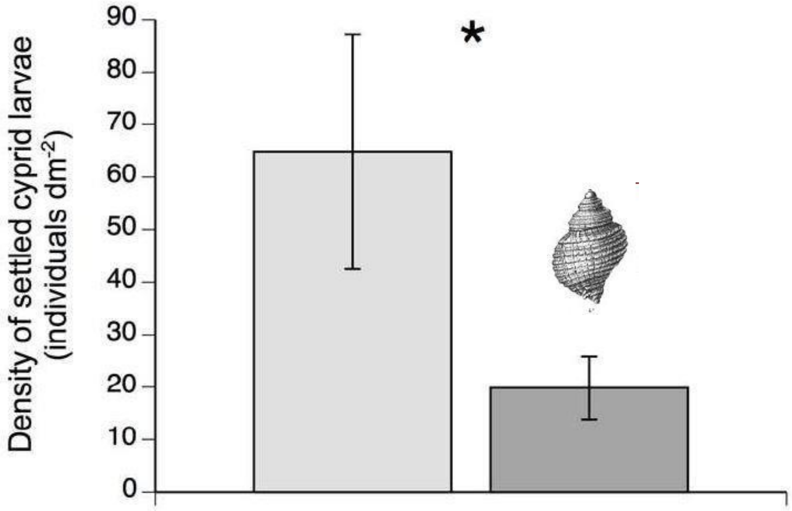
Pictures: [1]Charles Krebs, [2]Brianna Nelson, [3]Richard Palmer

Prey Larvae Settlement Responses to Predator Cues

Semibalanus balanoides cyprids

Semibalanus balanoides

Nucella lapillus



Nucella lapillus* presence limits *Semibalanus balanoides settlement.

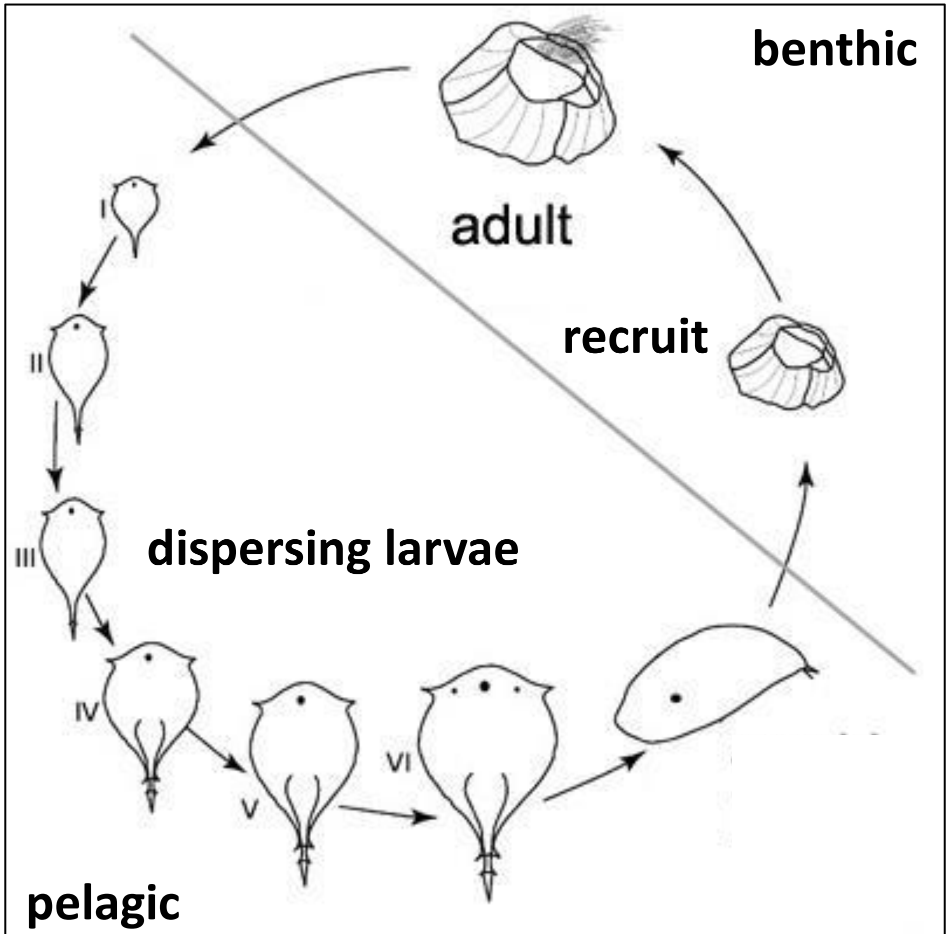
Ellrich et al. 2016

1st Research Question:

Do Predator NCEs Affect

Prey Demographic Rates?

Complex Life-Cycle



Settlement

larvae

Recruitment

cyprid larvae

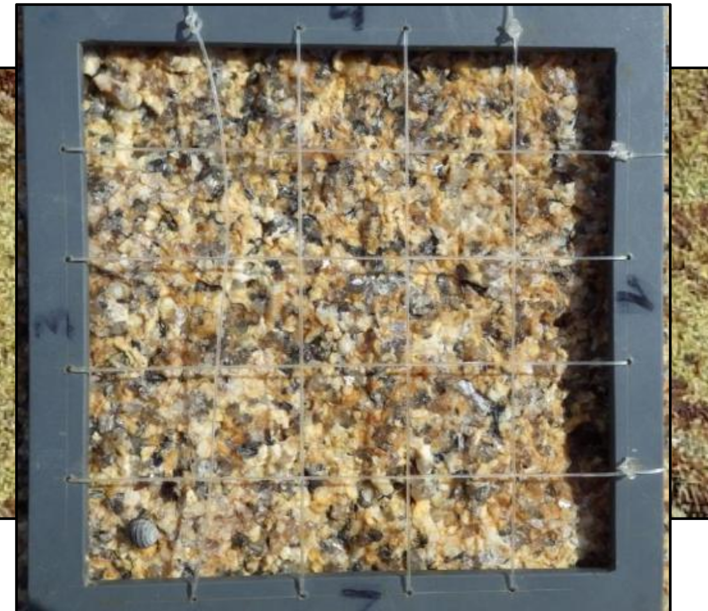
Metamorphosis

recruits

The appearance of new individuals in the population that have metamorphosed after settlement & that have reached an arbitrary size that allows to count them.

Atlantic coast, early May

Before Recruitment, early May



After Recruitment, late June

→ **Recruitment is a key demographic rate that determines population replenishment & persistence.**

1st: Do Predator NCEs affect prey demographic rates?

<u>Predator cues…</u>

- **repel larvae** (in lobster, crabs & sea urchins)

  (Bourget et al. 1993, Banks & Dinnel 2000, Metaxas & Bourdett-Coutts 2006)

- **decrease settlement** (in barnacles & crabs)

  (Johnson & Strathmann 1989, Tapia-Lewin & Pardo 2014)

However, recruits accumulate over <u>several weeks to months</u>

(Bertness et al. 1991, Kent et al. 2003, Menge & Menge 2013)

→ 2nd: Are there factors that affect predator NCEs on recruitment during that month lasting period?

Barnacle Recruit Density

<u>Cyprids are attracted by:</u>

- **Recent settlers & recruits**
  (Hills & Thomason 1998, Shanks 2009)
- **Cyprid footprints**
  (Yule & Walker 1985, Clare et al. 1994)
- **Attractive chemical cues**
  Arthropodin, Settlement-Inducing Protein Complex (SIPC)
  (Crisp & Meadows 1962, Matsumura et al. 2000, Dreanno et al. 2007)

Cyprids & Recruits[1]

→ High recruit density may weaken predator NCEs on recruitment.

[1]http://www.stuartjenkins.net

Food Supply

<u>High phytoplankton abundance enhances:</u>

- **larval development**
  (Emlet & Sadro 2006)
- **recruitment**
  (Menge et al. 2003, Cole et al. 2011)

Filter feeding barnacle[1]

→ Food supply may indirectly weaken predator NCEs on recruitment.

[1]zottoli.wordpress.com/saltmarshes/mud-flats-zone-1/

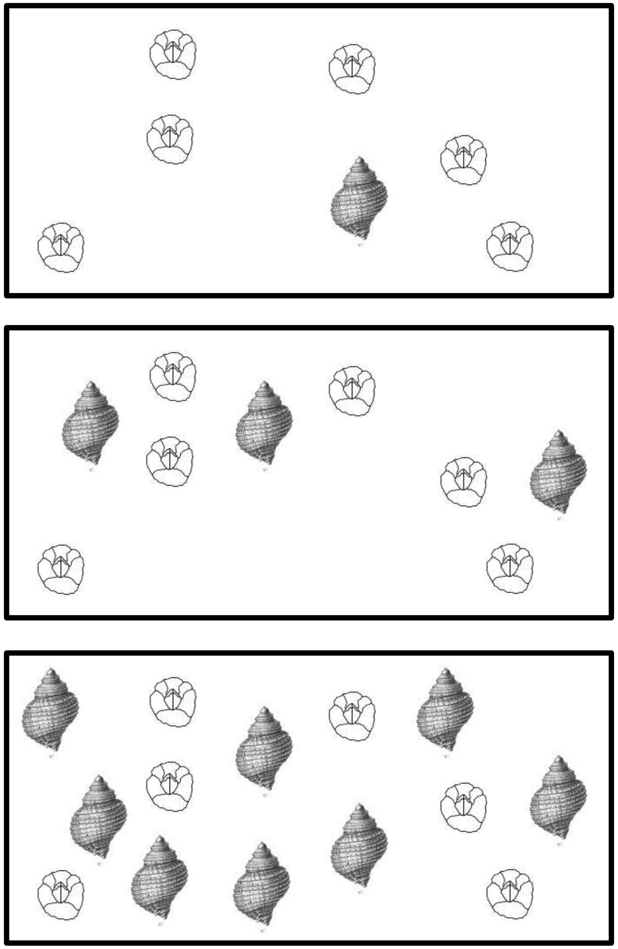
Predator Density

Predator NCEs on prey behavior & morphology increase…

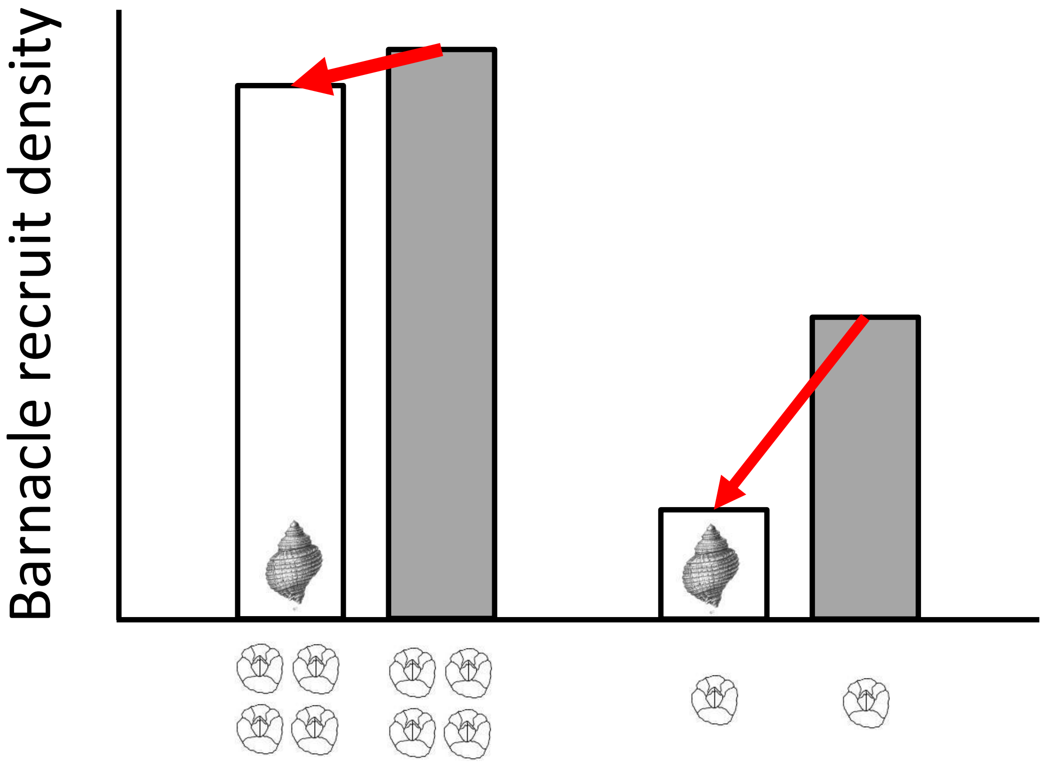
- **with predator density**
  (backswimmer: Silberbush & Blaustein 2011,
  crab: Hill & Weissburg 2013)

- **with predator cue concentration**
  (fish: von Elert & Ponert 2000,
  dragonfly: Ferland-Raymond et al. 2010)

→ **Dogwhelk NCEs on barnacle recruitment may increase with dogwhelk density.**

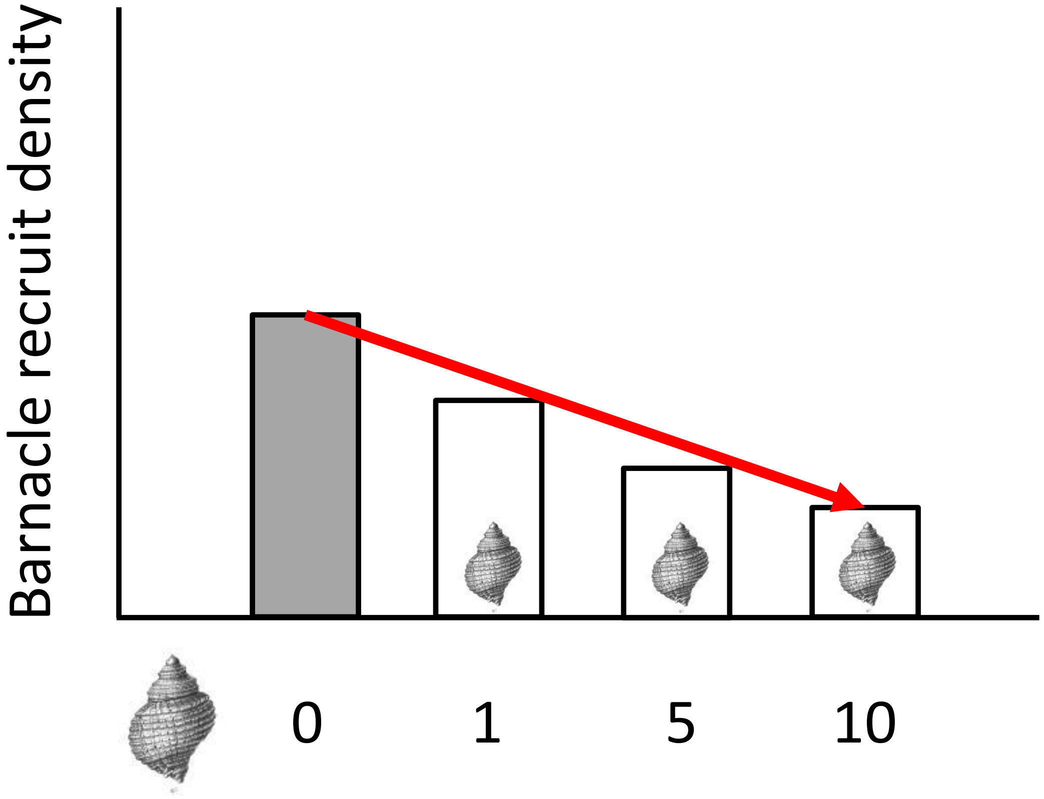


Hypotheses



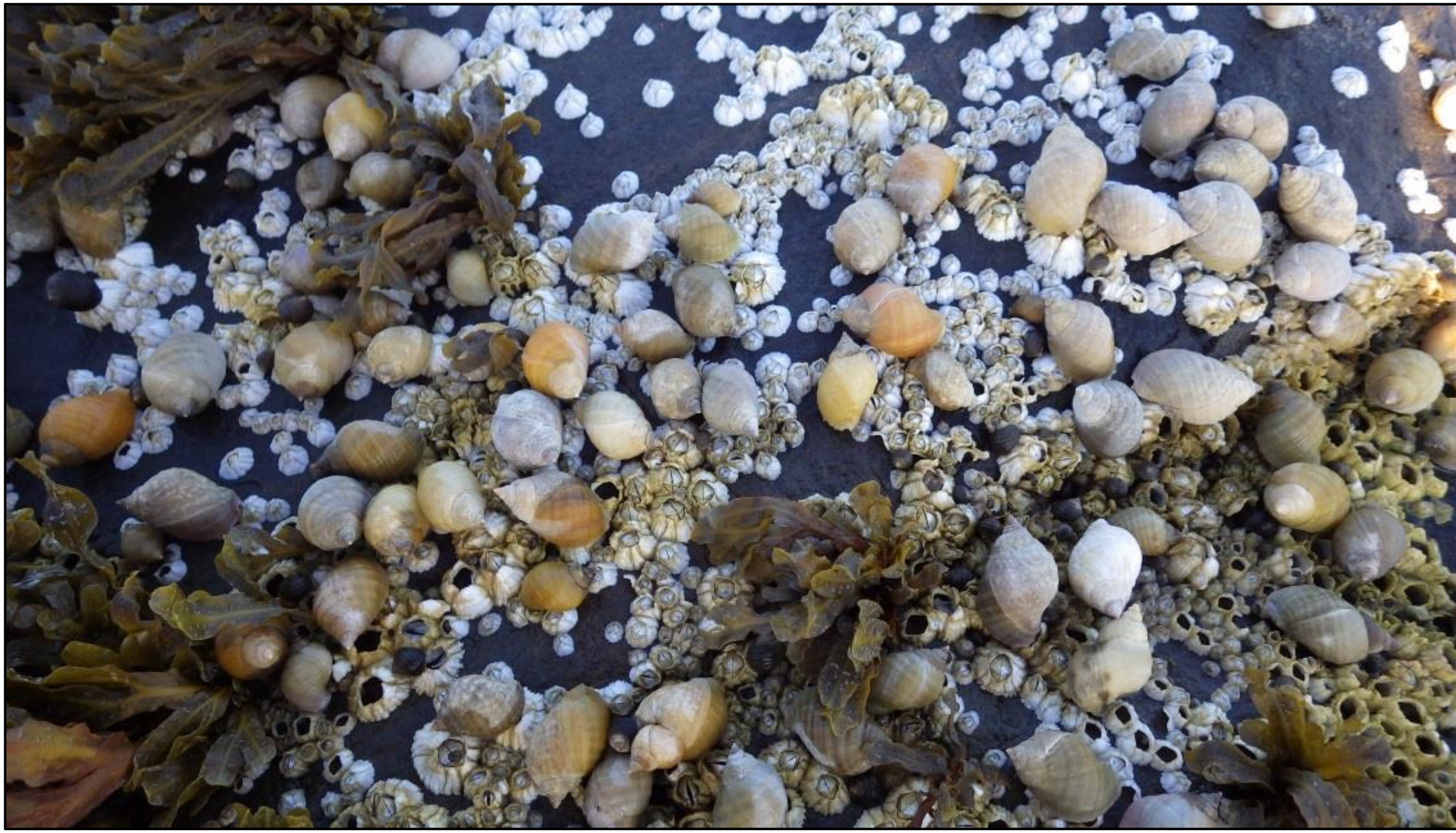
Predator NCEs on barnacle recruitment weaken with recruit density.

Hypotheses



Predator NCEs on barnacle recruitment increase with dogwhelk density.

Predator-Prey Model System



Dogwhelks *Nucella lapillus* (L. 1753) & barnacles *Semibalanus balanoides* (L. 1767)

Dogwhelks

- common intertidal snail
- active: April – November:
- barnacle & mussel predators
- drilling or prising attack
- slow moving
- easy to collect in high amounts
- easy to manipulate dogwhelk occurrence

Nucella lapillus

Review on dogwhelk biology: Crothers 1985

Barnacles

Semibalanus balanoides
adults and recruits

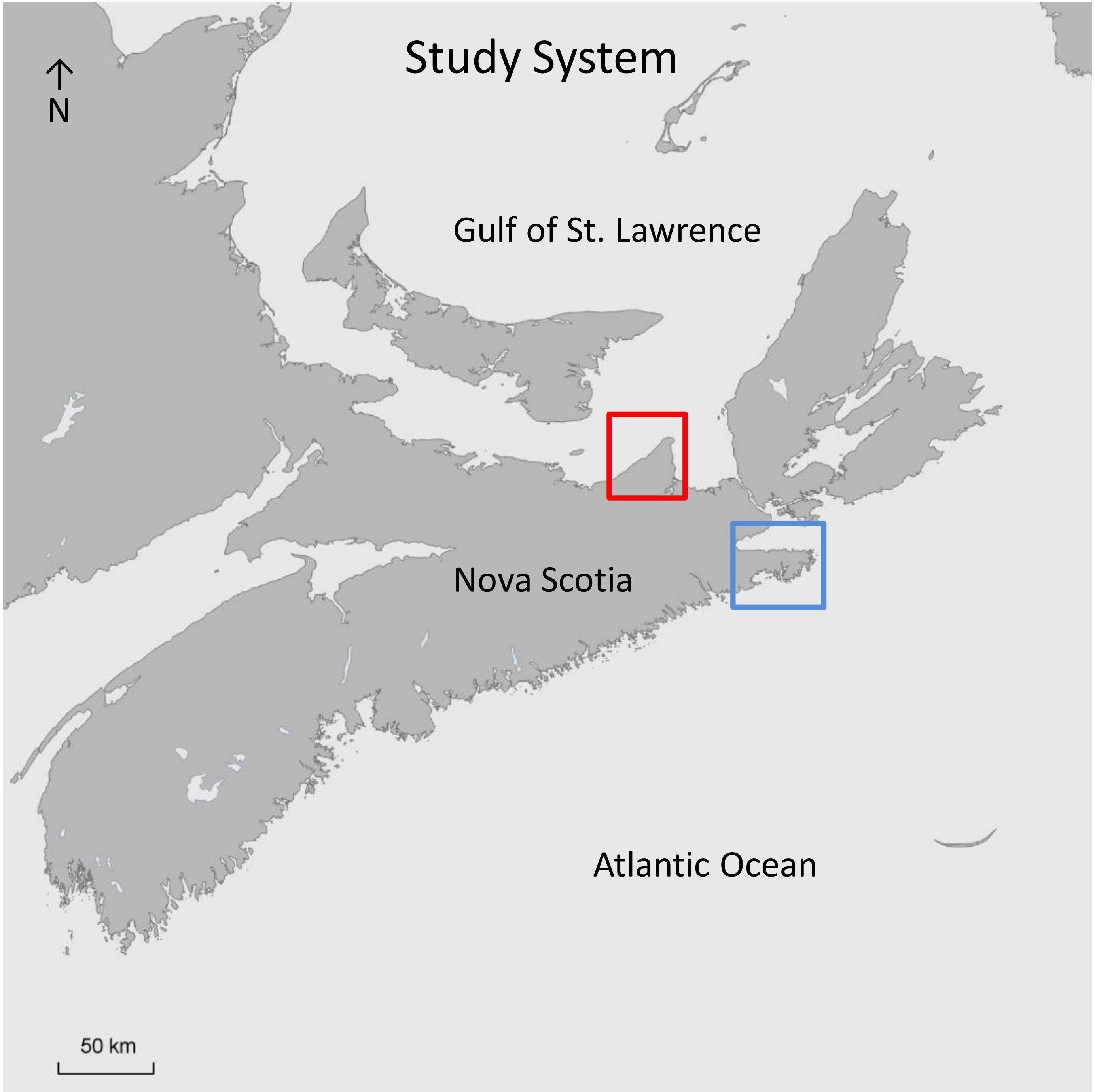
Ecological Relevance

- Facilitators of seaweeds, mussels & periwinkles
  (e.g. Van Tamelen 1987, Petraitis 1987, Harley 2006)
- Bentho-pelagic coupling
  (Menge et al. 2003, Cole et al. 2011)
- Food for predators
  (Largen 1967, Palmer 1983)

Semibalanus balanoides

- only intertidal barnacle species in Nova Scotia
  (Heaven & Scrosati 2007)
- recruitment: May & June
  (Macpherson et al. 2008, Cole et al. 2011)

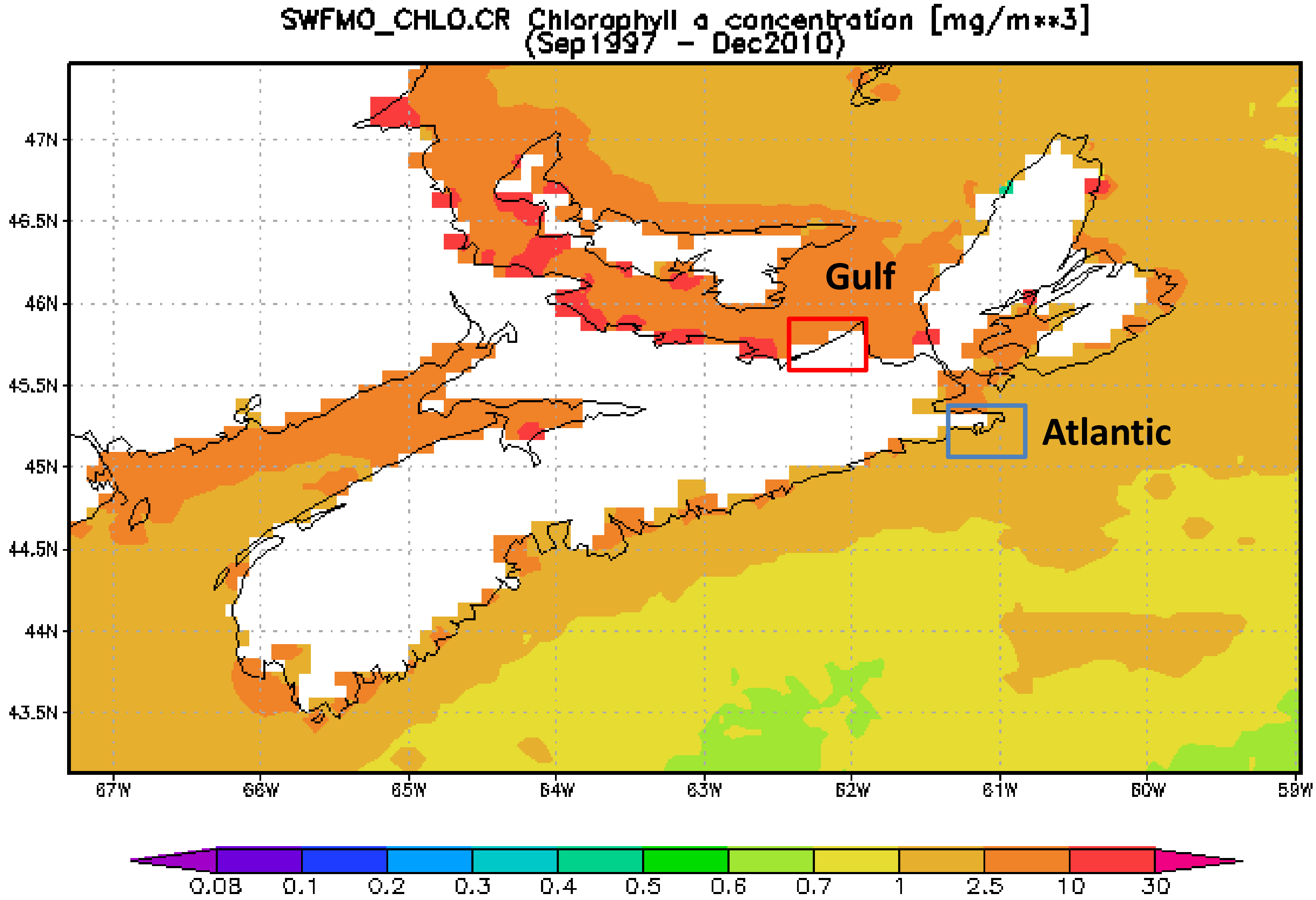
Manipulative Field Experiment



Study System
N
Gulf of St. Lawrence
Nova Scotia
Atlantic Ocean
50 km

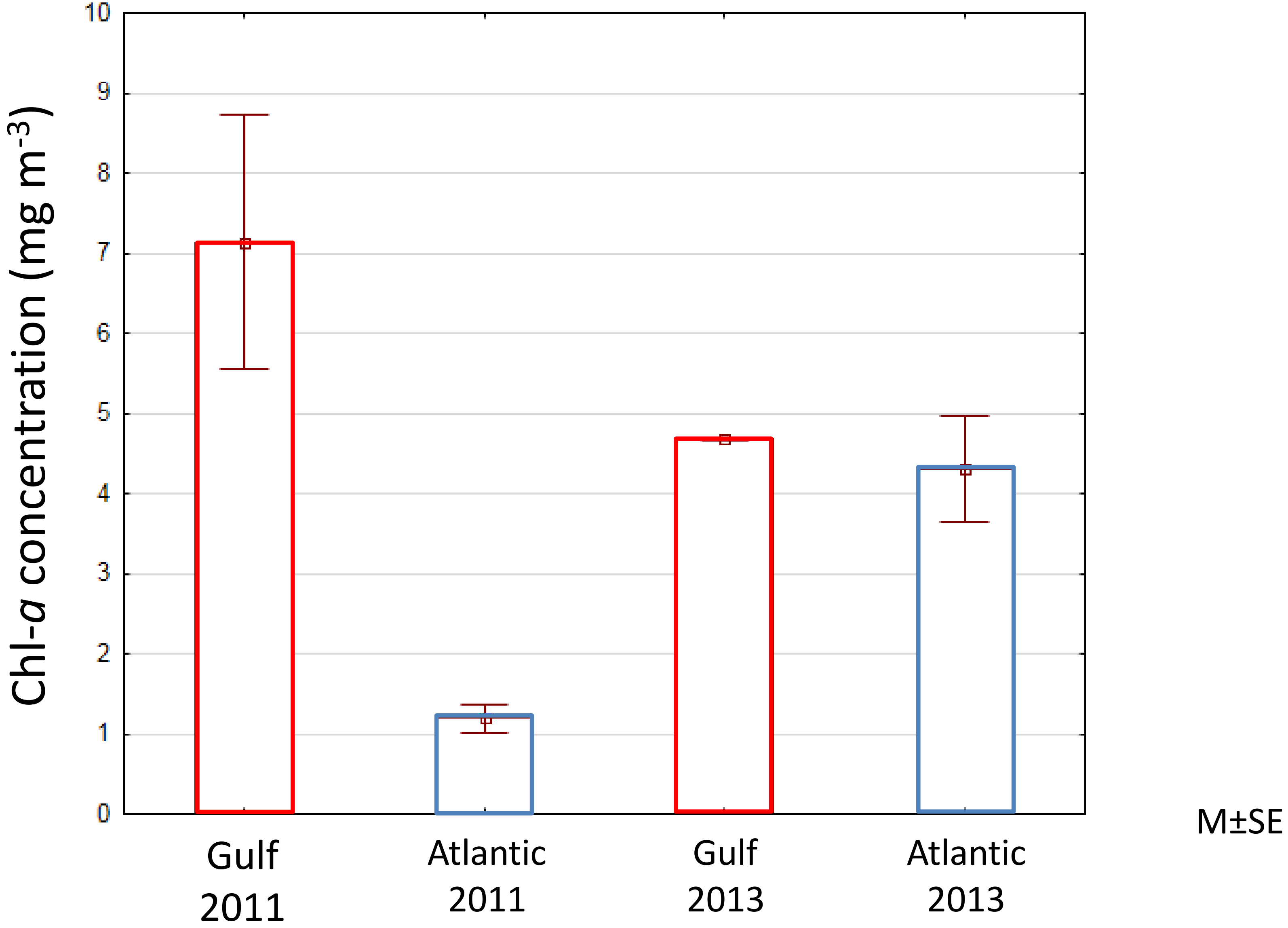
Food Supply

Chl-*a* concentration: Phytoplankton biomass



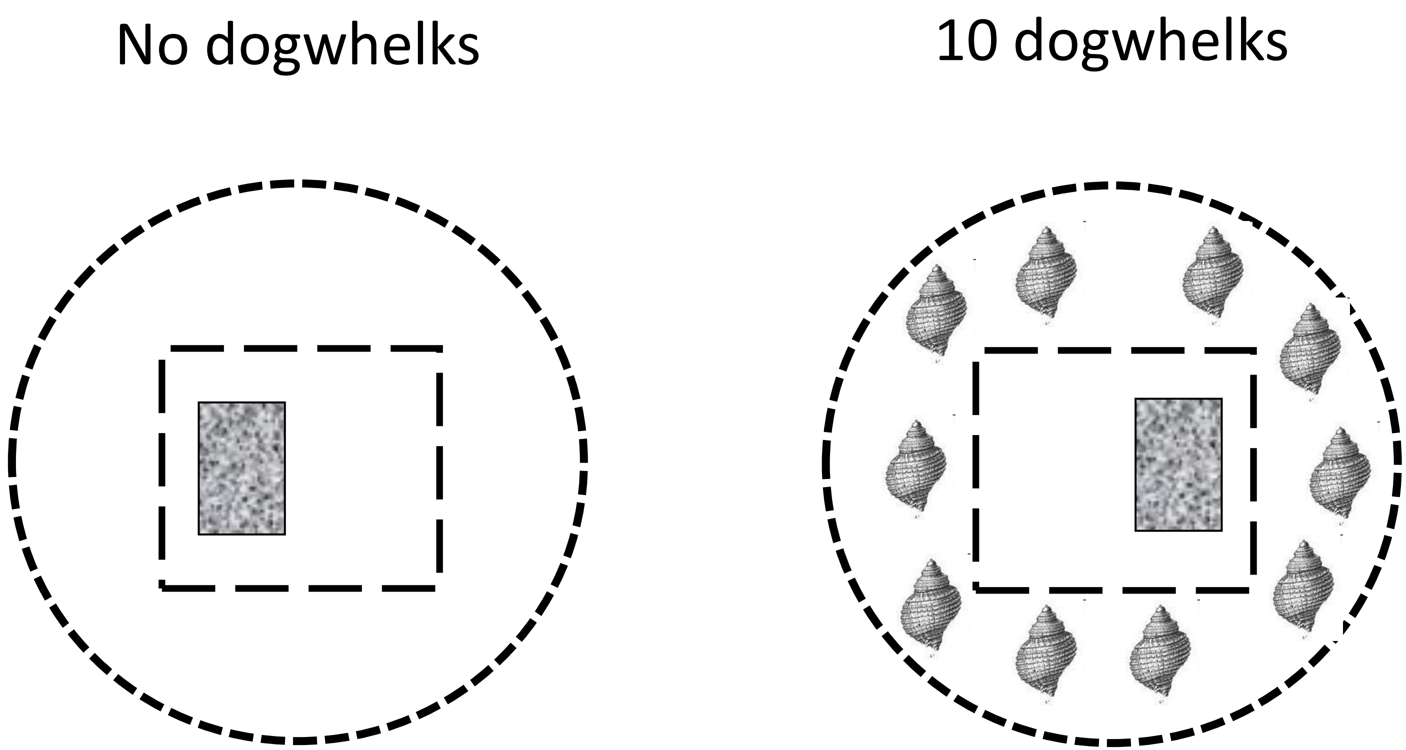
http://giovanni.gsfc.nasa.gov/giovanni/

Food Supply

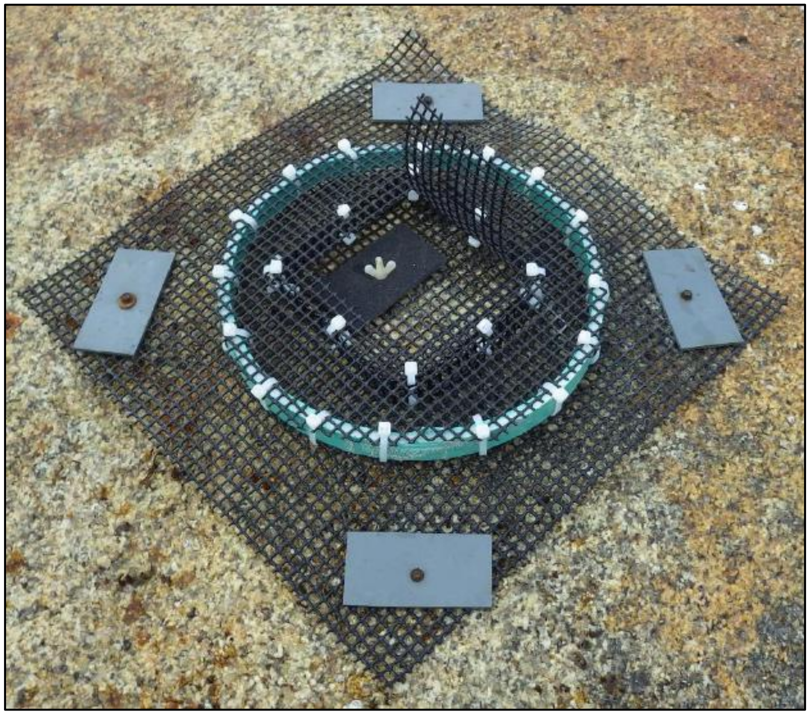


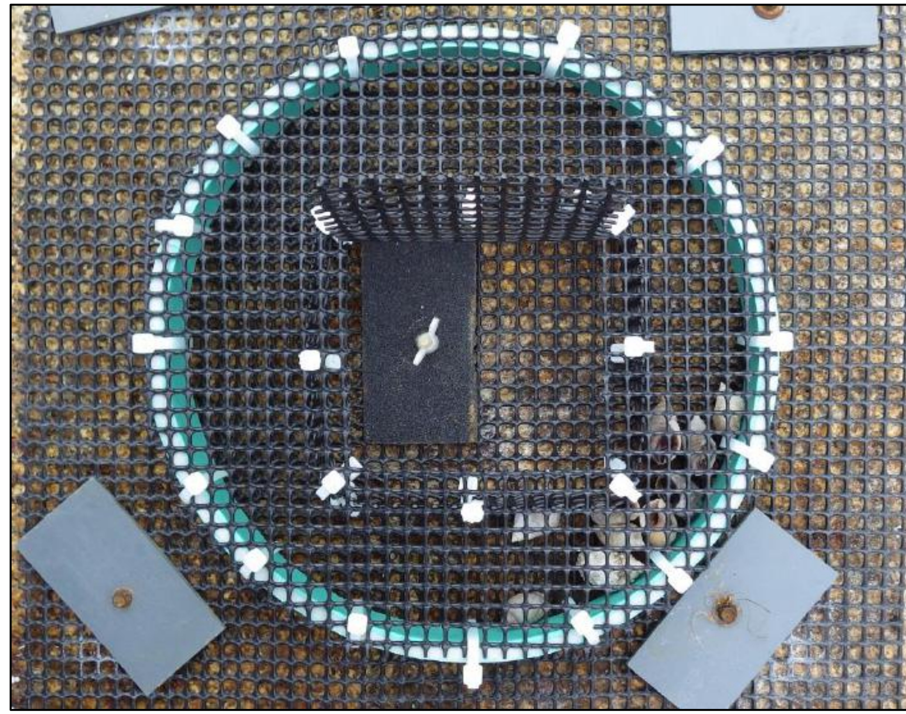
Ellrich et al. 2015

Predator Presence

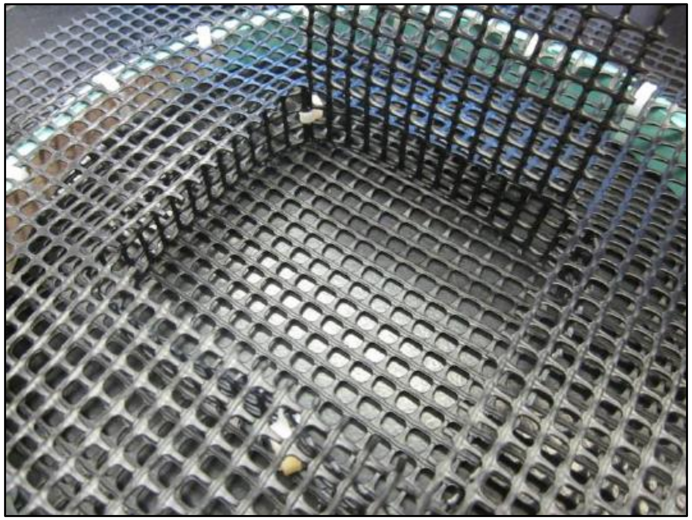


Cage Design

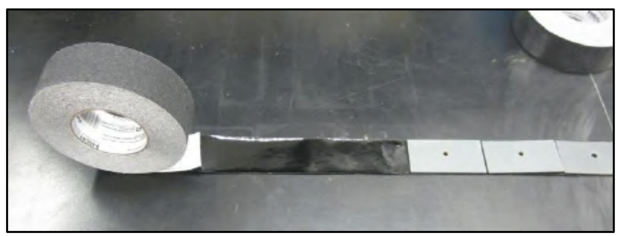




Laboratory Work

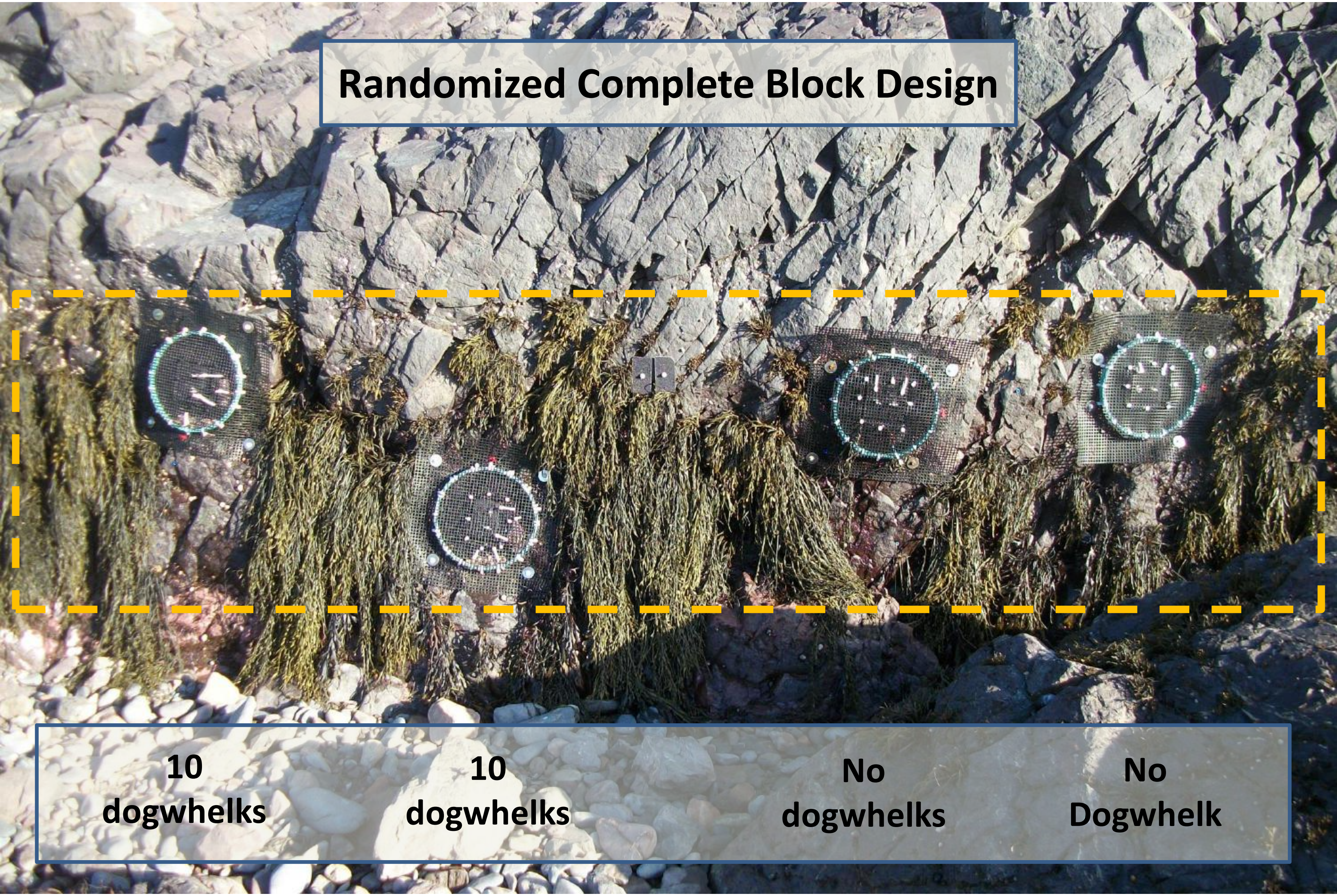


Laboratory Work



Gulf of St. Lawrence coast

Atlantic coast


Randomized Complete Block Design
10 dogwhelks
10 dogwhelks
No dogwhelks
No Dogwhelk

Whelk Collection

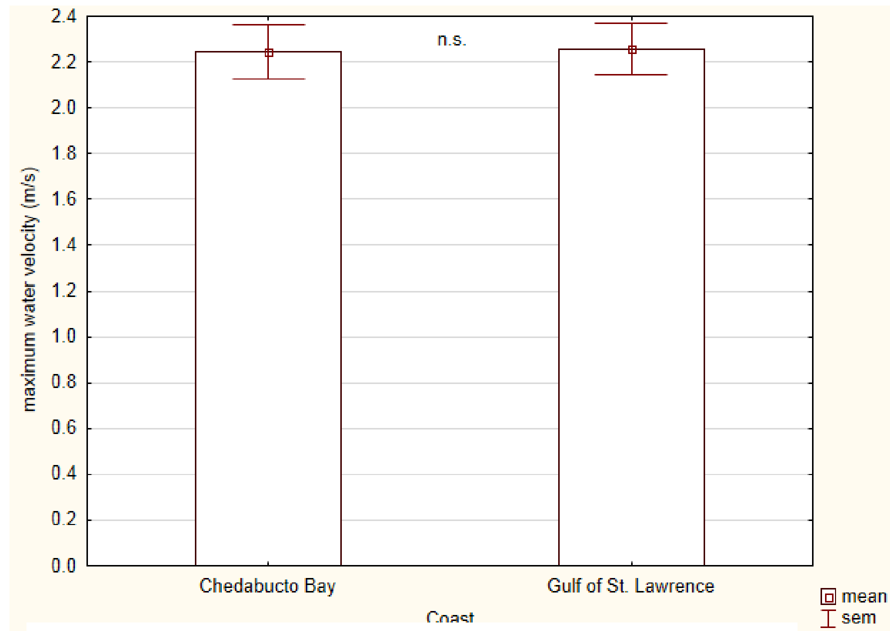
Starting the Experiment

Maximum Water Velocity During the Recruitment Season

Dynamometers

Dynamometer on the Gulf coast

Maximum water velocity (m/s)

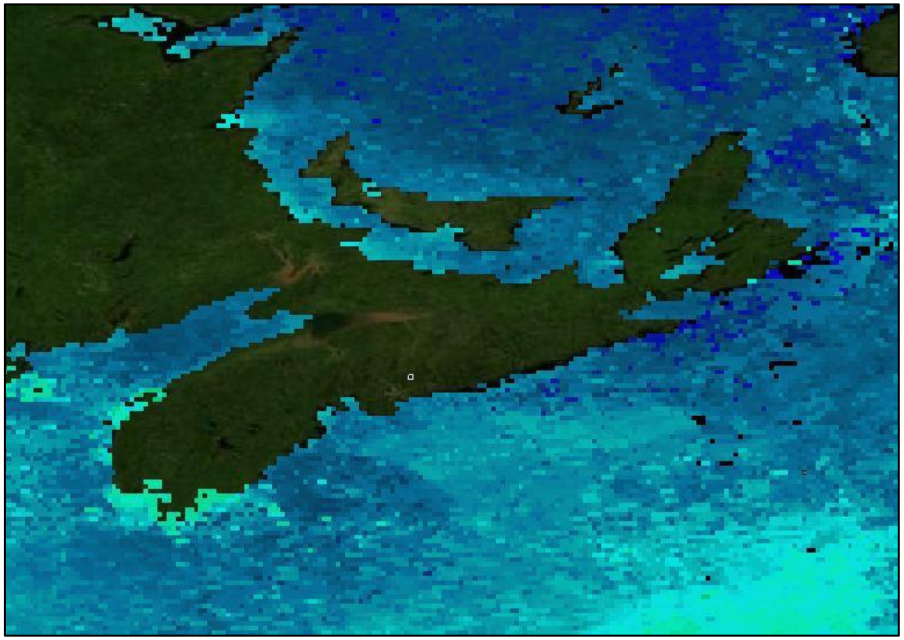


Atlantic Gulf

for dynamometer design: Bell & Denny 1994, JEMBE

Ellrich et al. 2015, Ecology

Sea Surface Temperature (SST) during the Recruitment Season



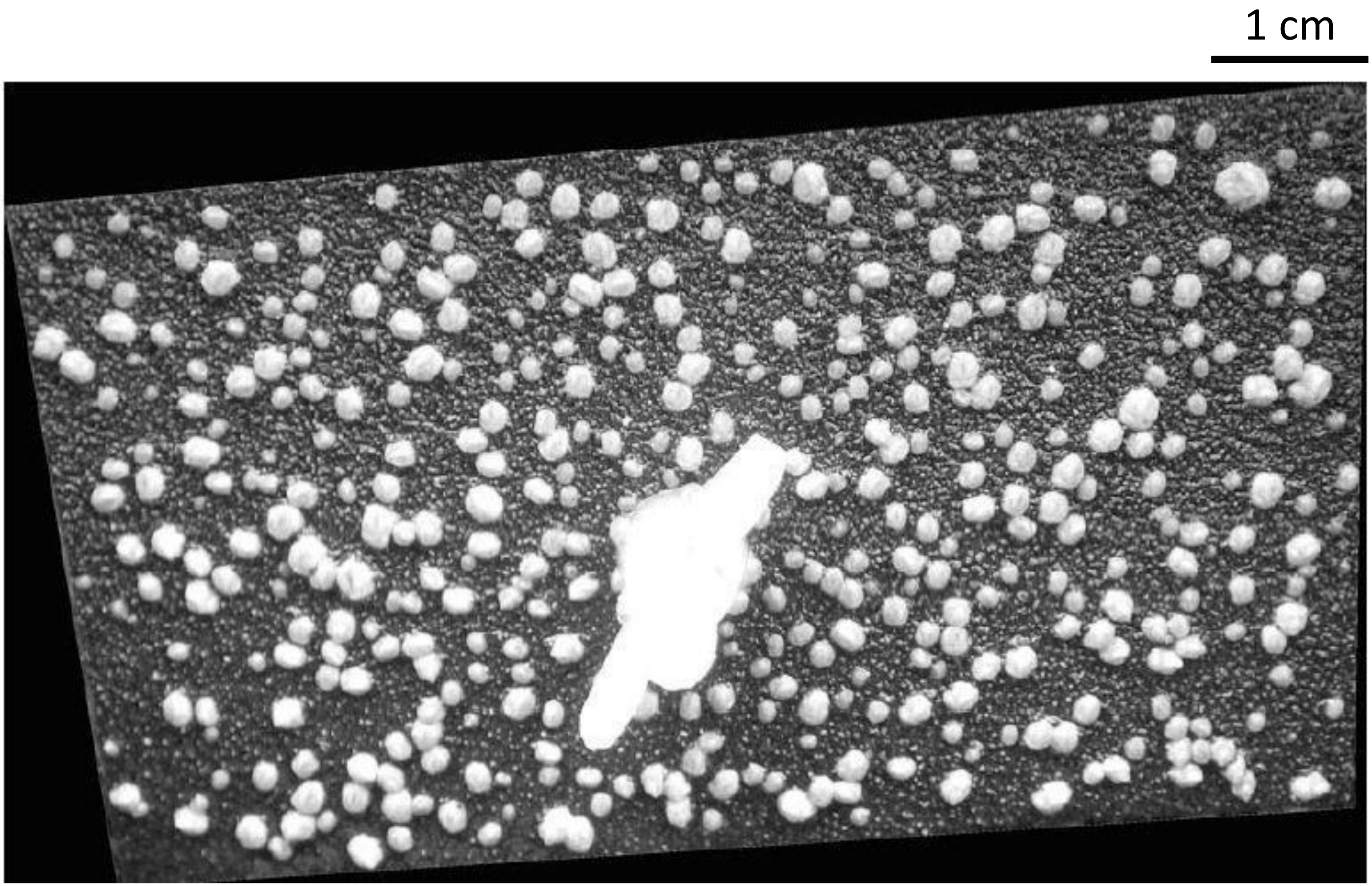
Modis Aqua SST satellite data

Average SST (mean ± standard error)

7.68 ± 1.28 °C	**5.98 ± 1.18 °C**	**8.88 ± 1.98 °C**	**8.48 ± 1.68 °C**
Gulf 2011	Atlantic 2011	Gulf 2013	Atlantic 2013

Ellrich et al. 2015, Ecology

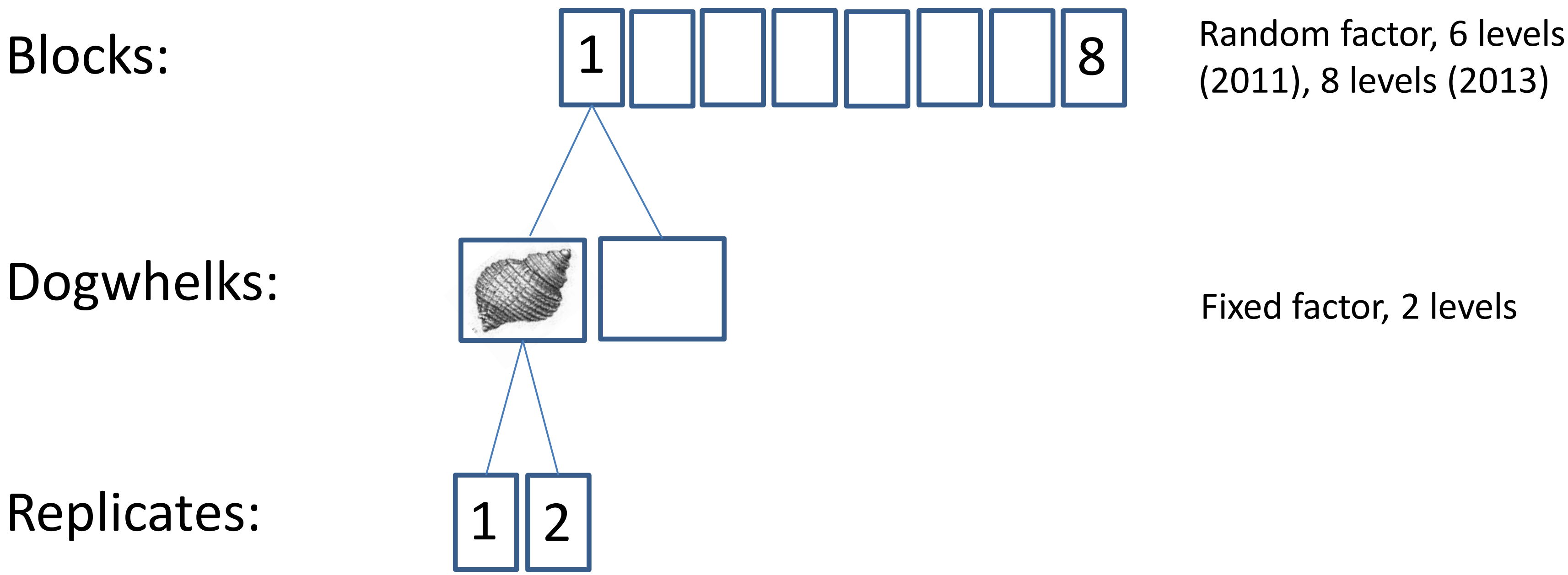
Sampling of Recruits



End of Recruitment: Mid-June

Ellrich et al. 2015, Ecology

Effects of Barnacle Recruit Density



→ 4 separate 2-factorial ANOVAs

Comparative Experimental Approach (Menge et al. 1994)

Effects of Dogwhelk Density

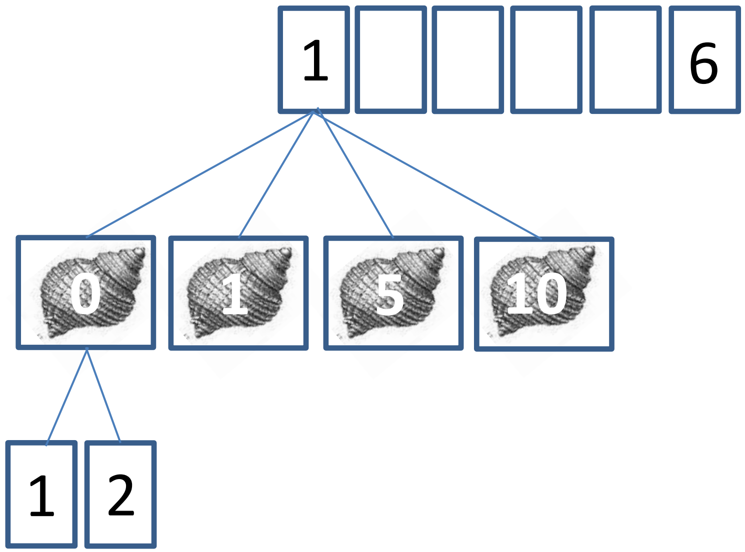
Blocks:

Random factor,
6 levels

Dogwhelk density:

Fixed factor,
4 levels

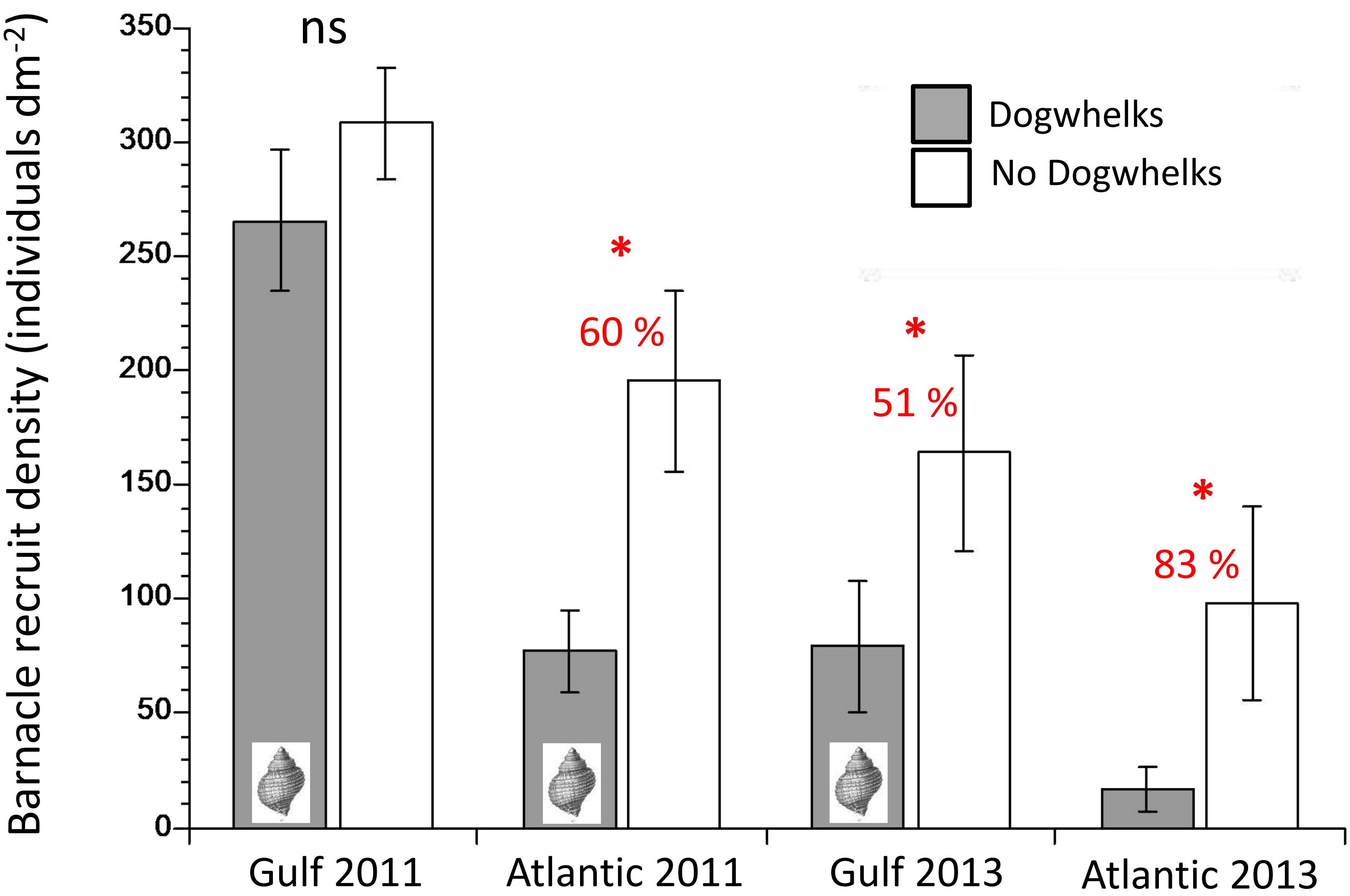
Replicates:



→ 2-factorial ANOVA, Fisher's LSD test

Results

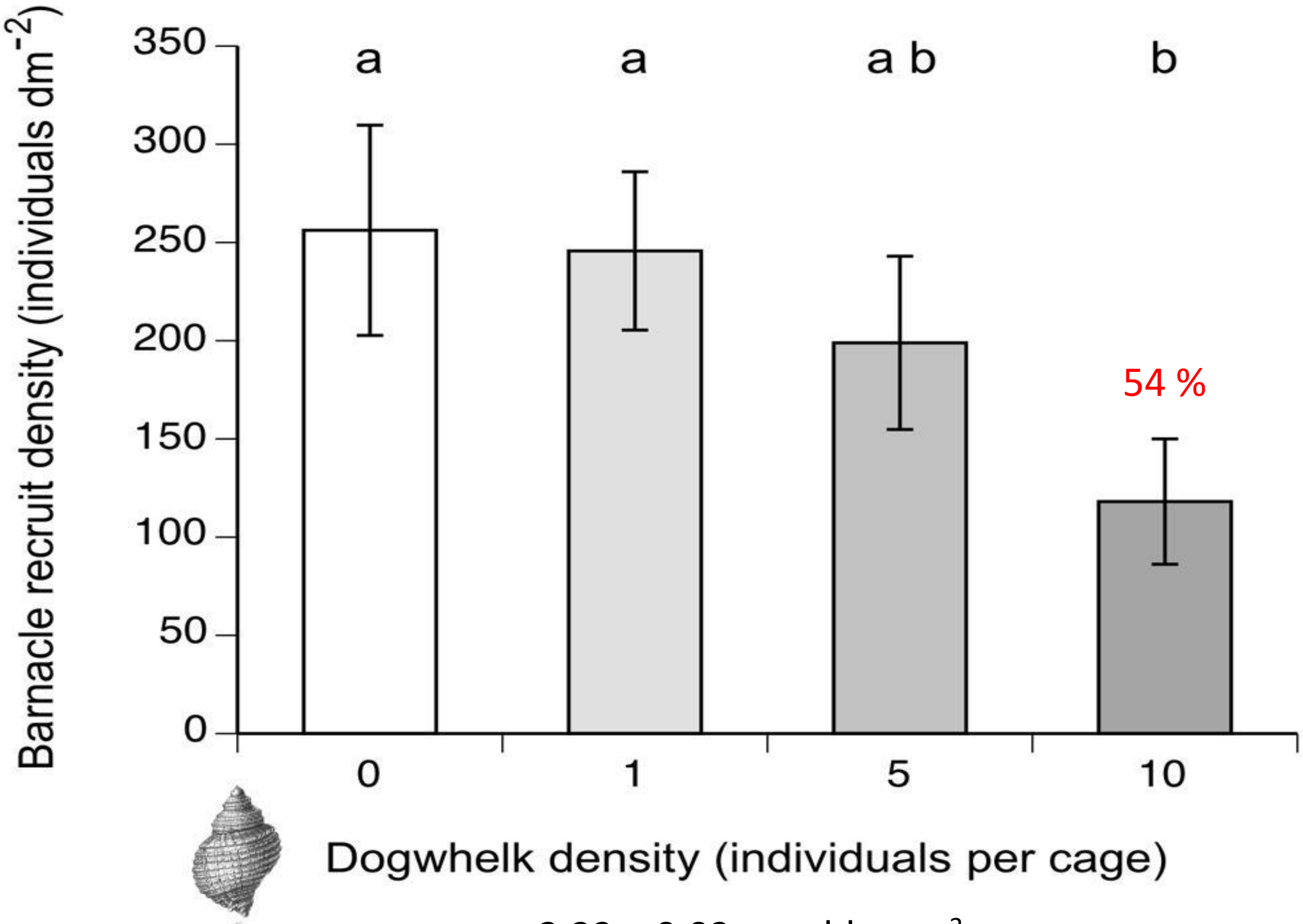
Effects of Barnacle Recruit Density



Chl-*a* (mg m^{-3}) 7.14 ± 1.58 1.19 ± 0.18 4.68 ± 0.01 4.30 ± 0.66 M ± SE

Ellrich, Scrosati & Molis 2015, *Ecology*

Effects of Dogwhelk Density



M ± SE

3.22 ± 0.02 mg chl-*a* m^{-3}

Ellrich, Scrosati & Petzold 2015, Journal of Experimental Marine Biology and Ecology

Conclusions

Recruit Density

- **Dogwhelk NCEs limit barnacle recruitment**
- **High barnacle recruit density neutralizes dogwhelk NCE**s

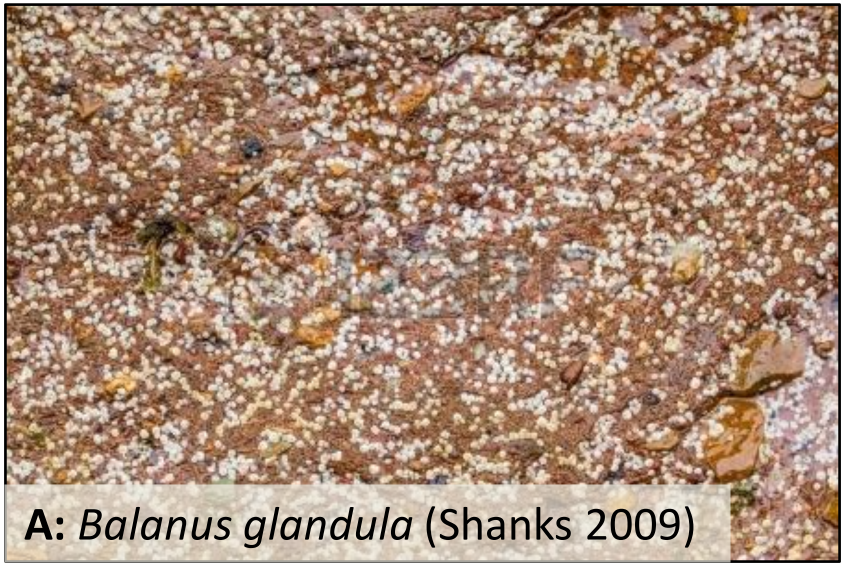
  → *Attractive recruit cues may counteract predator cues*

  → *Cyprids may experience a lower predation risk per capita in presence of recruits*

- **High recruit density is related to high phytoplankton abundance**

  → *Bottom-up factor may determine occurrence of predator NCEs on recruitment*

Recruit Density



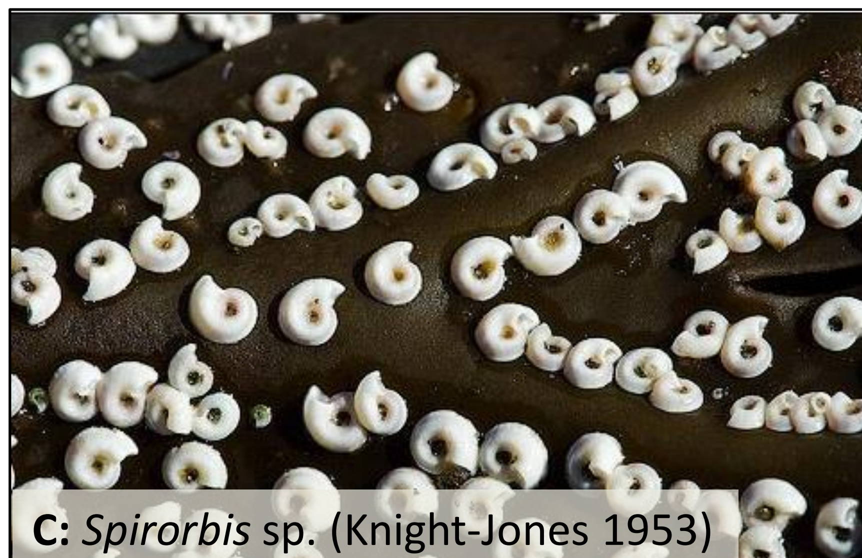
A: *Balanus glandula* (Shanks 2009)

- **Recruits attract larvae**

  → *High recruit density limiting NCEs recruitment may be common in sessile invertebrates.*

  → *Food supply regulating NCEs on recruitment may be common among filter feeders.*

B: *Crassostrea virginica* (Hidu 1967)



C: *Spirorbis* sp. (Knight-Jones 1953)

Dogwhelk Density

- **Predator NCEs on barnacle recruitment increase with dogwhelk density**

- **Higher recruit density neutralizes NCEs of 10 dogwhelks**

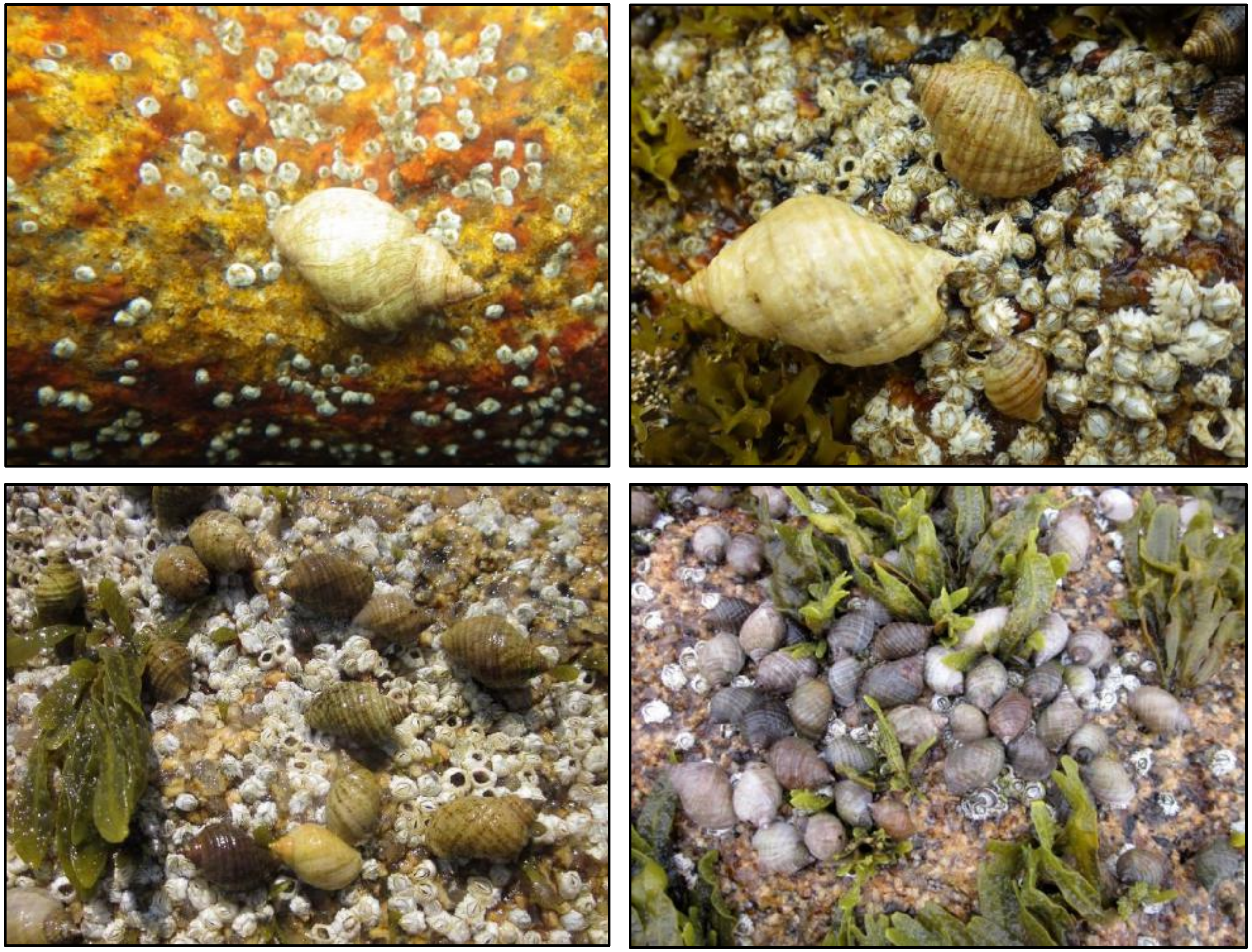
→ *Occurrence of predator NCEs on recruitment*
may depend on the balance between
predator & prey density

Dogwhelk Density

- **Habitat heterogeneity enhances dogwhelk density** (Johnson et al. 1998)
- **Food supply enhances barnacle recruitment** (Cole et al. 2011)

→ *The Interplay of habitat heterogeneity & food supply may determine the occurrence of NCEs on a coastal scale.*

Dogwhelk Density



- Patchiness in dogwhelks may determine patchiness in NCEs on a local scale.

Summary: NCEs…

- … can affect movement and settlement in prey larvae.
- … can limit prey recruitment by reducing settlement.
- … on prey recruitment weaken with recruit density.
- … on prey recruitment increase with predator density.
- … depend on the balance of predator an prey density.

CHECK OUT THESE 2 PAPERS FROM THE COURSE WEBSITE

Ecology, 96(3), 2015, pp. 611–616

Predator nonconsumptive effects on prey recruitment weaken with recruit density

Julius A. Ellrich,[1] Ricardo A. Scrosati,[1,3] and Markus Molis[2]

[1]*St. Francis Xavier University, Department of Biology, Antigonish, Nova Scotia B2G 2W5 Canada*
[2]*Alfred Wegener Institute, Helmholtz-Zentrum für Polar- und Meeresforschung, Am Handelshafen 12, 27570 Bremerhaven, Germany*

Journal of Experimental Marine Biology and Ecology 472 (2015) 72–76

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Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Predator density affects nonconsumptive predator limitation of prey recruitment: Field experimental evidence

CrossMark

Julius A. Ellrich, Ricardo A. Scrosati *, Willy Petzold

St. Francis Xavier University, Department of Biology, Antigonish, Nova Scotia B2G 2W5, Canada

II. Predator NCEs on Prey Demography: Predator Nonconsumptive Limitation of Prey Recruitment

Ehlers, S. M., R. A. Scrosati & J. A. Ellrich (2017) Nonconsumptive predator effects on prey demography: Dogwhelk cues decrease benthic mussel recruitment. *BioRxiv*. doi: https://doi.org/10.1101/172692

Predator Consumptive & Nonconsumptive Effects (NCEs)

Predation

Predator cues

Killing

Predator

Chemical, tactile, visual & audible cues

Prey

prey density changes

Prey responses / trait changes

- Behavior
- Demography
- Morphology

that may limit predation risk

Prey Behavioral Responses to Predator Cues

REVIEW / SYNTHÈSE

Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus[1]

Maud C.O. Ferrari, Brian D. Wisenden, and Douglas P. Chivers

Can. J. Zool. **88**: 698–724 (2010) doi:10.1139/Z10-029 Published by NRC Research Press

Original Articles

The scent of death: Chemosensory assessment of predation risk by prey animals

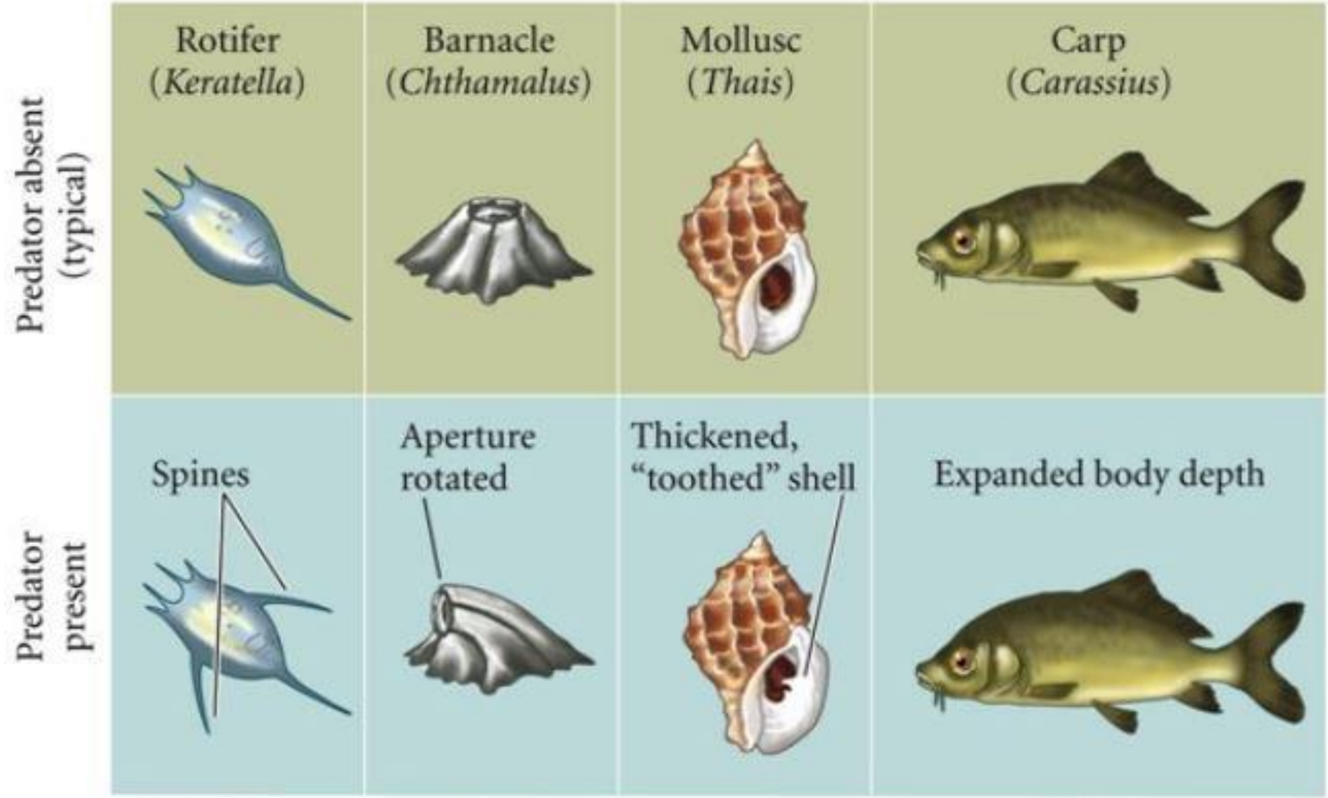
Lee B. Kats & Lawrence M. Dill

Pages 361-394 | Received 13 Aug 1996, Accepted 30 Aug 1997, Published online: 24 Mar 2016

Download citation http://dx.doi.org/10.1080/11956860.1998.11682468

Prey behavioral responses to predator cues have been widely studied.

Prey Morphological Responses to Predator Cues

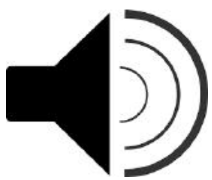


Prey morphological responses to predator cues have been widely studied.

Scott F. Gilbert, Developmental Biology

Prey Demographic Responses to Predator Cues Have Received Comparatively Little Attention

Prey: Song sparrow (*Melospiza melodia*)



Playbacks with predator calls

Decreased hatching

Increased Nestling Mortality

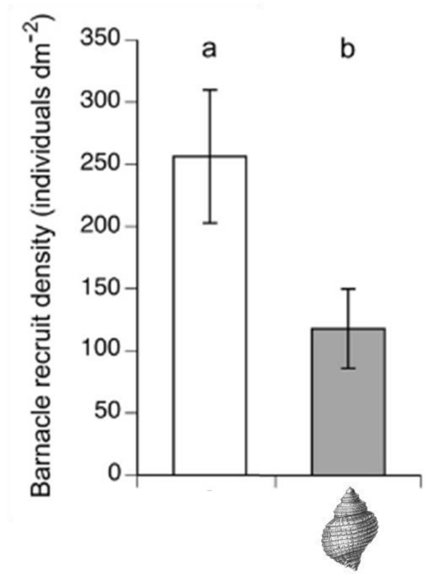
Zanette et al. 2011*, Science*

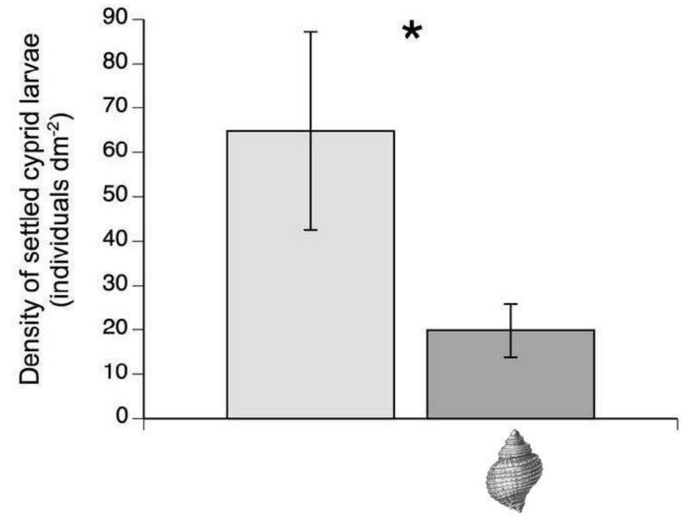
Dogwhelk Cues Limit Barnacle Recruitment by Reducing Barnacle Settlement

Semibalanus balanoides cyprids

Semibalanus balanoides

Nucella lapillus





Ellrich et al. 2015, 2016

Mussel larvae avoid waterborne chemical cues by dogwhelks
(Lab experiment, Morello & Yund 2016)

Hypothesis: Dogwhelk cues may limit mussel recruitment.

Benthic Prey Mobility

Barnacles are strictly sessile

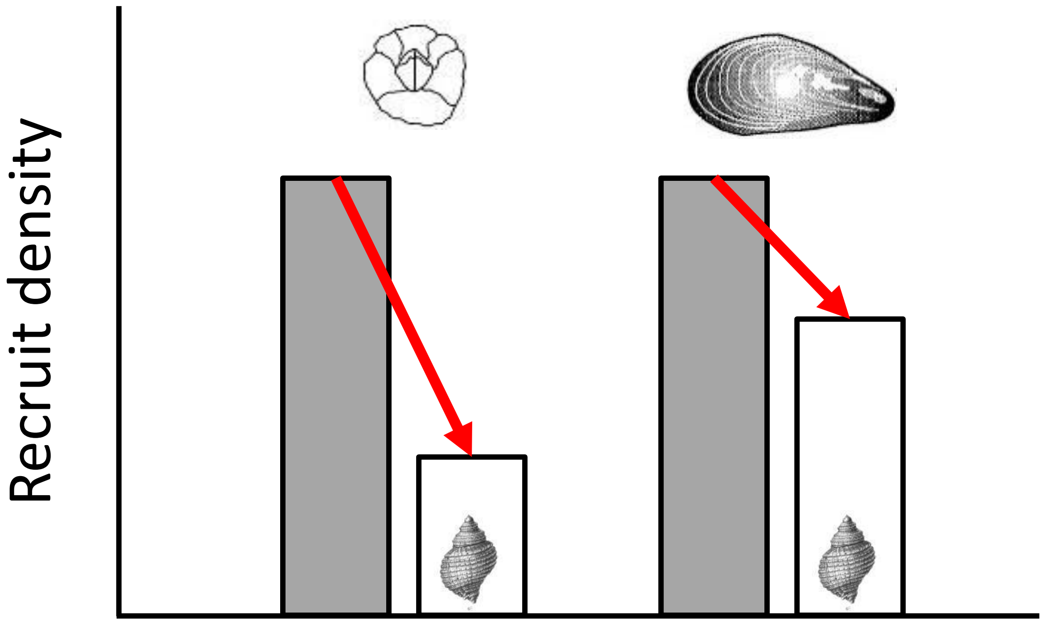
Mussels remain mobile

Video: “How Mussels Move”

Video: van den Berg et al. 2011, https://www.youtube.com/watch?v=MaMBiRoZYvs

Mussels remain capable to escape from dogwhelk predation.

Prediction



Dogwhelk NCEs on recruitment are stronger for barnacles than for mussels.

Predator-Prey Model System

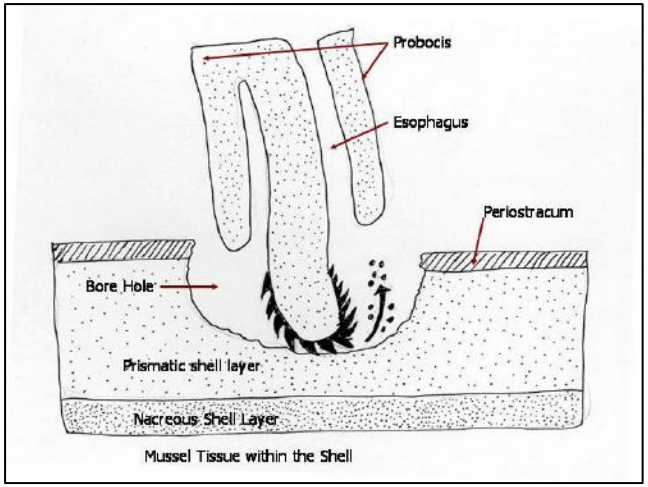
Predatory dogwhelks *Nucella lapillus* (L. 1753) & blue mussels *Mytilus* spp.

Dogwhelks

- common intertidal snail
- active: April – November
- barnacle & mussel predators
- drilling or prising attack
- slow moving
- easy to collect in high amounts
- easy to manipulate dogwhelk occurrence

Nucella lapillus

N. lapillus borehole



Dogwhelk radula drilling

Review on dogwhelk biology: Crothers 1985; Radula picture: https://www.bigelow.org/archive/mitzi/mid_12.html

Blue Mussels

<u>Ecological Relevance:</u>

- Bentho-pelagic coupling
  (Menge & Menge 2013)

- Food for predators
  (Largen 1967, Crothers 1985)

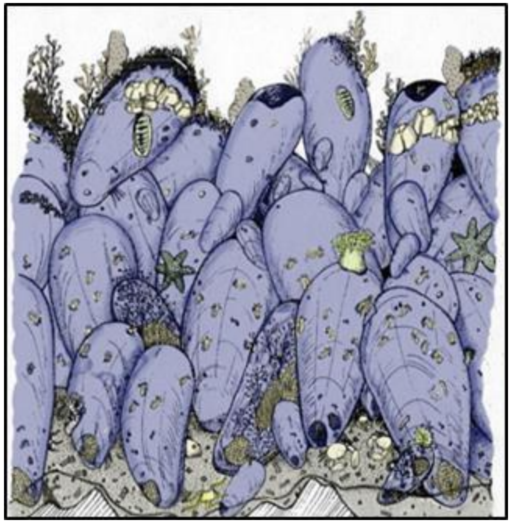
- Ecosystem engineers
  (Arribas et al. 2014, Altieri & van de Koppel 2014)

<u>Blue mussel species in Atlantic Nova Scotia:</u>

- *Mytilus edulis* & *M. trossulus*
  (Tam & Scrosati 2011)

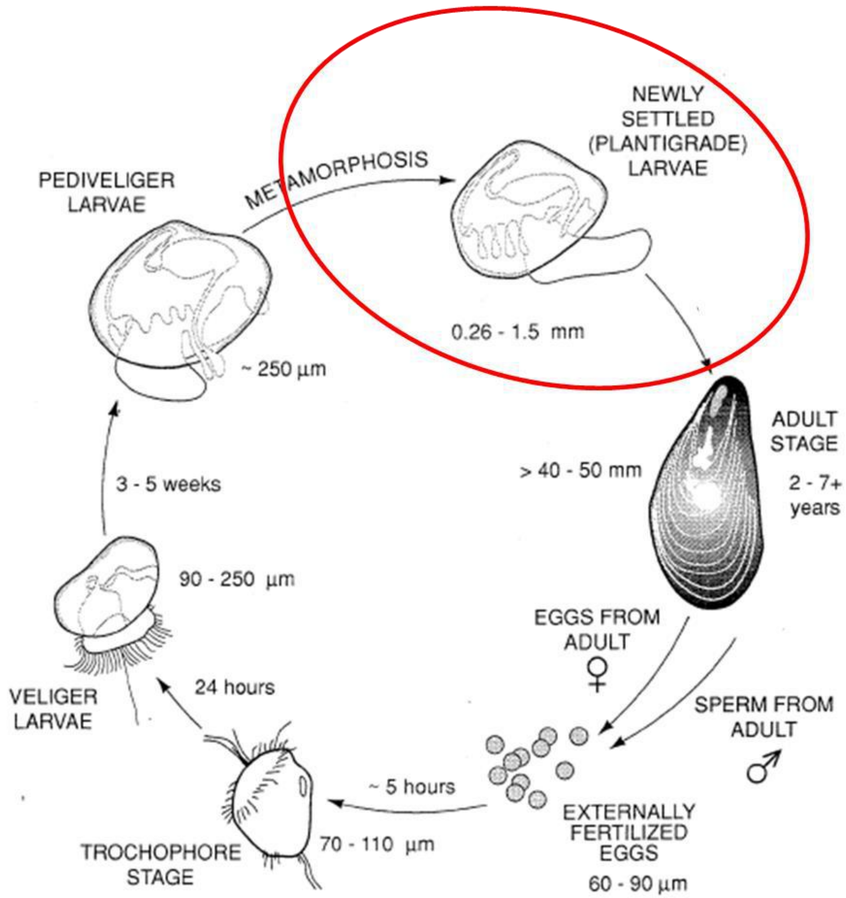
- Recruitment: mid-April to October
  (Scrosati & Petzold 2016)

Mussel patch



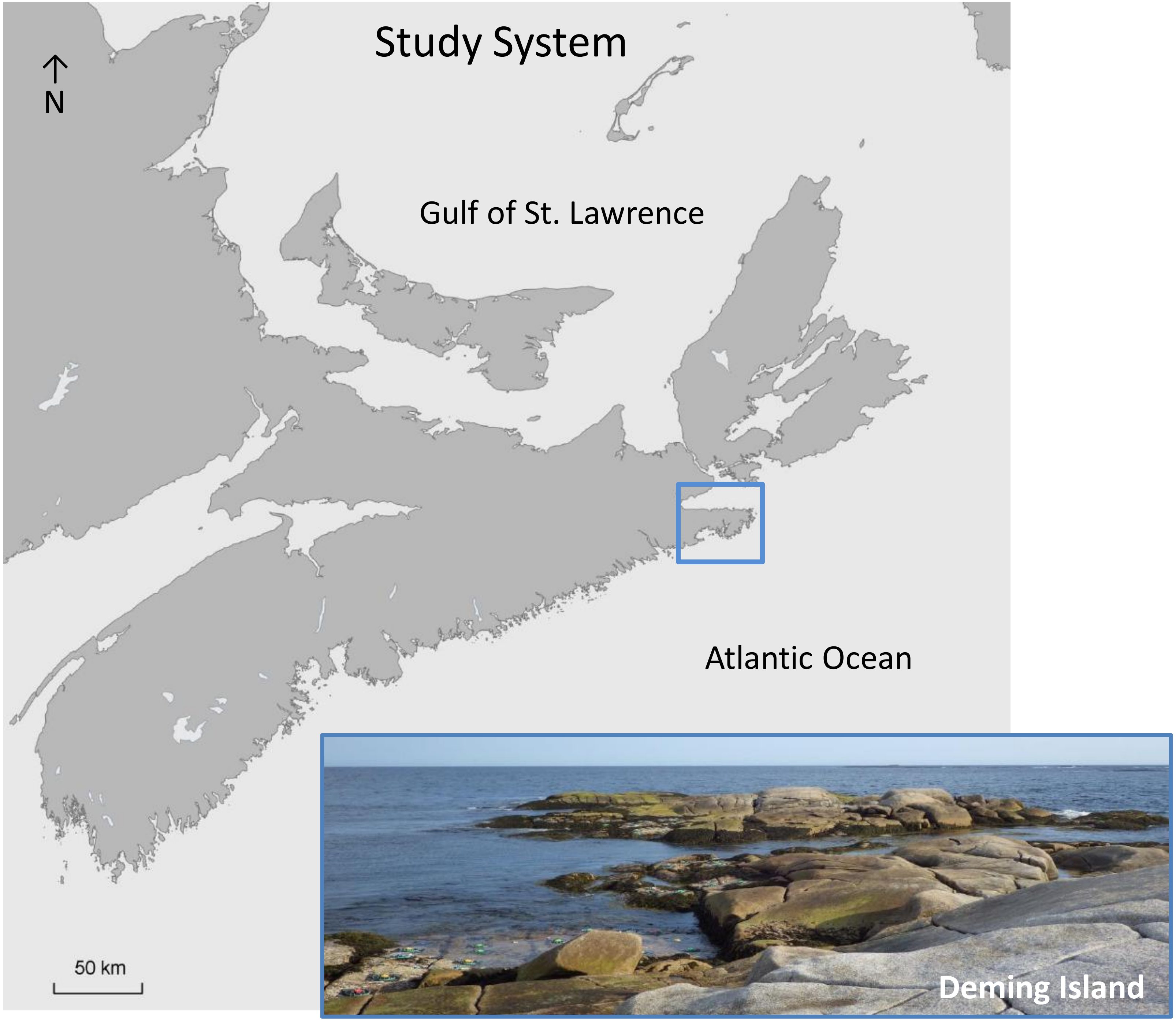
Picture: Suchanek 1992

Blue Mussel Life-Cycle



Mussel life-cycle picture: Stewart 1994

Manipulative Field Experiment


Study System
N
Gulf of St. Lawrence
Atlantic Ocean
50 km
Deming Island

Experimental Units

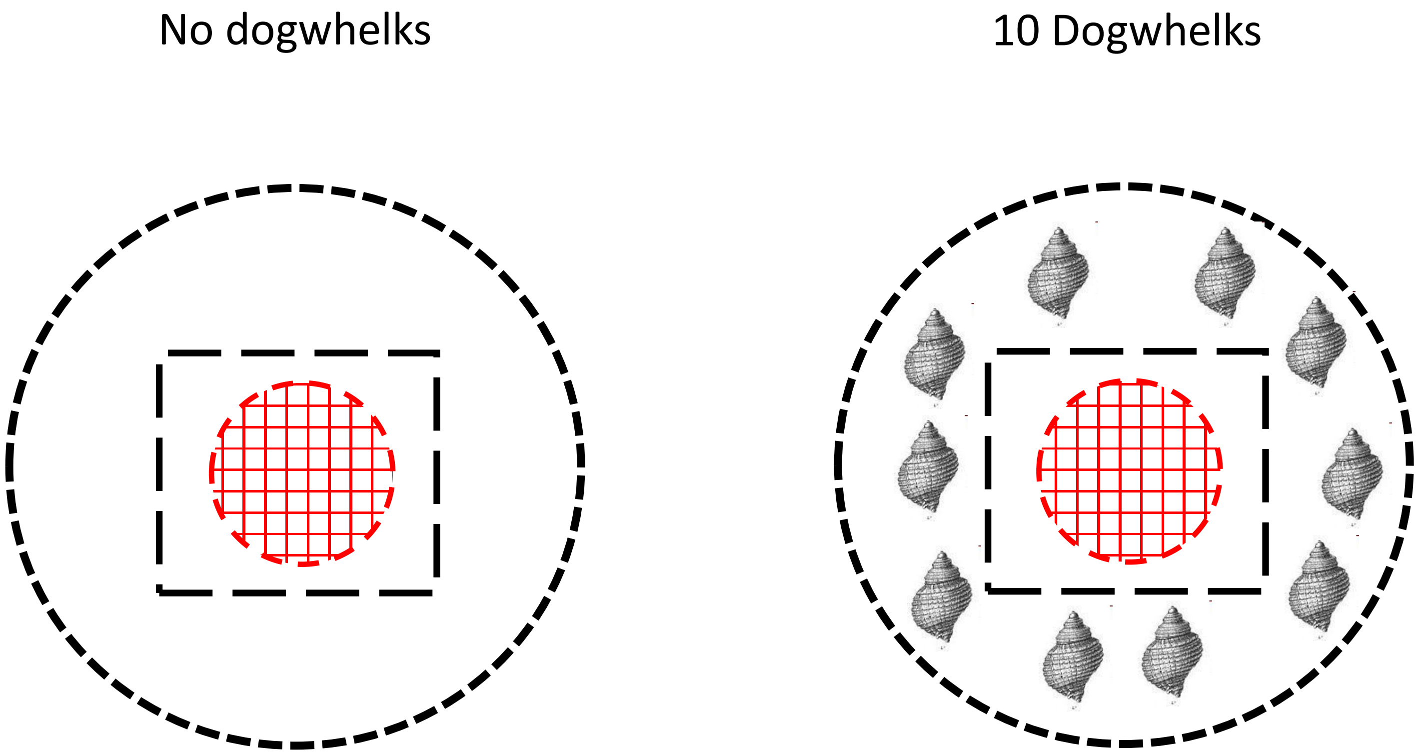
n= 48 cages in total, diameter: 25 cm, height: 2.5 cm

Randomized Block Design

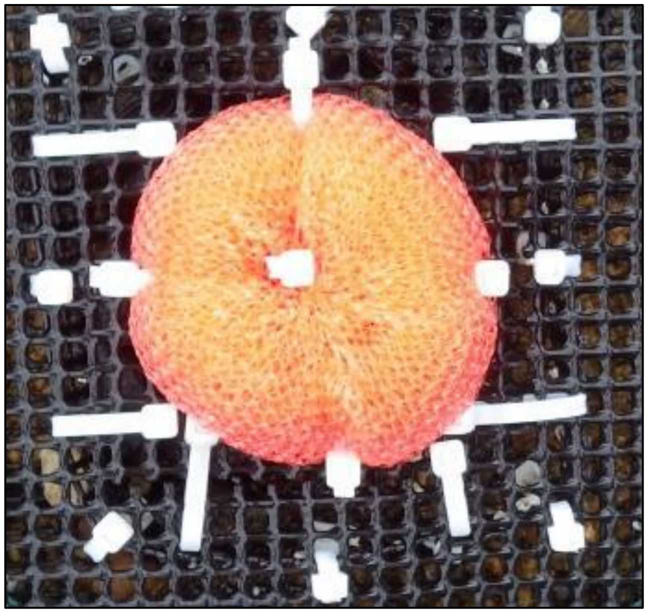
2 replicates per dogwhelk treatment within each block

Submerged Experimental Units During High Tide

Predator Presence & Absence



Mesh Scourer



Mesh scourer

Mussels on filamentous algae

Menge et al. 2009, South 2016

Field Setup



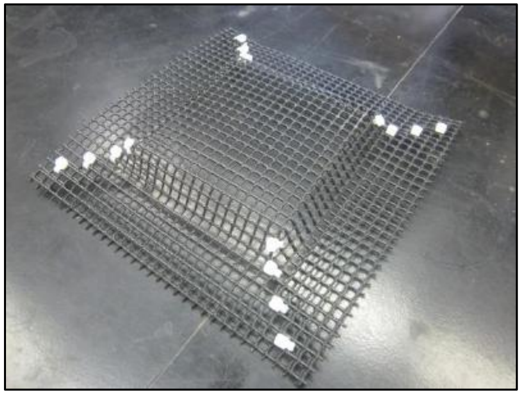

Experimental Cage Installation Video

https://www.youtube.com/watch?v=ztx_7VLZT8o&feature=youtu.be

Dogwhelk Field Collection

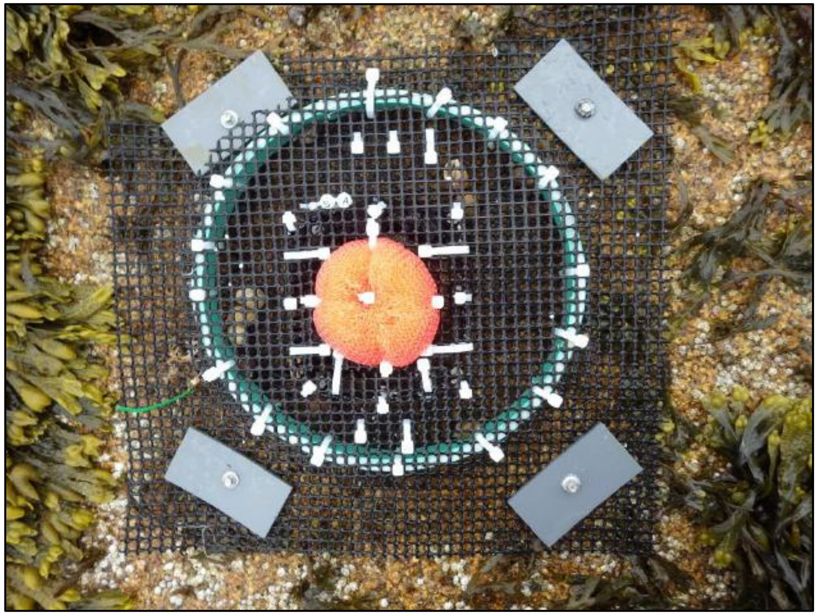
Ehlers SM & Ellrich JA. 2017. First visual record of rare purple-colored dogwhelks (*Nucella lapillus*) on the Atlantic coast of Nova Scotia, Canada. F1000 Research 5:2435.

Dogwhelk Field Maintenance

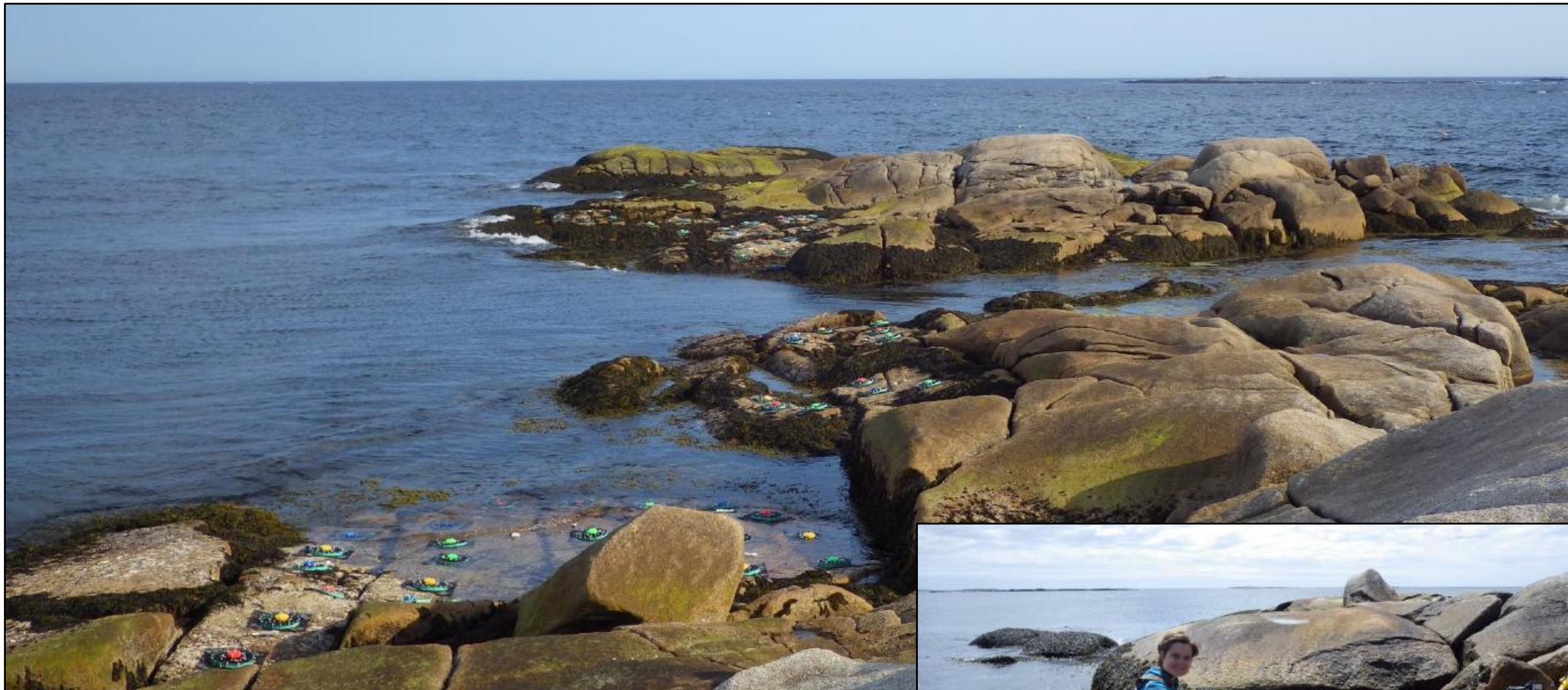


Dogwhelks were kept on a mussel diet.

Start of the Field Experiment, 21 May 2016



Maintenance of the Field Experiment



Regular exchange of dogwhelks & removal of wild dogwhelks from the experimental area.

Measurements of intertidal temperature using 7 submersible loggers.

Average temperature was:
12.8 ± 0.1 °C (mean ± SE)

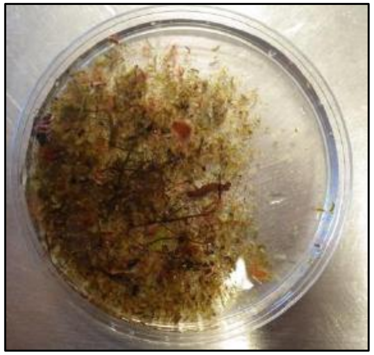
Mesh Scourer Collection, 29 July 2016

Individually bagged and tagged mesh scourers.

Laboratory Analyses of Mesh Scourers

Mesh scourer

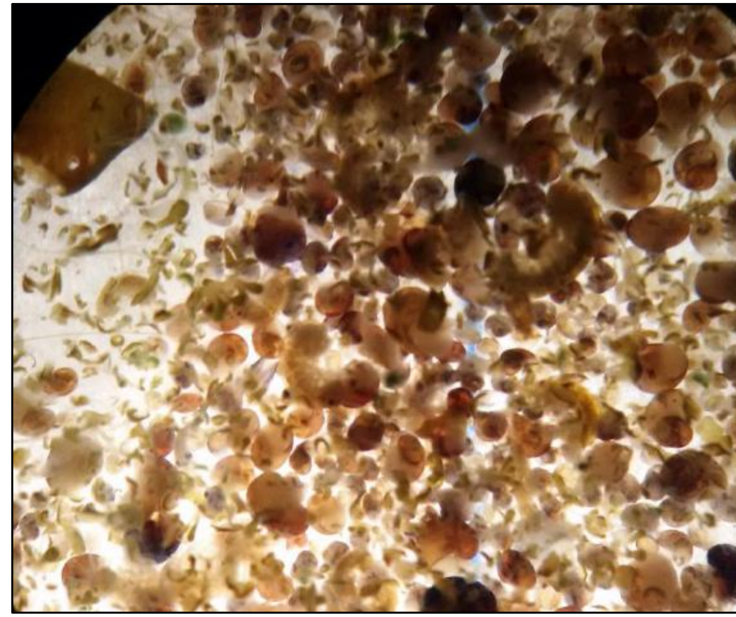
Rinsing scourers contents onto
a sieve (opening size: 0.212 mm x 0.212 mm).



Scourer content
in a Petri dish

Microscopic Assessment of Mussel Recruit Number

Counting mussel recruits

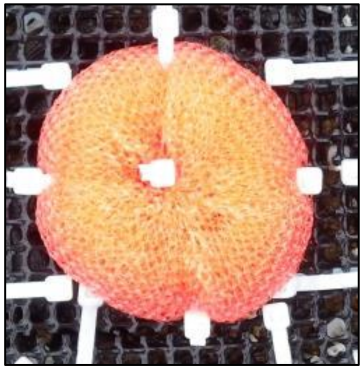


Mesh scourer content

Mussel recruit

Calculation of Mussel Recruit Density

Mesh scourer



Unrolled mesh scourer

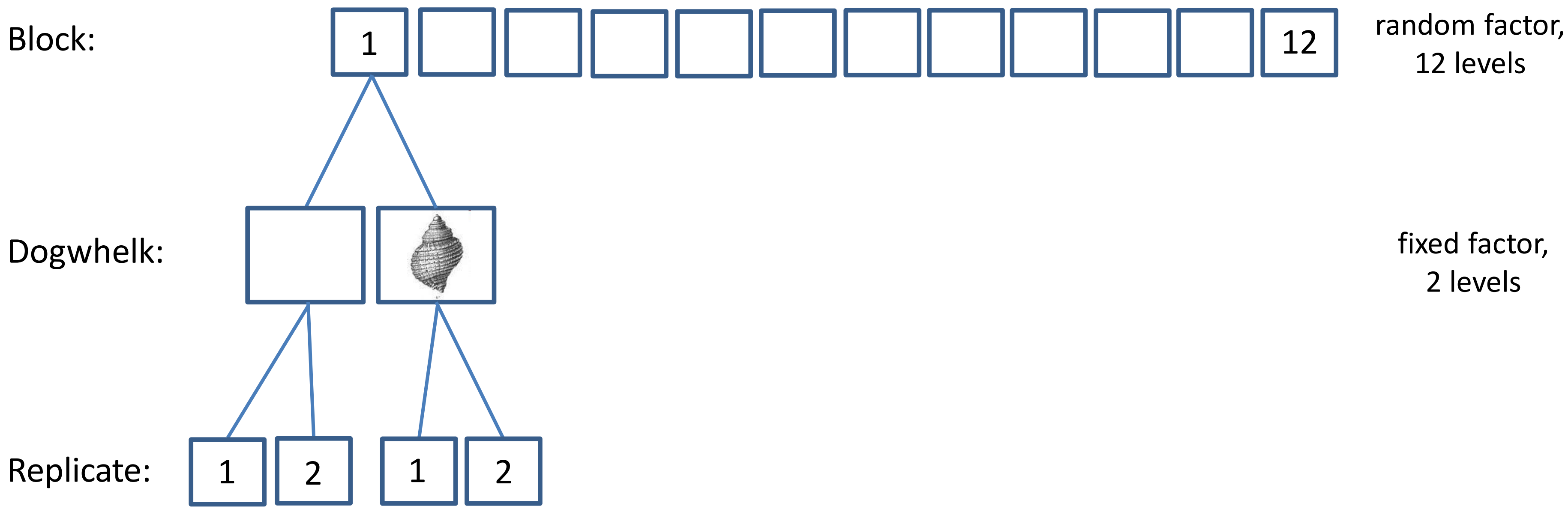
Width

Length

Scourer area = length x width x 4

Mussel recruit density =
mussel recruit individuals per dm^2 mesh scourer

Statistical Analysis: Analysis of Variance (ANOVA)



→ Response variable: mussel recruit density

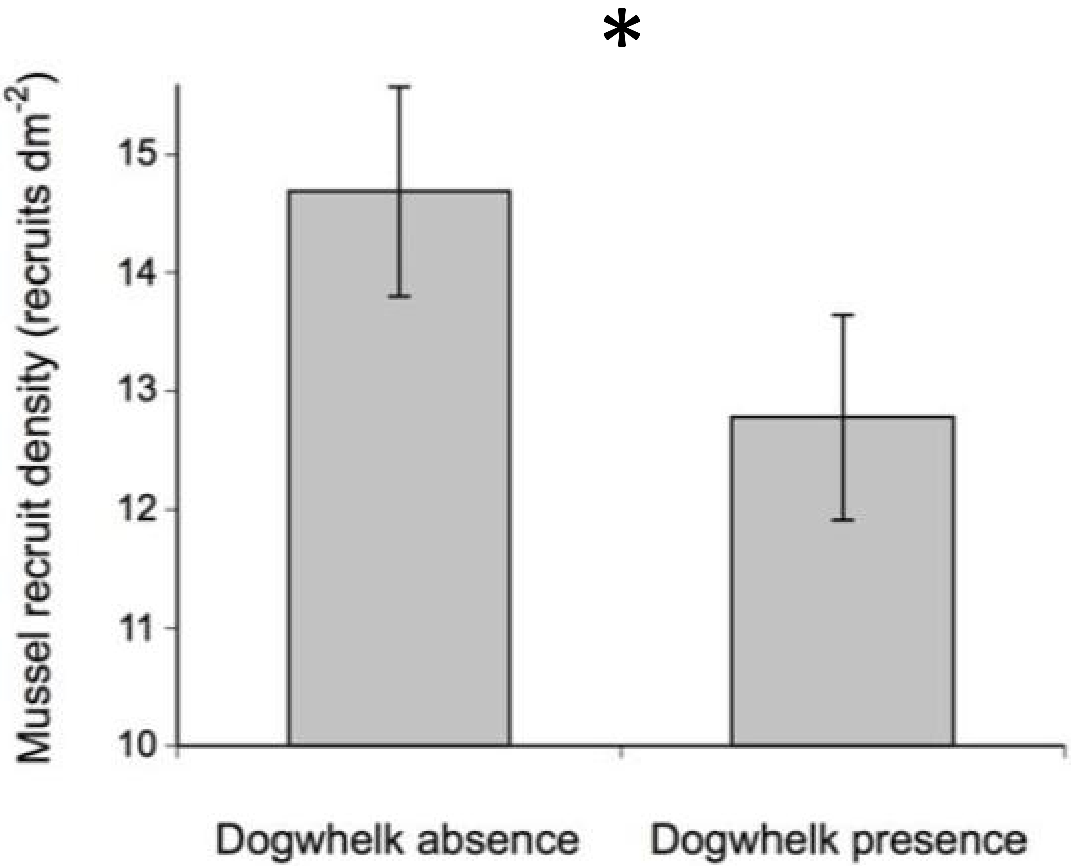
Results

ANOVA table

Source of variation	df	SS	MS	F	P	
Dogwhelks	1	43.86	43.86	7.37	0.020	*
Blocks	11	401.36	36.49	2.29	0.044	*
Dogwhelks x Blocks	11	65.50	5.96	0.37	0.954	
Residual	24	382.70	15.95			

Ehlers, S. M., R. A. Scrosati & J. A. Ellrich. 2017. Nonconsumptive predator effects on prey demography: Dogwhelk cues decrease benthic mussel recruitment. *BioRxiv*. doi: https://doi.org/10.1101/172692

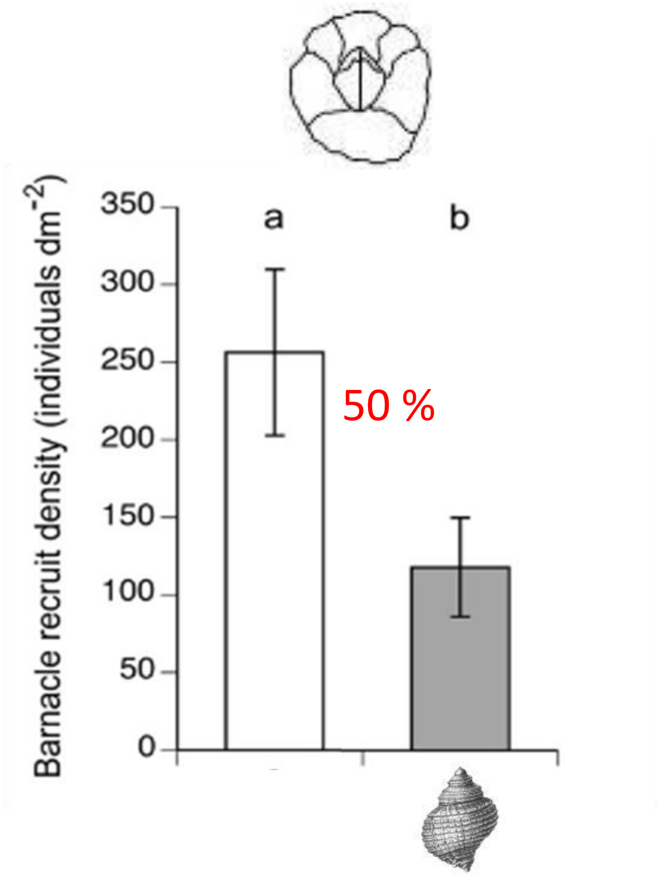
Dogwhelk Cues Decrease Benthic Mussel Recruitment



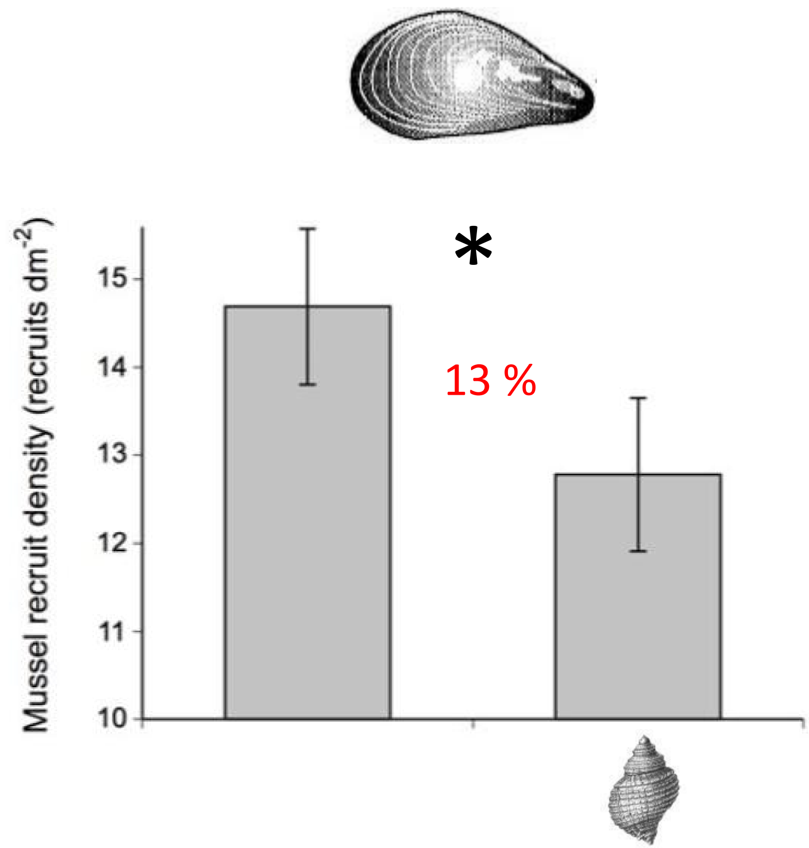
Ehlers, S. M., R. A. Scrosati & J. A. Ellrich. 2017. Nonconsumptive predator effects on prey demography: Dogwhelk cues decrease benthic mussel recruitment. *BioRxiv*. doi: https://doi.org/10.1101/172692

Discussion

Dogwhelk NCEs on Recruitment are Stronger for Barnacles Than for Mussels



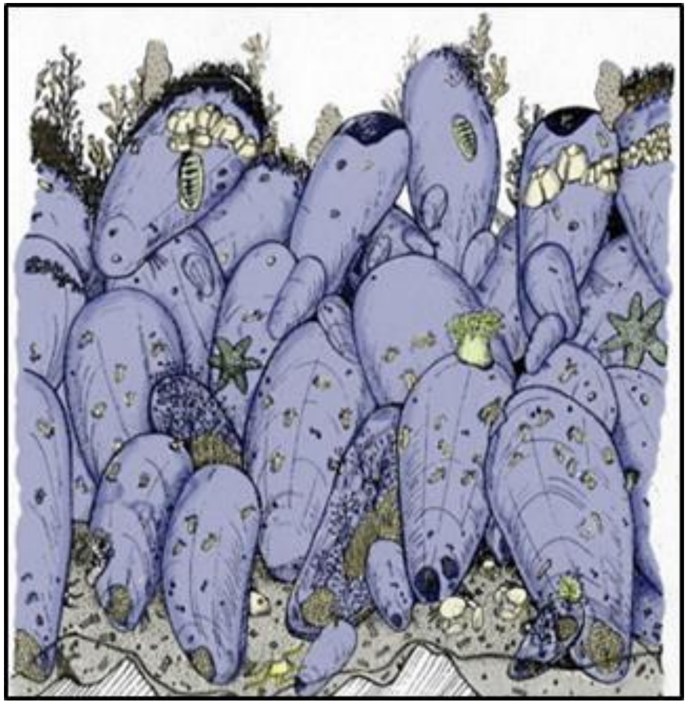
Ellrich et al. 2015



Ehlers et al. 2016

→ Mussel recruitment responses to dogwhelk cues may be weaker than barnacle responses because mussels can still relocate, whereas barnacles are strictly sessile once they became recruited.

Mussels are Ecosystem Engineers that form Mussel Beds



Picture: Suchanek 1992

By decreasing mussel recruitment, dowhelk cues may indirectly affect the composition of mussel bed communities.

Cold Spring Harbor Laboratory

bioRxiv beta

THE PREPRINT SERVER FOR BIOLOGY

New Results

Nonconsumptive predator effects on prey demography: Dogwhelk cues decrease benthic mussel recruitment

Sonja M. Ehlers, Ricardo A. Scrosati, Julius A. Ellrich

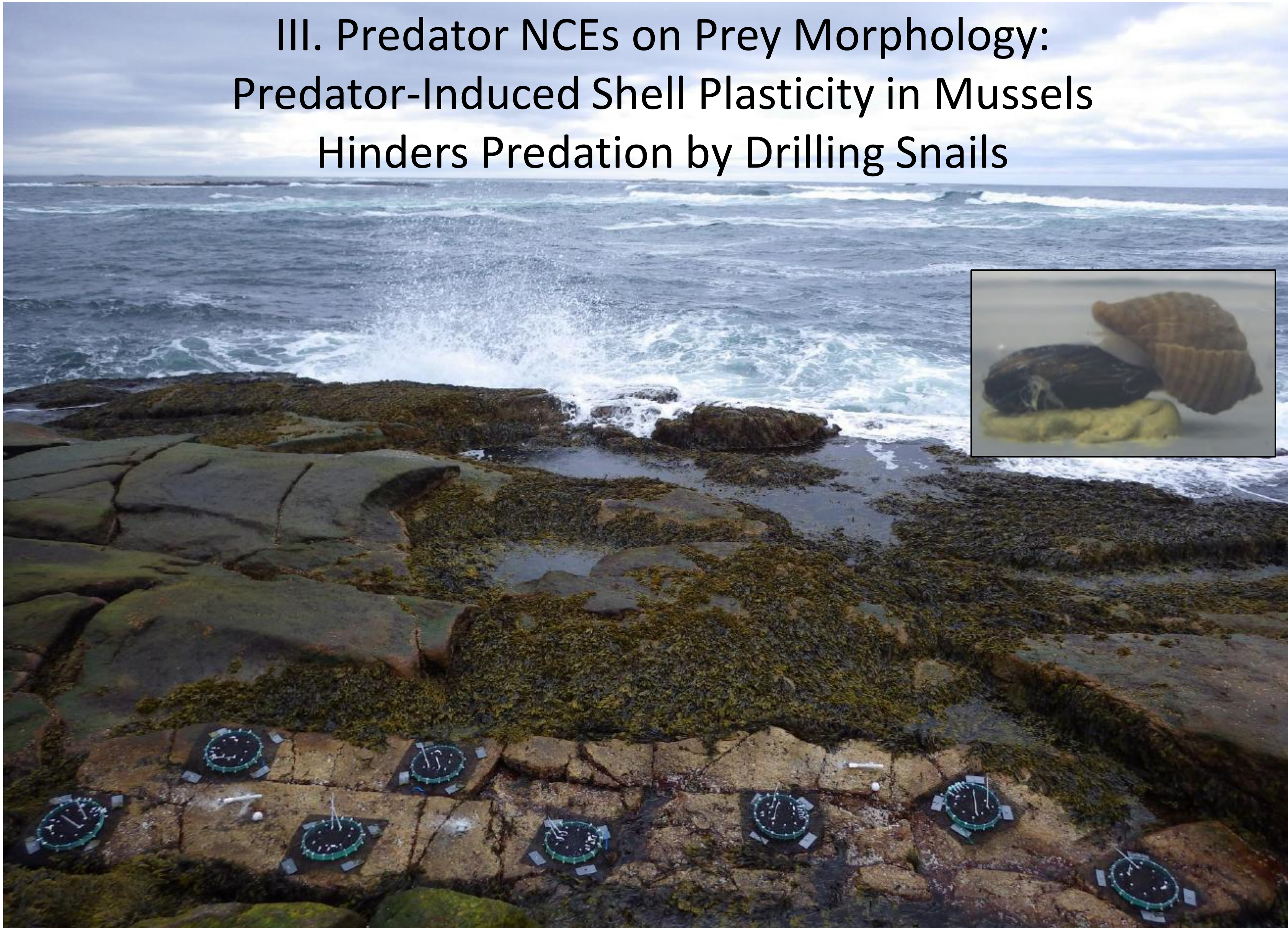
doi: https://doi.org/10.1101/172692

Sonja Ehlers

Ricardo Scrosati

Julius Ellrich

III. Predator NCEs on Prey Morphology: Predator-Induced Shell Plasticity in Mussels Hinders Predation by Drilling Snails



Sherker, Z. T., J. A. Ellrich, and R. A. Scrosati. 2017. Marine Ecology Progress Series.
573: 167-175. DOI 10.3354/meps12194

Short-term Prey Responses to Predator Cues

<u>Behavioral responses:</u>

Reduced feeding & mating activity

Prey moving away from predators

Green crab

Periwinkles

Trussell et al. 2004, Koch et al. 2007, Molis et al. 2011

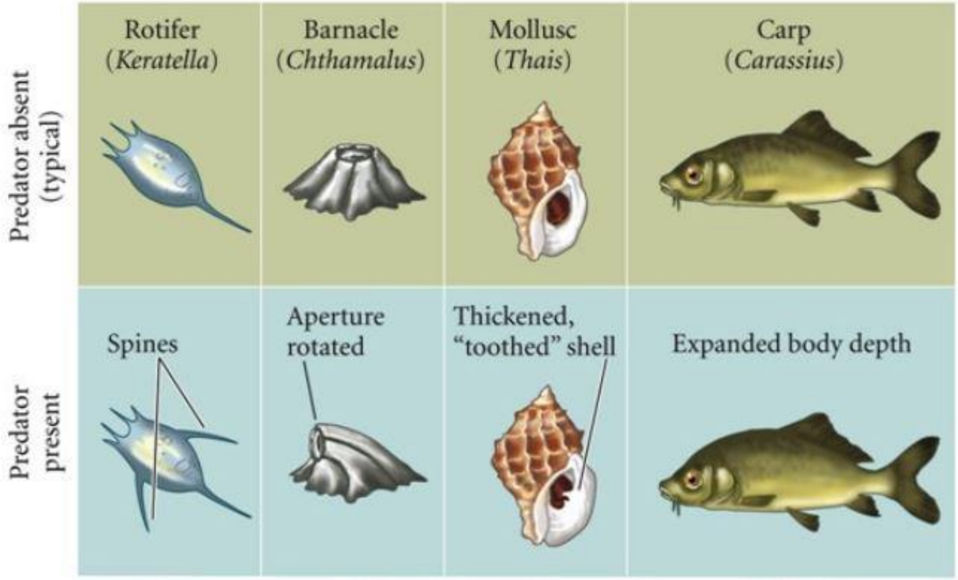
Long-term Prey Responses to Predator Cues

Changes in prey demographic rates
(Ellrich et al. 2015, Ehlers et al. 2017)

Barnacles

Blue mussels

Changes in prey morphology
(Lively 1986, Appleton & Palmer 1988,
Brönmark et al. 1999, Gilbert 1999)



Scott F. Gilbert, Developmental Biology

Blue Mussel Morphological Responses to Predator Cues

Crushing green crab

Prying sea star

Drilling dogwhelk

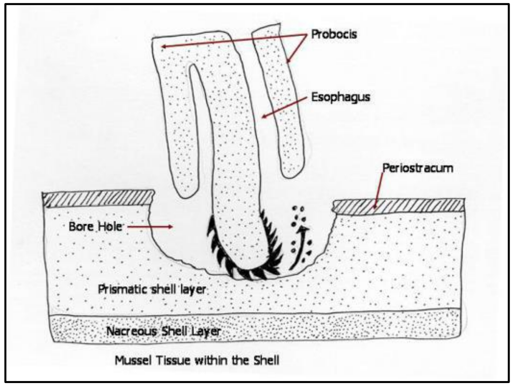
Crushing green crab	Prying sea star	Drilling dogwhelk
Mussel responses in lab experiments		
Shell thickening	Shell thickening	Shell thickening
Decrease in linear growth	Adductor muscle strengthening	
Increase in byssal production	Increase in byssal production	
Functional Significance - Predation hindrance		
Yes	Yes	**unknown**

Boulding 1984, Leonard et al. 1999, Freeman 2007, Lowen et al. 2013, Babarro et al. 2016

Sea star picture: http://leesonphoto.photoshelter.com/image/I00003XIkDojjeYY

Model System

Dogwhelk (*Nucella lapillus*)

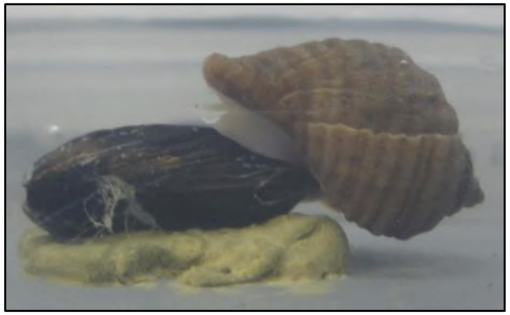


Radula drilling

Field experiment: examining dogwhelk NCEs on mussel traits

Blue mussels (*Mytilus* spp.)

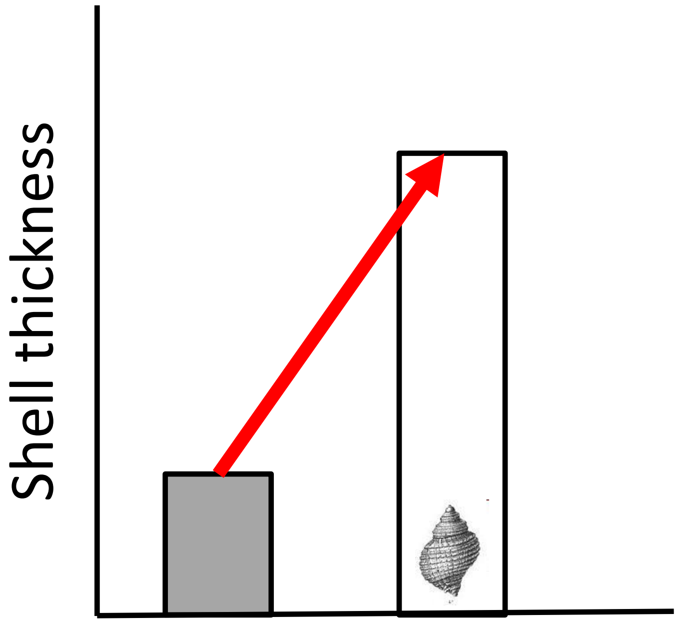
Dogwhelk borehole

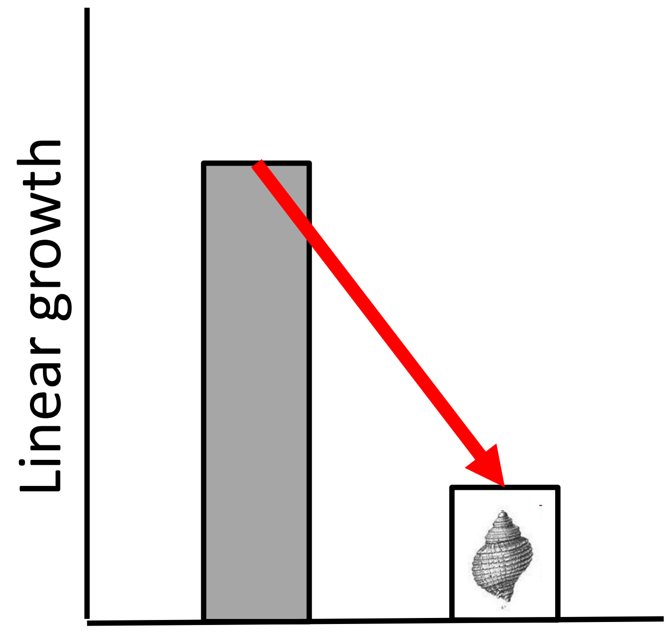


Lab experiment: examining predator hindrance by thickened mussel shells

Radula picture: https://www.bigelow.org/archive/mitzi/mid_12.html

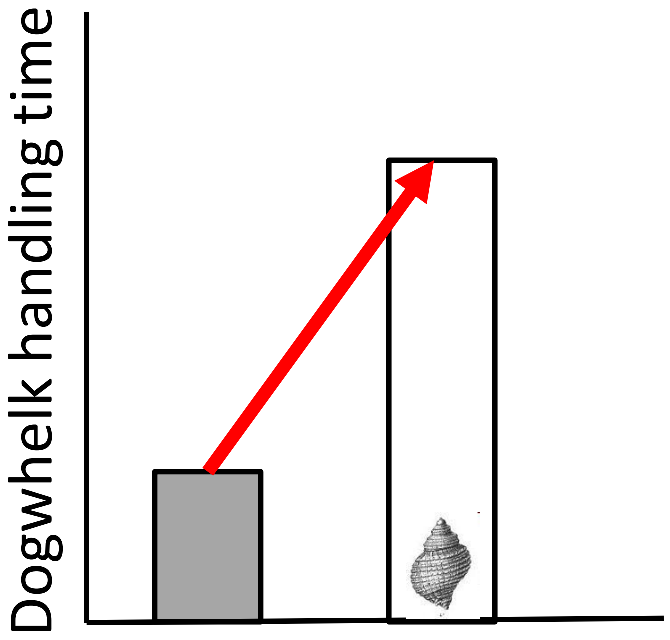
Field Experiment: Hypotheses





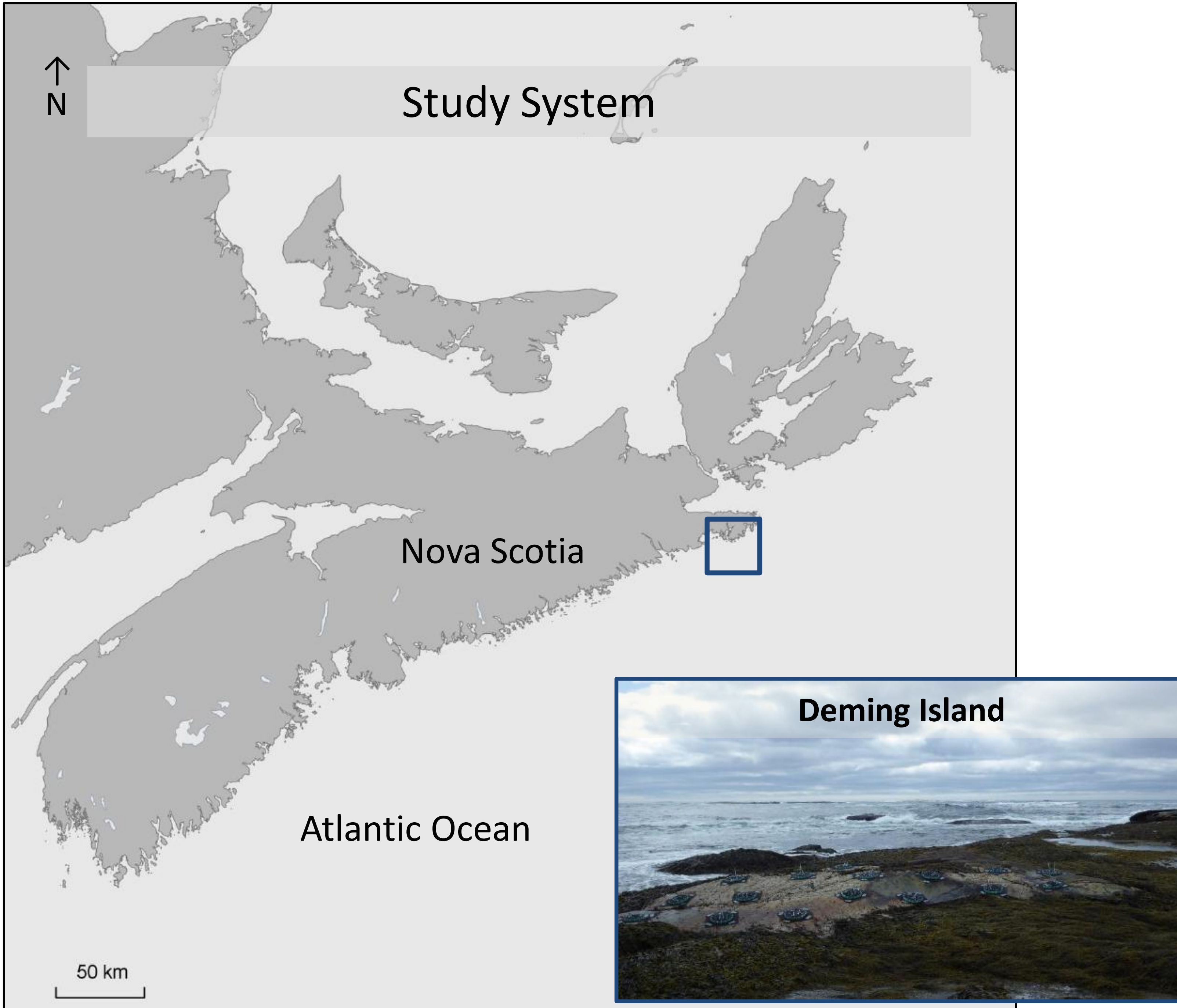
In presence of dogwhelk cues, mussels will thicken their shells but limit shell elongation.

Lab Experiment: Hypothesis

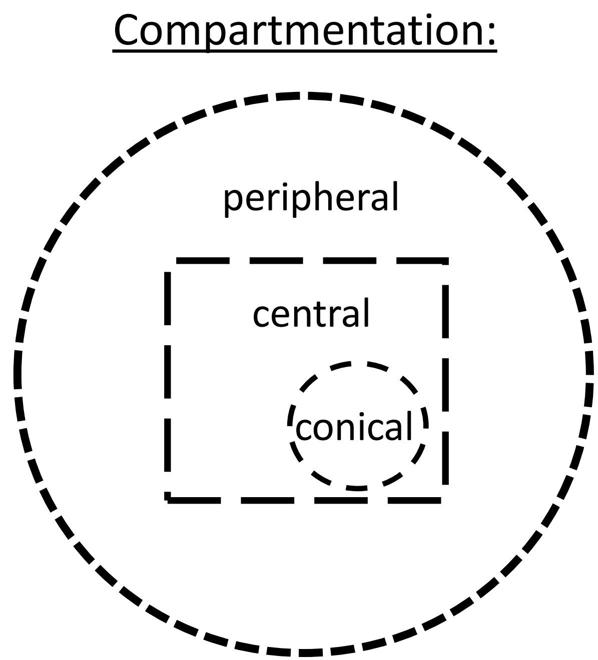


Dogwhelk cue-induced mussel shell thickening will increase the handling time required by a drilling predator.

Manipulative Field Experiment: Dogwhelk NCEs on Mussel Traits


Study System
N
Nova Scotia
Atlantic Ocean
50 km
Deming Island

Experimental Unit

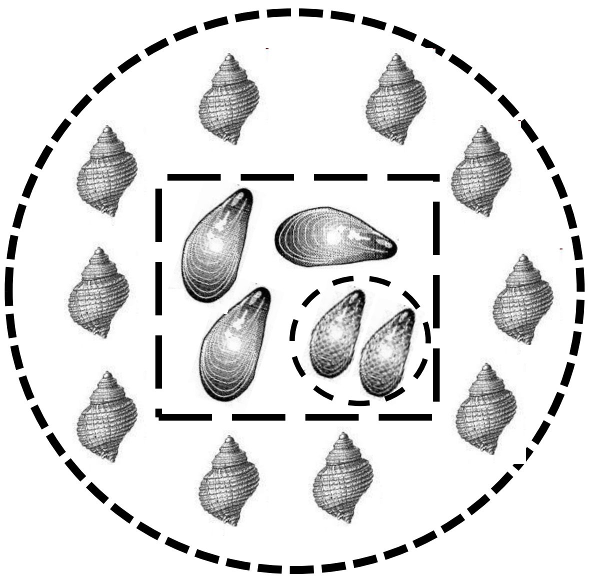


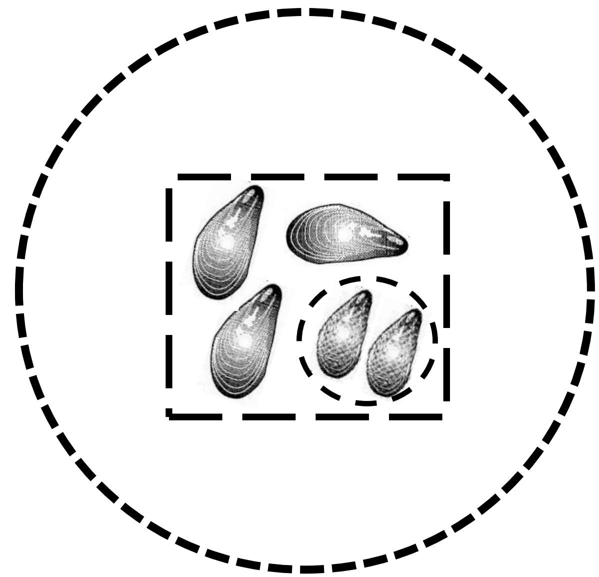
n= 60 cages, diameter: 25 cm, height: 2.5 cm

Predator Treatments

10 dogwhelks present

Dogwhelks absent





n= 30 replicates

n= 30 replicates

2 experimental mussels per conical compartment, average length: 1.86 ± 0.01 cm (± se)
18 mussels per central compartment, simulating a natural mussel patch

Randomized Complete Block Design

15 Blocks, each including 2 replicates of the 2 predator treatments = 60 cages

Dogwhelk Maintenance on a Mussel Diet

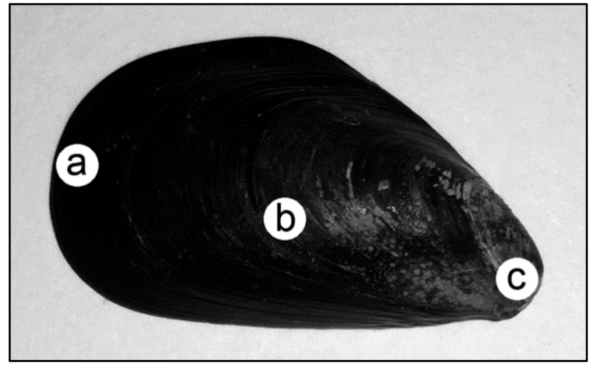
Supply cage containing dogwhelks and mussels.

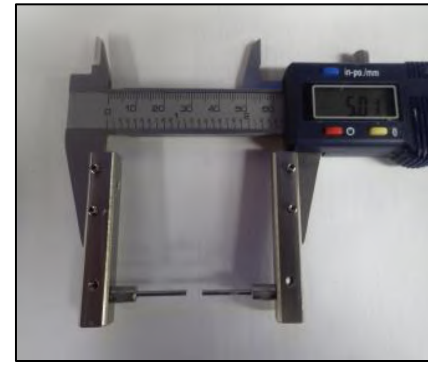
Starting the Field Experiment

Field Experiment: 06 June – 16 August 2016 (10 weeks)

Sampling Mussel Traits

Shell thickness measured at the **lip** (a) **center** (b) & **base** (c) of the mussel



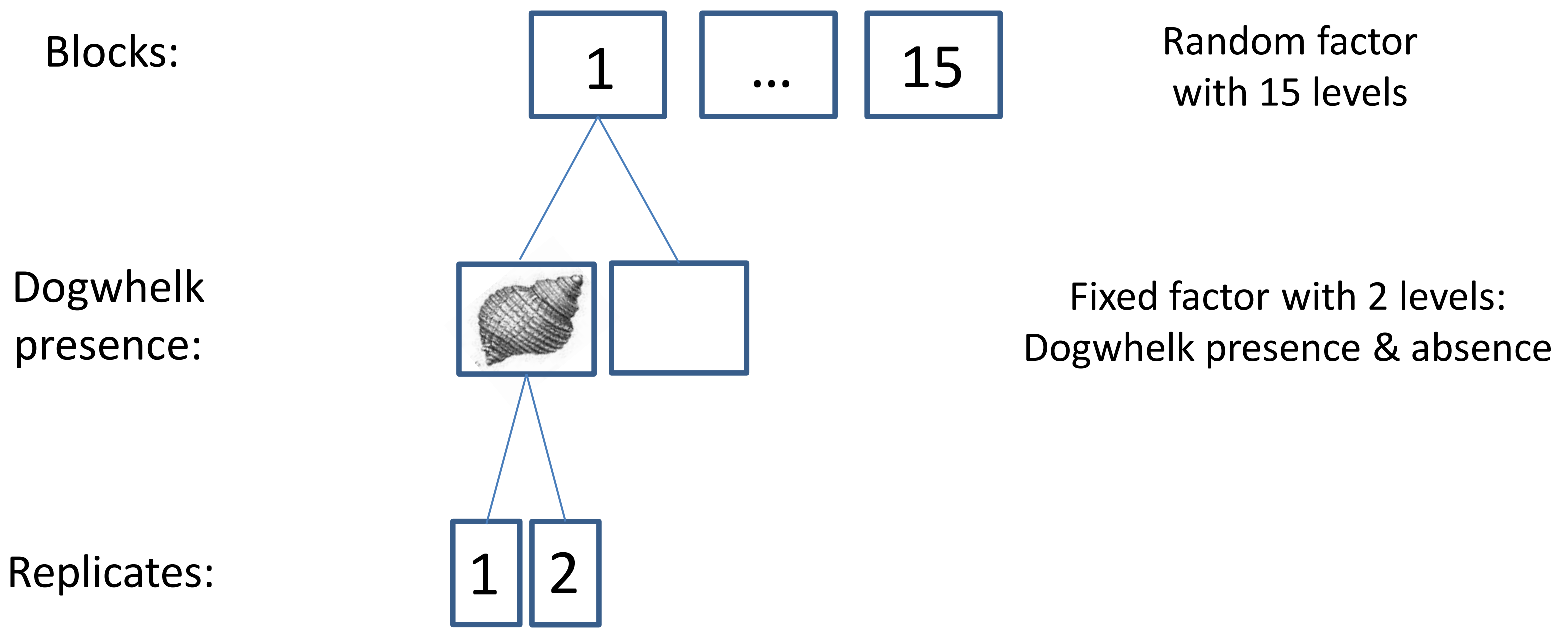


Shell length measured along the anterior-posterior axis of the mussel

Shell dry mass & **soft tissue dry mass measured** with a balance

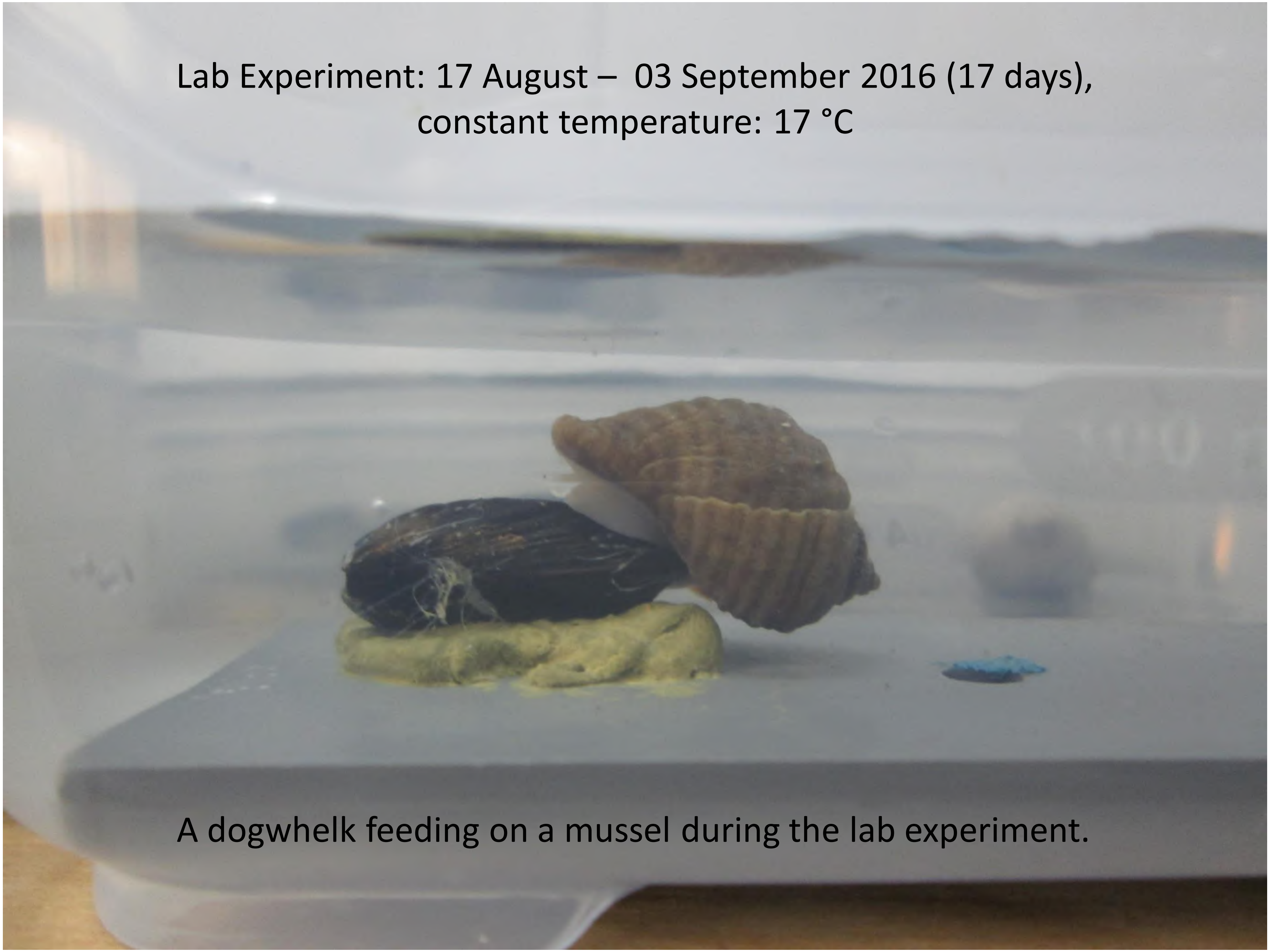
N= 30 mussels grown in **dogwhelk presence**
N= 30 mussels grown in **dogwhelk absence**

ANOVAs Examining Dogwhelk NCEs on Mussel Traits



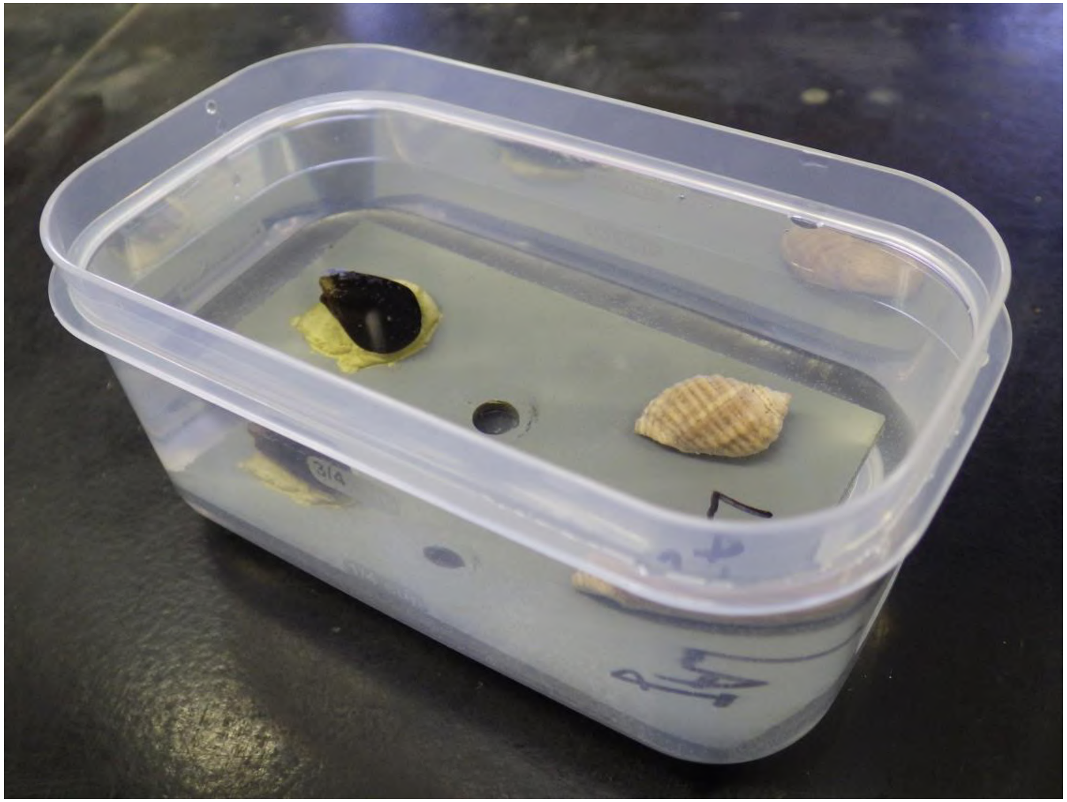
Mussel traits were analysed by 6 separate 2-factorial ANOVAs.

Manipulative Lab Experiment: Effects of Mussel Shell Thickness on Dogwhelk Handling Time



A dogwhelk feeding on a mussel during the lab experiment.

Experimental Unit

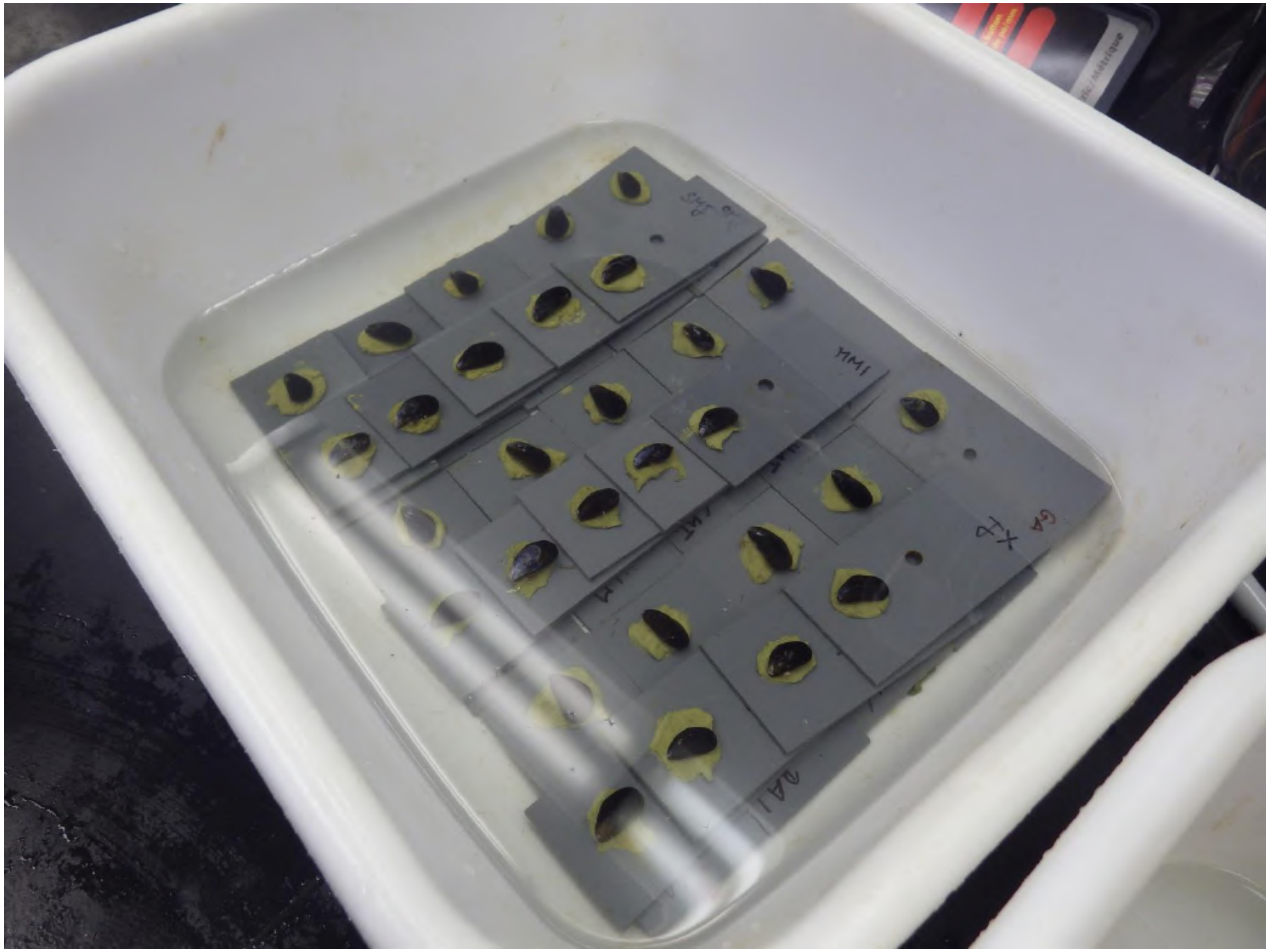


plastic container (250 ml seawater)

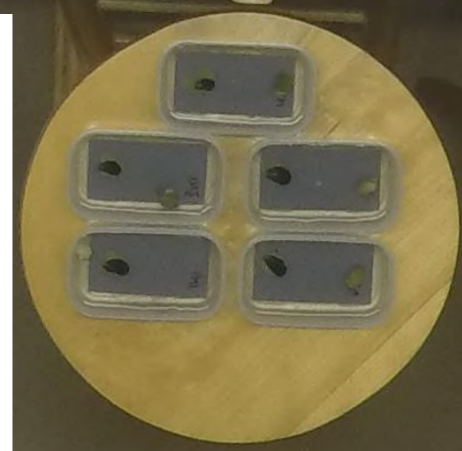
1 mussel attached to PVC tile

1 dogwhelk (2.22 ± 0.01 cm shell length), previously starved for 10 days

Preparing the Mussel Tiles



Complete Randomized Design



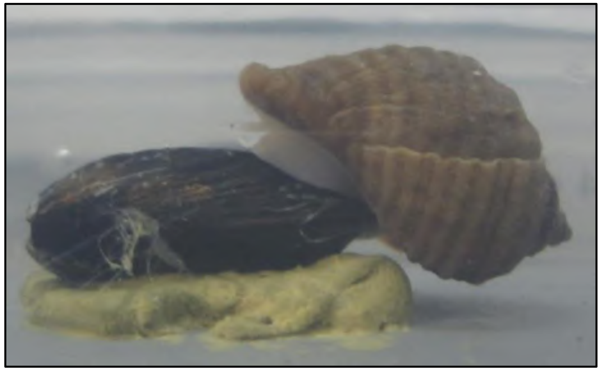
N= 26 mussels previously grown in **dogwhelk presence**

N= 22 mussels previously grown in **dogwhelk absence**

<u>GoPro camera monitoring:</u>

1 picture every 30 sec.

Handling Time
& Mussel Shell Thickness at the Borehole



Handling time:

The period between the moment when
the dogwhelk mounted the mussel and
the moment when the dogwhelk left the drill hole.

A *t*-test compared the handling times of mussels grown in dogwhelk presence and absence.

Mussel Shell Thickness at the Borehole:

A t-test compared shell thickness at the borehole of mussels grown in dogwhelk presence and absence.

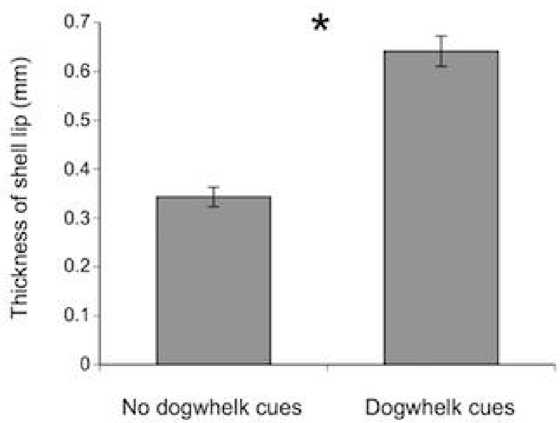
Comparing Mussel Shell Thickness at the Borehole With Shell Thickness in Intact Areas

Paired *t*-tests compared the shell thickness at the borehole with shell thickness in intact areas (5 randomly picked spots) in mussels grown in dogwhelk presence and absence.

Results

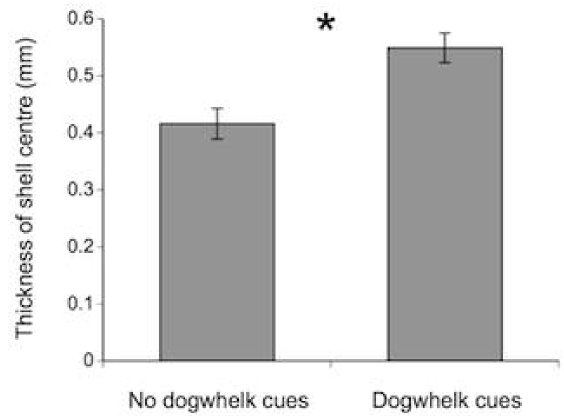
Field: Mussel Shell Thickening

87 %



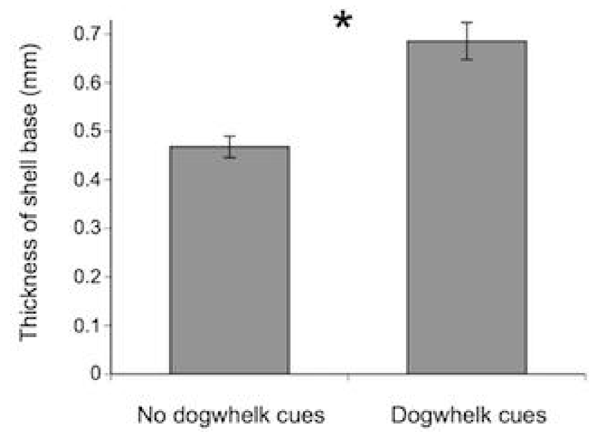
Shell Lip Thickness (mm)

32 %



Shell Centre Thickness (mm)

47 %

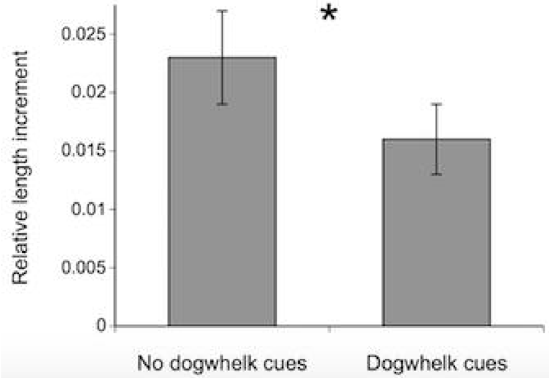


Shell Base Thickness (mm)

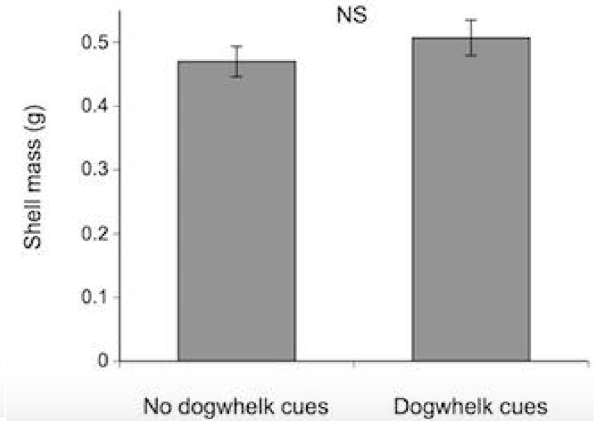
Dogwhelks cues induced shell thickening of the mussel lip, center and base, with most pronounced thickening in the thinnest part of the shells.

Sherker, Ellrich & Scrosati 2017 *Marine Ecology Progress Series*

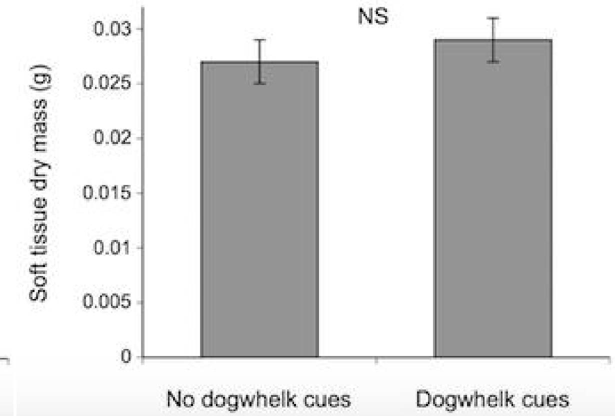
Field: Mussel Elongation, Shell Mass & Tissue Mass



Relative shell elongation



Shell mass (g)

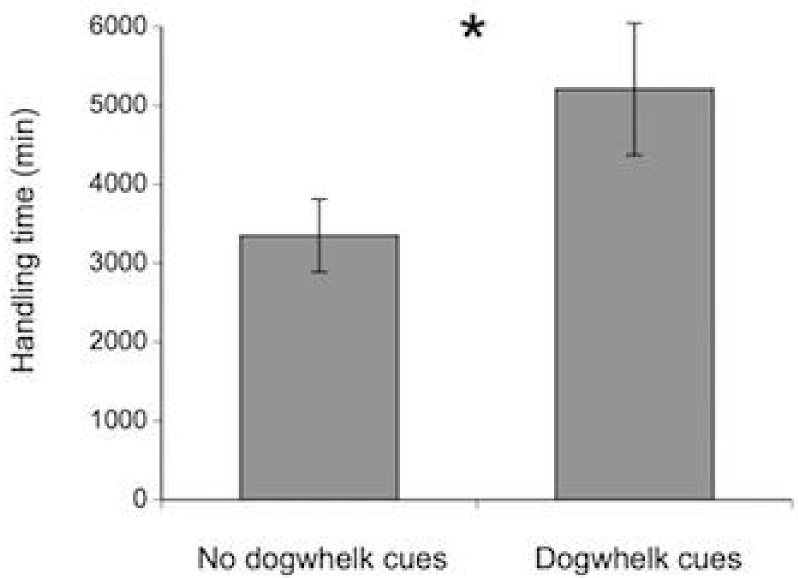


Soft tissue dry mass (g)

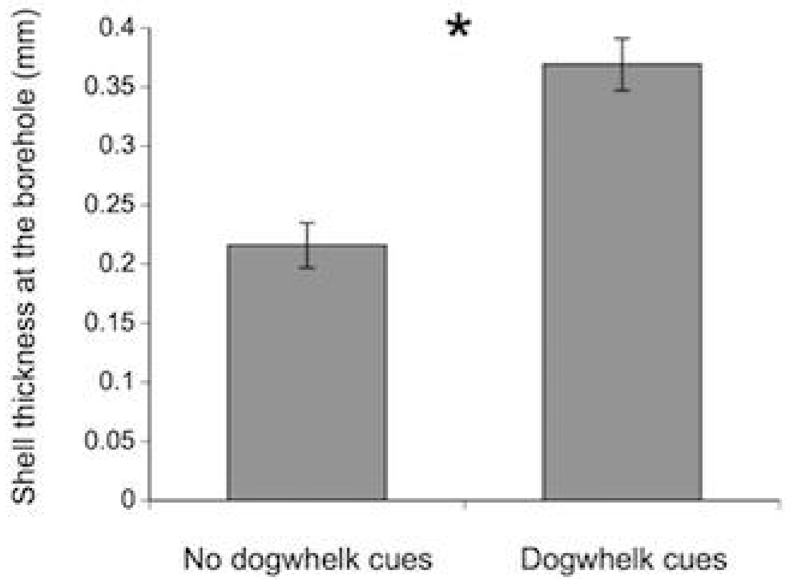
Dogwhelk cues limited shell elongation,
but did not affect shell mass & soft tissue dry mass,
indicating a trade of between shell thickening & elongation.

Sherker, Ellrich & Scrosati 2017 *Marine Ecology Progress Series*

Lab : Handling Time & Mussel Shell Thickness at the Borehole



Handling time (min)

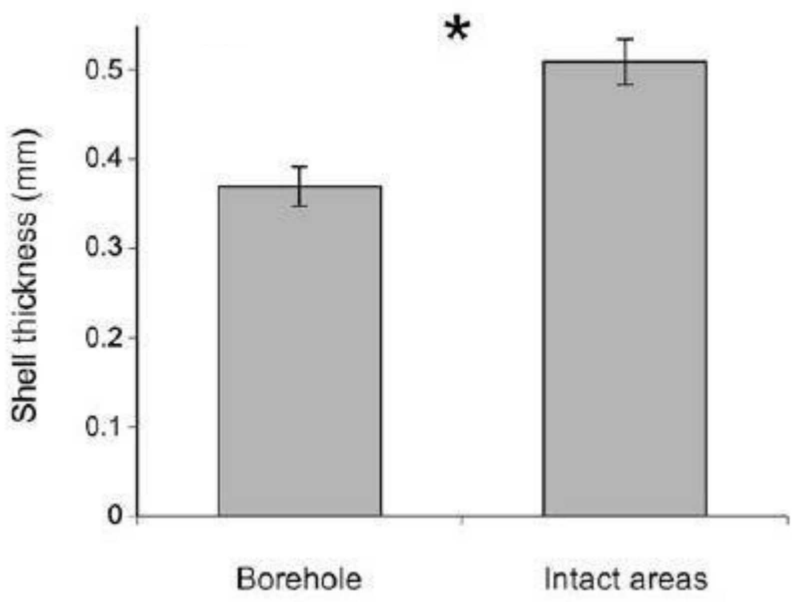


Shell thickness at the borehole (mm)

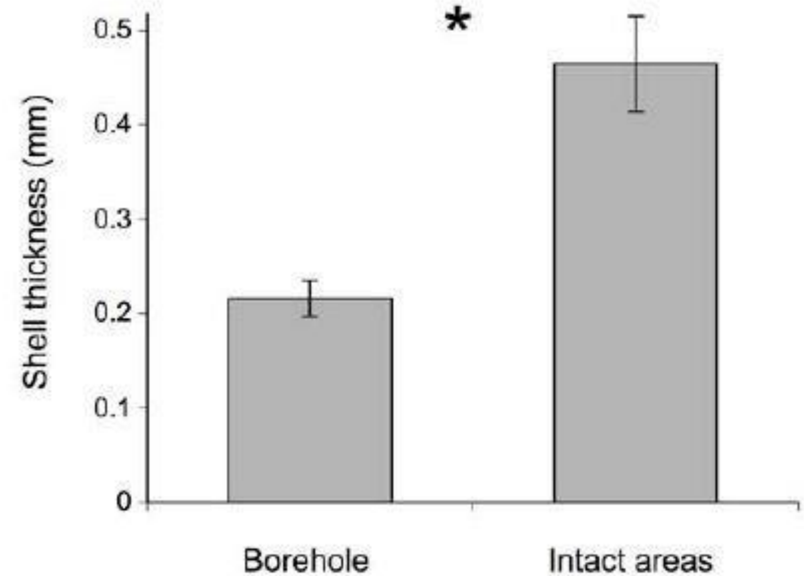
Dogwhelk handling time increased for mussels previously exposed to dogwhelk cues.
Consumed mussels previously exposed to dogwhelk cues had thicker shells than mussels unexposed to dogwhelk cues.

Sherker, Ellrich & Scrosati 2017 *Marine Ecology Progress Series*

Lab :
Comparing Mussel Shell Thickness at the Borehole With Shell Thickness in Intact Areas



Mussels grown in
dogwhelk presence



Mussels grown in
dogwhelk absence

Dogwhelks consistently drilled mussels in areas of low thickness.

Sherker, Ellrich & Scrosati 2017 *Marine Ecology Progress Series*

Conclusions

Exposed to dogwhelk cues, mussels increased shell thickness & limited elongation,
(but did not change shell mass & soft tissue dry mass)

→ *trade-off between shell thickening and elongation*

Shell thickening occurs throughout the entire mussel shell,
but varies across the shell with most pronounced thickening in the thinnest areas

→ *potentially the parts most vulnerable to predation*

Mussel shell thickening increased dogwhelk handling time (by 55 %)

→ *reveals that drilling predators are hindered*

Future research on European shores could examine if dogwhelk NCEs differ to some extent between *M. edulis, M. trossulus* & the European *M. galloprovincialis* to examine the generality of the findings.

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https://doi.org/10.3354/meps12194

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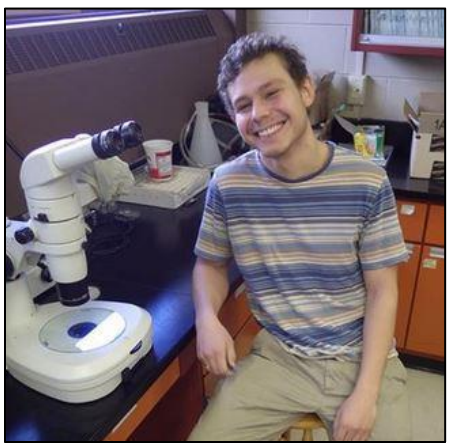
Published June 21

Predator-induced shell plasticity in mussels hinders predation by drilling snails

Zachary T. Sherker, Julius A. Ellrich, Ricardo A. Scrosati*

Department of Biology, St. Francis Xavier University, 2320 Notre Dame Avenue, Antigonish, Nova Scotia B2G 2W5, Canada

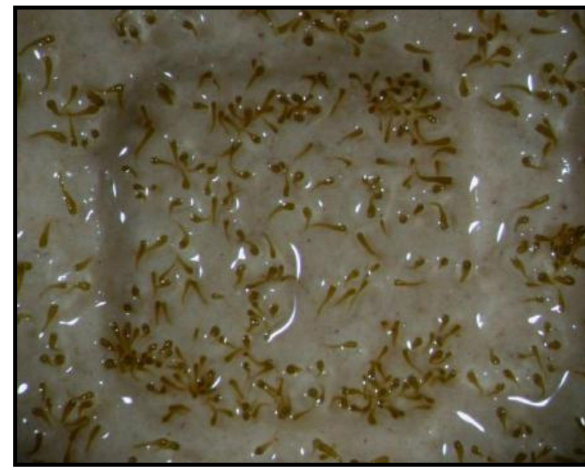


Zachary Sherker

Julius Ellrich

Ricardo Scrosati

Predator Nonconsumptive Effects & Trait-Mediated Indirect Interactions in Intertidal Systems



IV. Trait-Mediated Indirect Interactions in Benthic Food Chains

Predator Consumptive & Nonconsumptive Effects

Predation

Predator cues

Direct effects

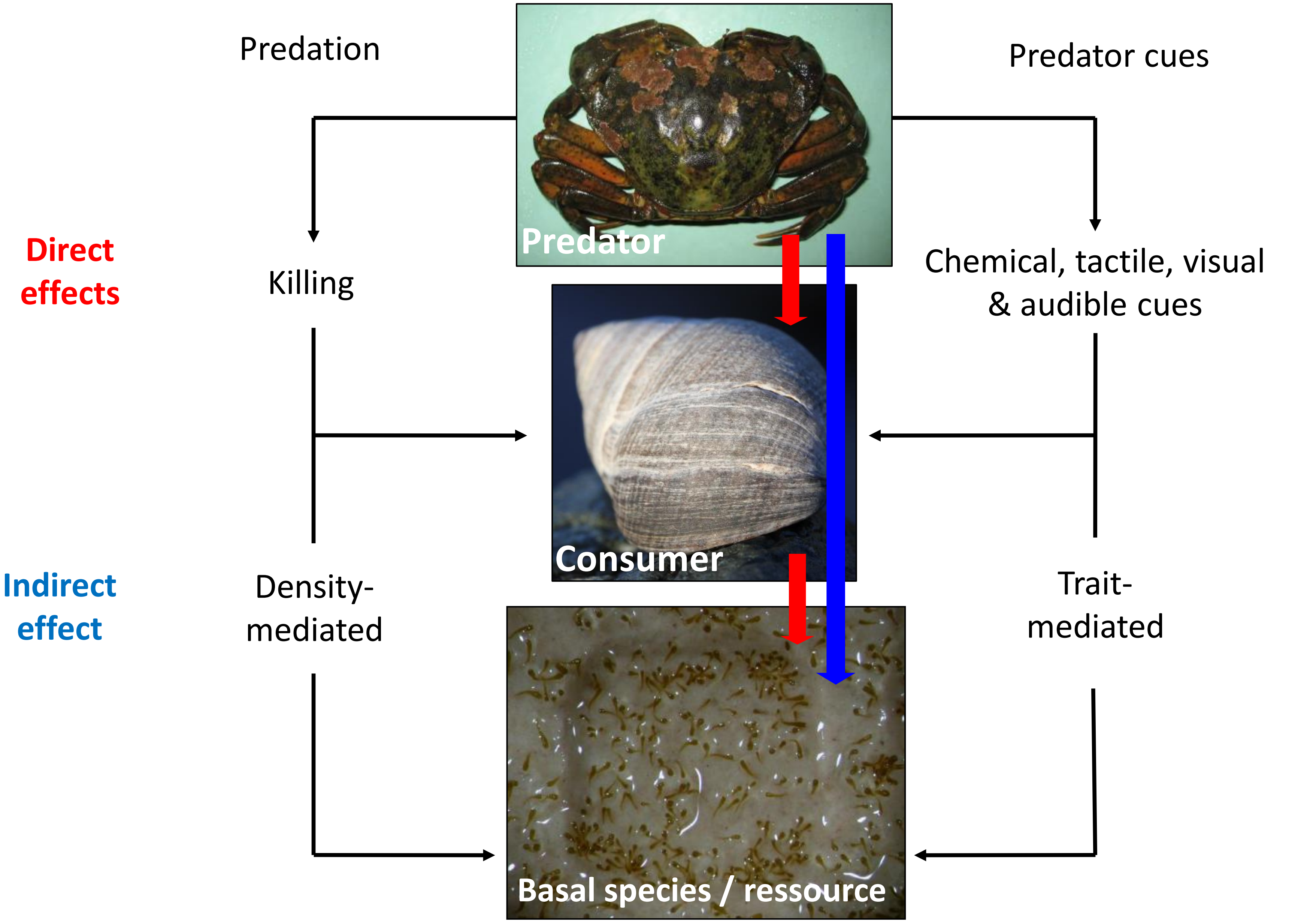
Killing

Chemical, tactile, visual & audible cues

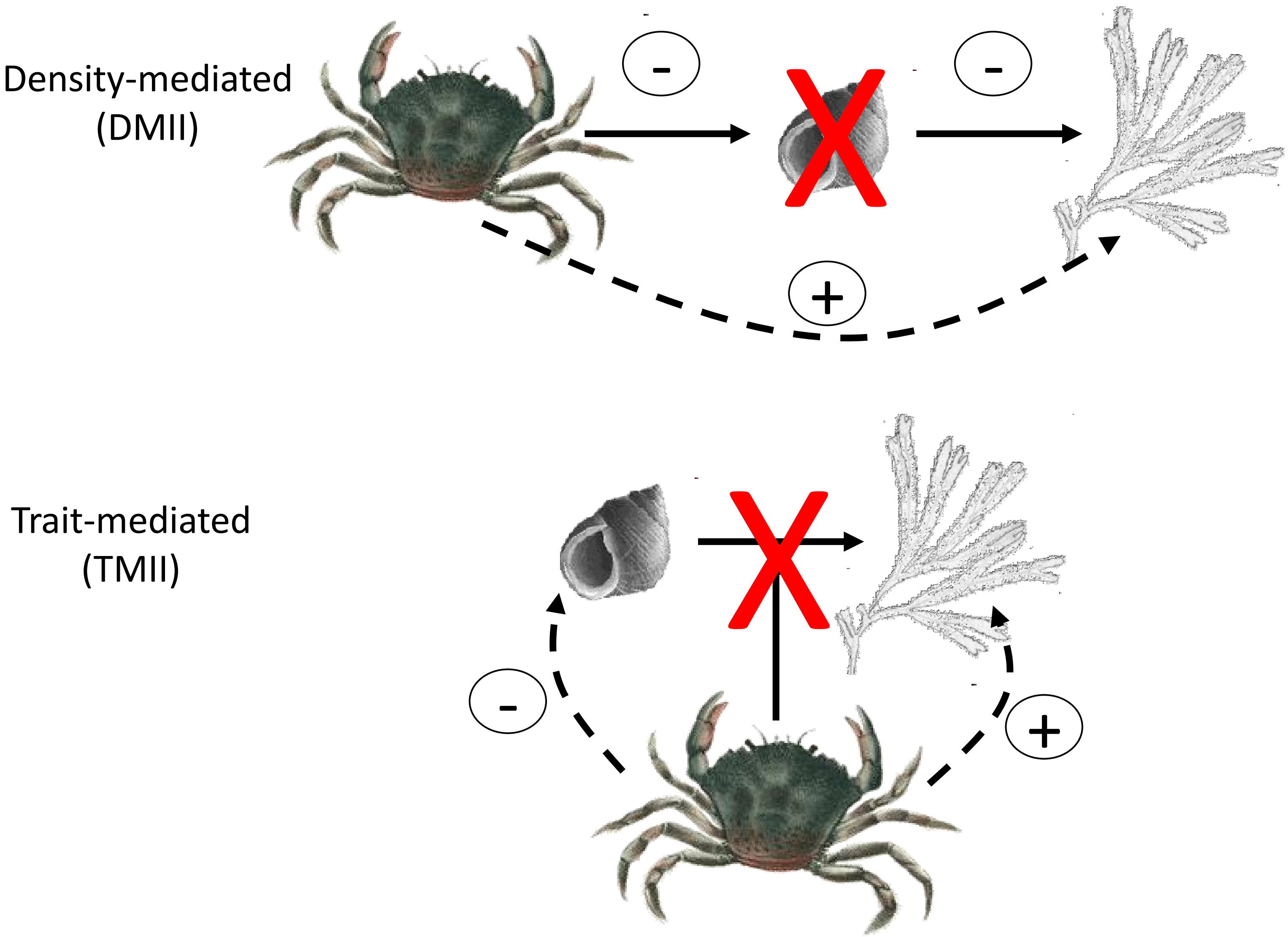
Changes in prey traits:
(prey responses)

- Behaviour, activity, physiology
- Habitat shift, reproductive output
- Morphology
- Demography

Density- & Trait-Mediated Indirect Interactions (DMII, TMII)



Indirect Interactions

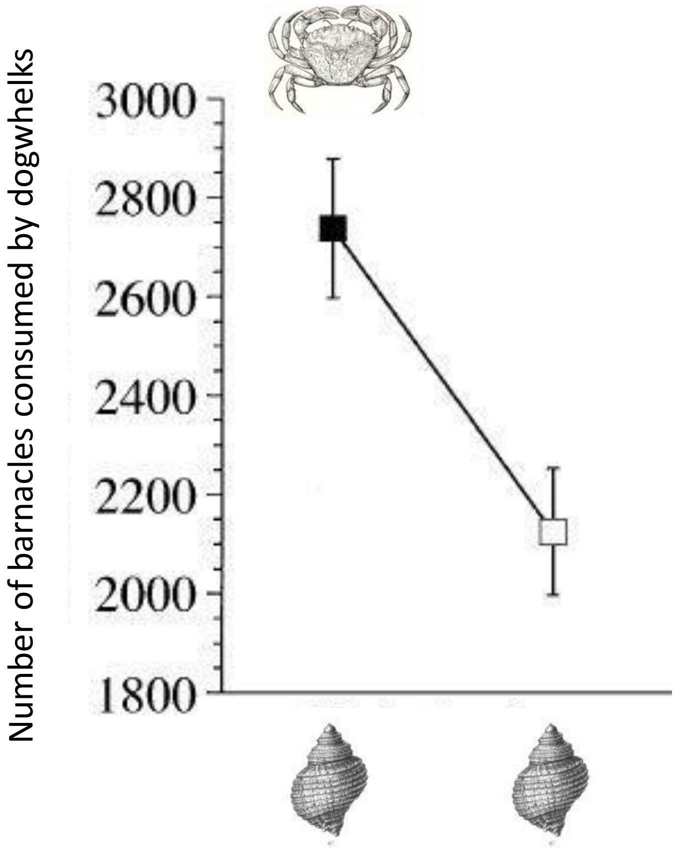


Predator NCEs limit prey feeding activity

Predator: green crab, *Carcinus maenas*

Crab prey: dogwhelk, *Nucella lapillus*

Dogwhelk prey: barnacle, *Semibalanus balanoides*



Dogwhelks reduce feeding activity when exposed to predator cues.

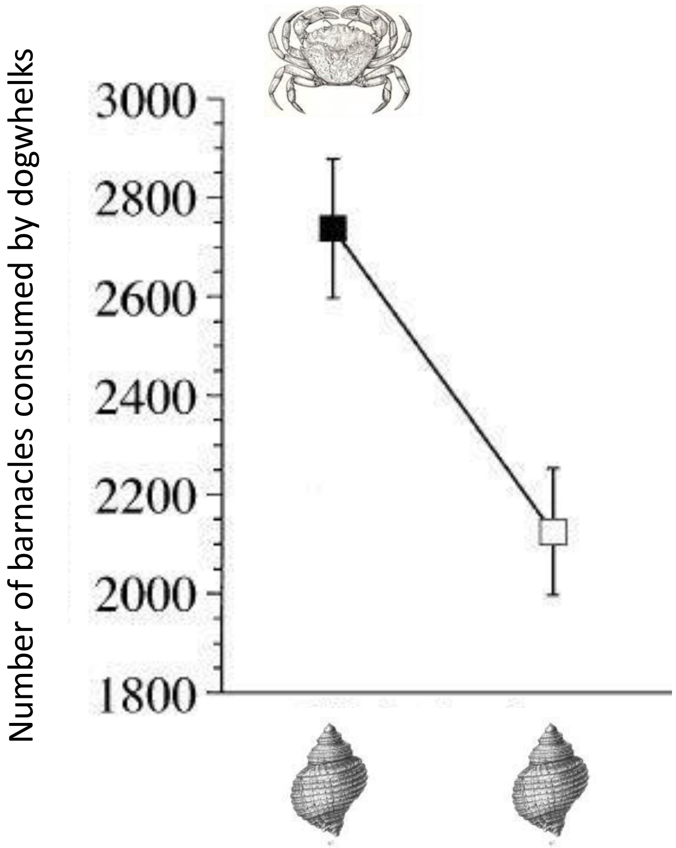
Trussell et al. 2003

TMII: Thereby, Predator NCEs Indirectly Increase Basal Species Survival

Predator: green crab,
Carcinus maenas

Crab prey: dogwhelk,
Nucella lapillus

Dogwhelk prey: barnacle,
Semibalanus balanoides



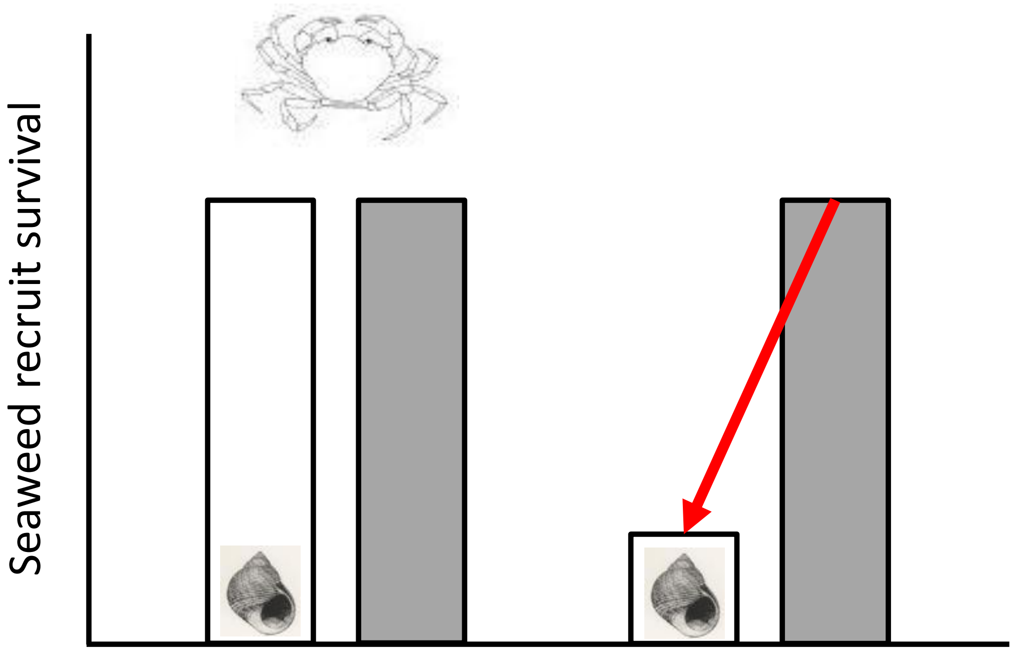
The predator cue-induced feeding reduction in dogwhelks indirectly increases barnacle survival.

Trussell et al. 2003

Research Question:

Do TMIIs occur in the ”green crab – periwinkle – seaweed” food chain from Helgoland, NE Atlantic?

Prediction



TMII: Green crab cues limit periwinkle feeding activity and, thus, indirectly enhance seaweed recruit survival.

Study System

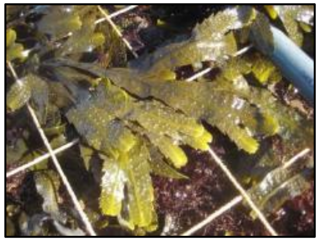
North East Atlantic

Picture: https://en.wikipedia.org/wiki/Heligoland#/media/File:Helgoland_Vogelperspektive_sx.jpg

Field Collection of Green Crabs, Periwinkles & Seaweeds at Nordostwatt, Helgoland

Predator: green crab,
Carcinus maenas

Consumers: periwinkles,
Littorina littorea



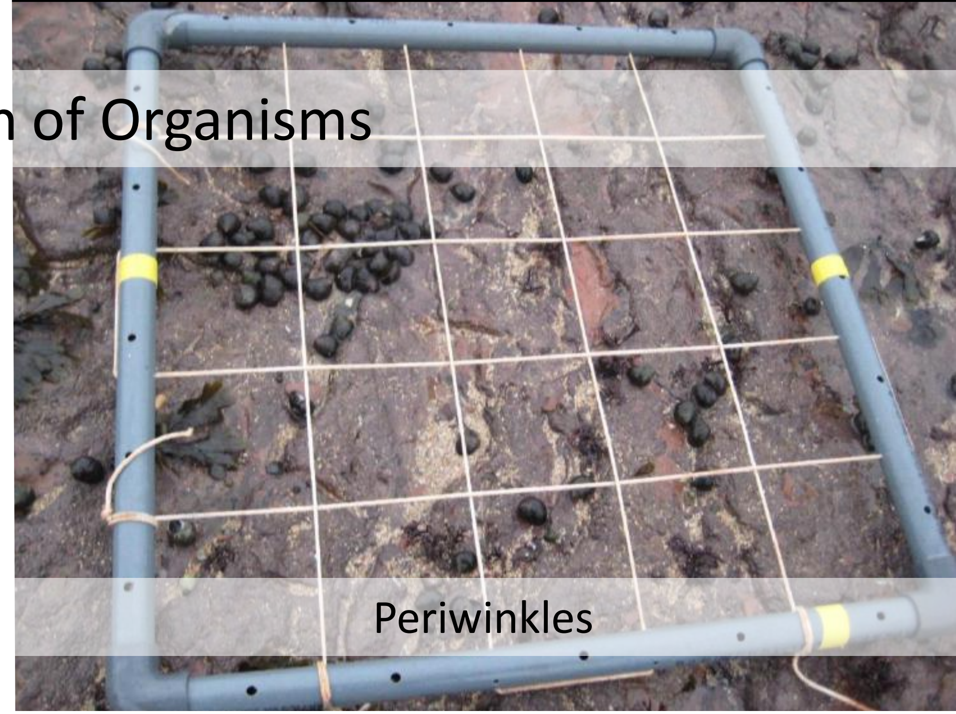
Basal species: seaweed,
Fucus serratus

Low & High Tide, Nordostwatt, Helgoland

Pictures: Thorsten Stegmann, https://naturfotografen-forum.de/o30849-Ebbe%20und%20Flut

Field Collection of Organisms

Crap trap



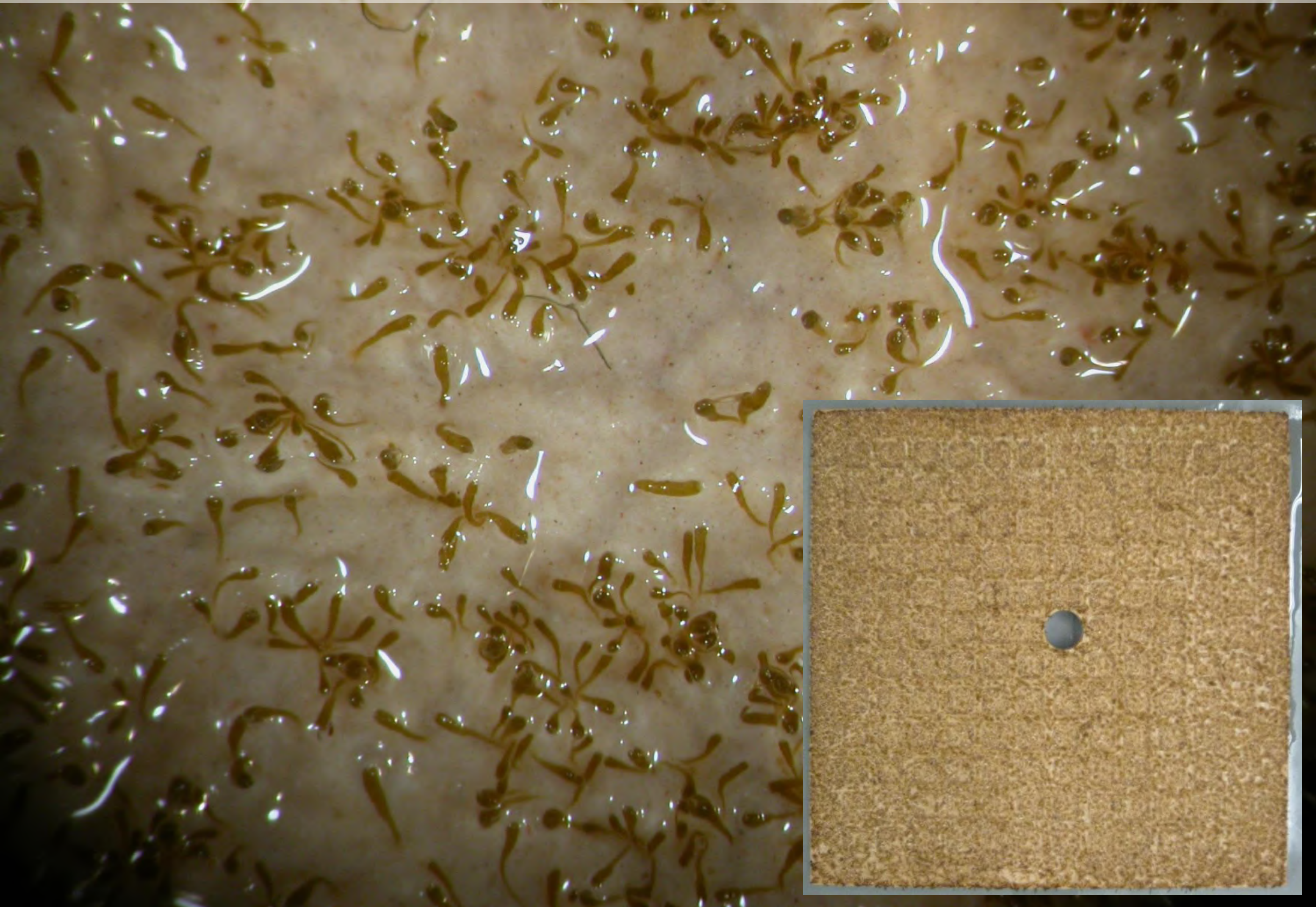
Periwinkles

Green crabs

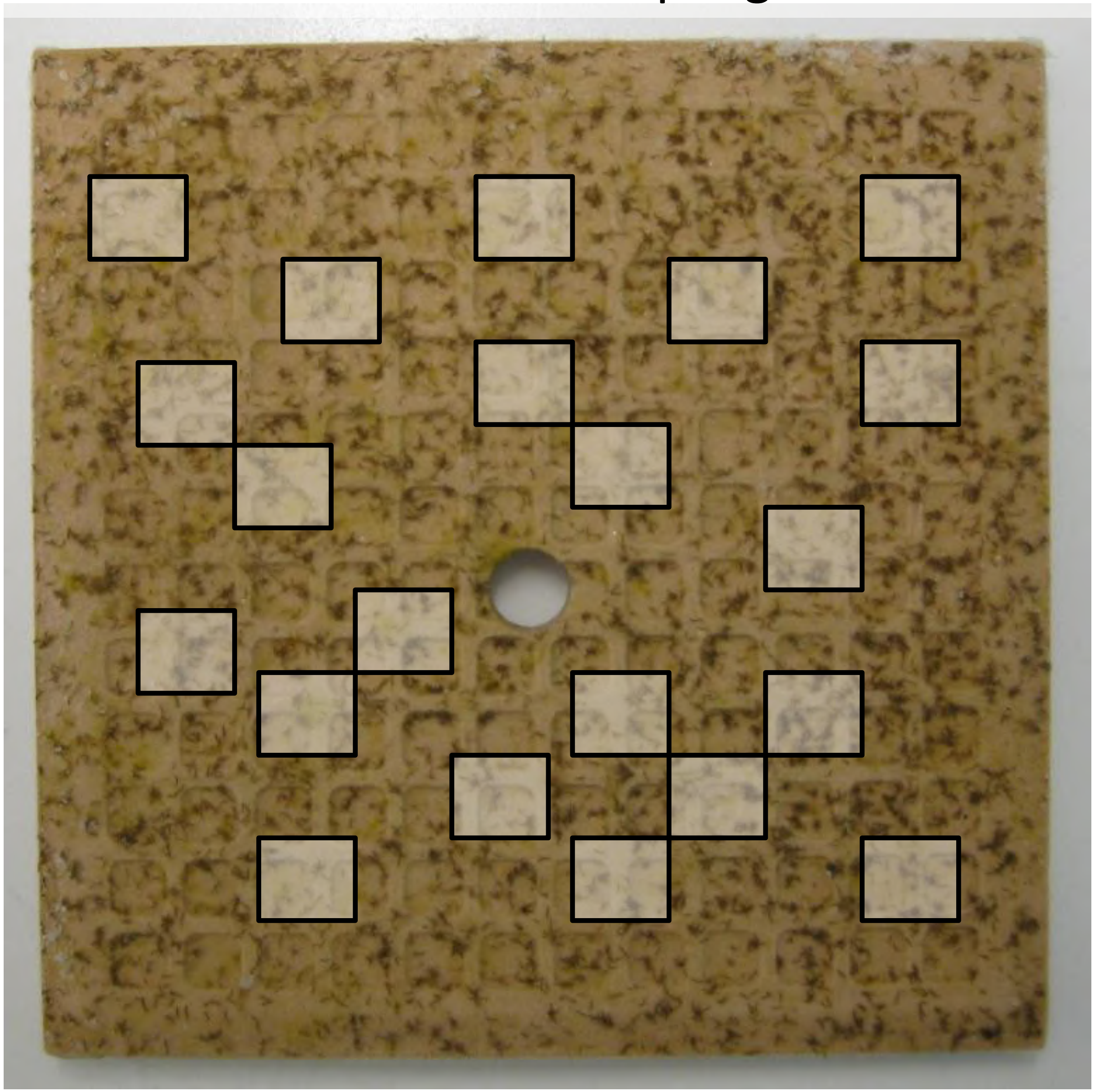
Seaweeds


Seaweed Recruit Cultivation
Seaweed collection
Separating male & female individuals
Freshwater triggered gamete release
Seaweed cultivation chamber

Seaweed Recruits (12 x Magnification)



Seaweed Sampling



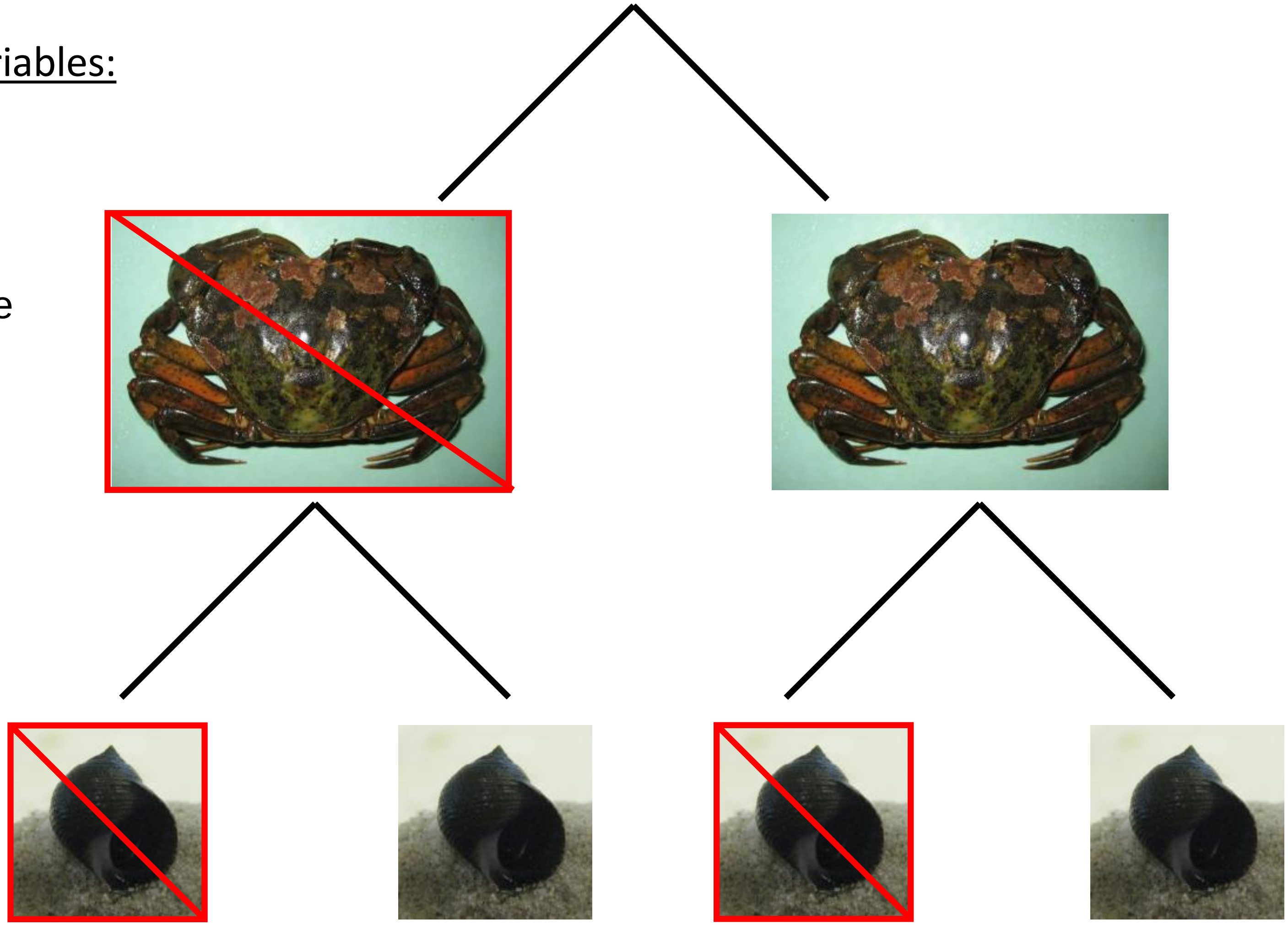
Seaweed survival (%) = final recruit density/initial recruit density *100

Manipulative Lab Experiment

Factorial Design

Independent variables:

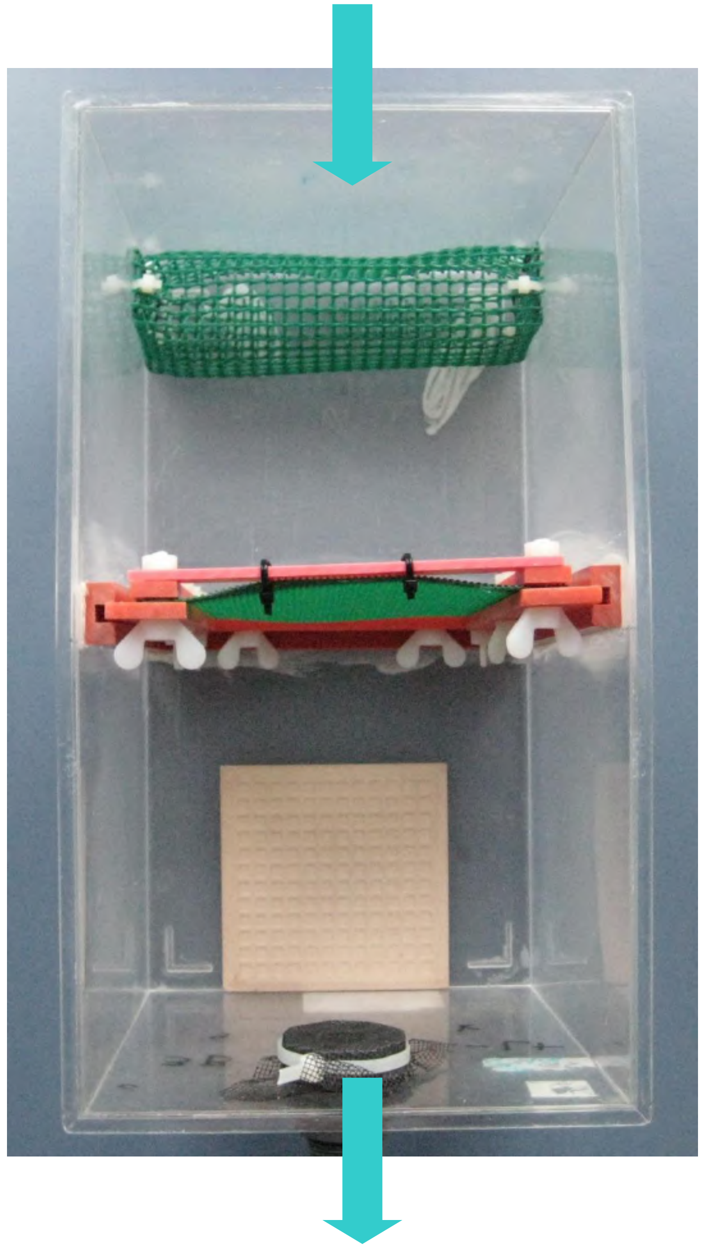
Predator presence
fixed factor
2 levels



Consumer presence,
fixed factor,
2 levels

Dependent variable: seaweed recruit survival (%)

Experimental Unit



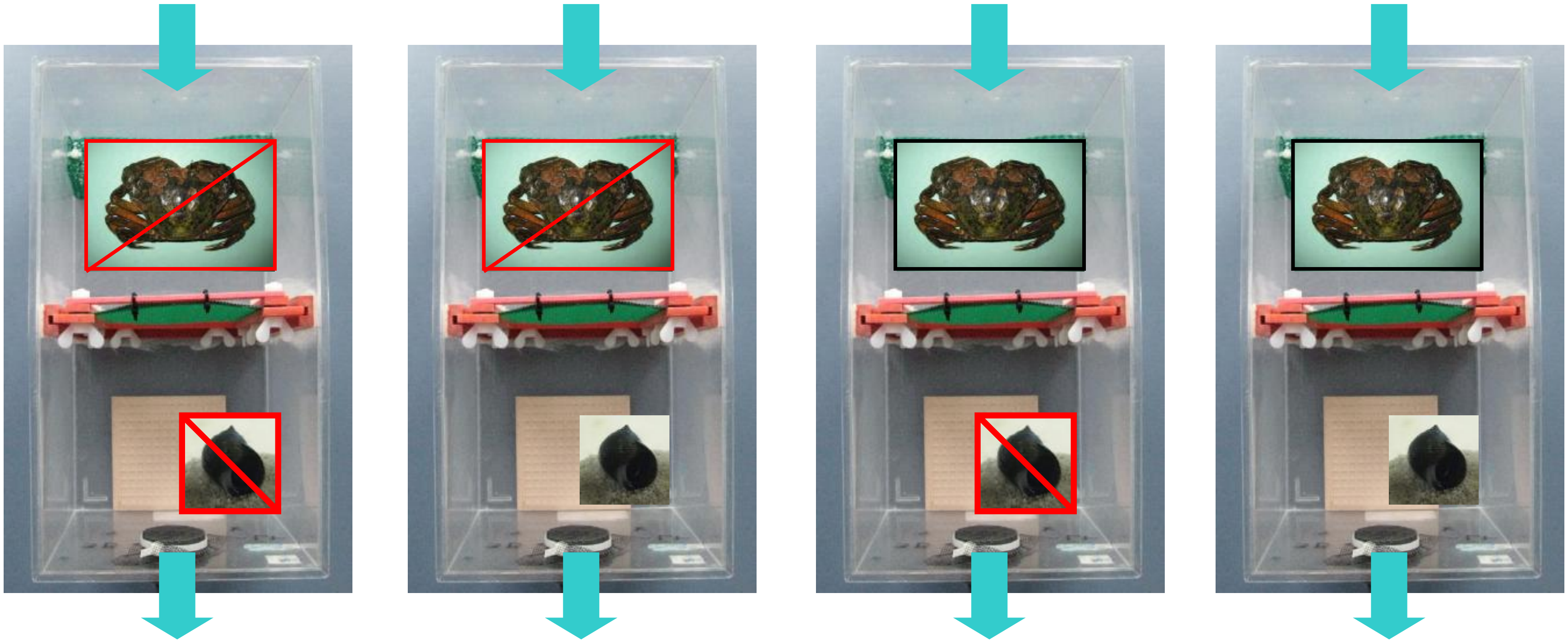
Predator compartment

Mesh divider

Consumer compartment with seaweed tile

Unidirectional water flow

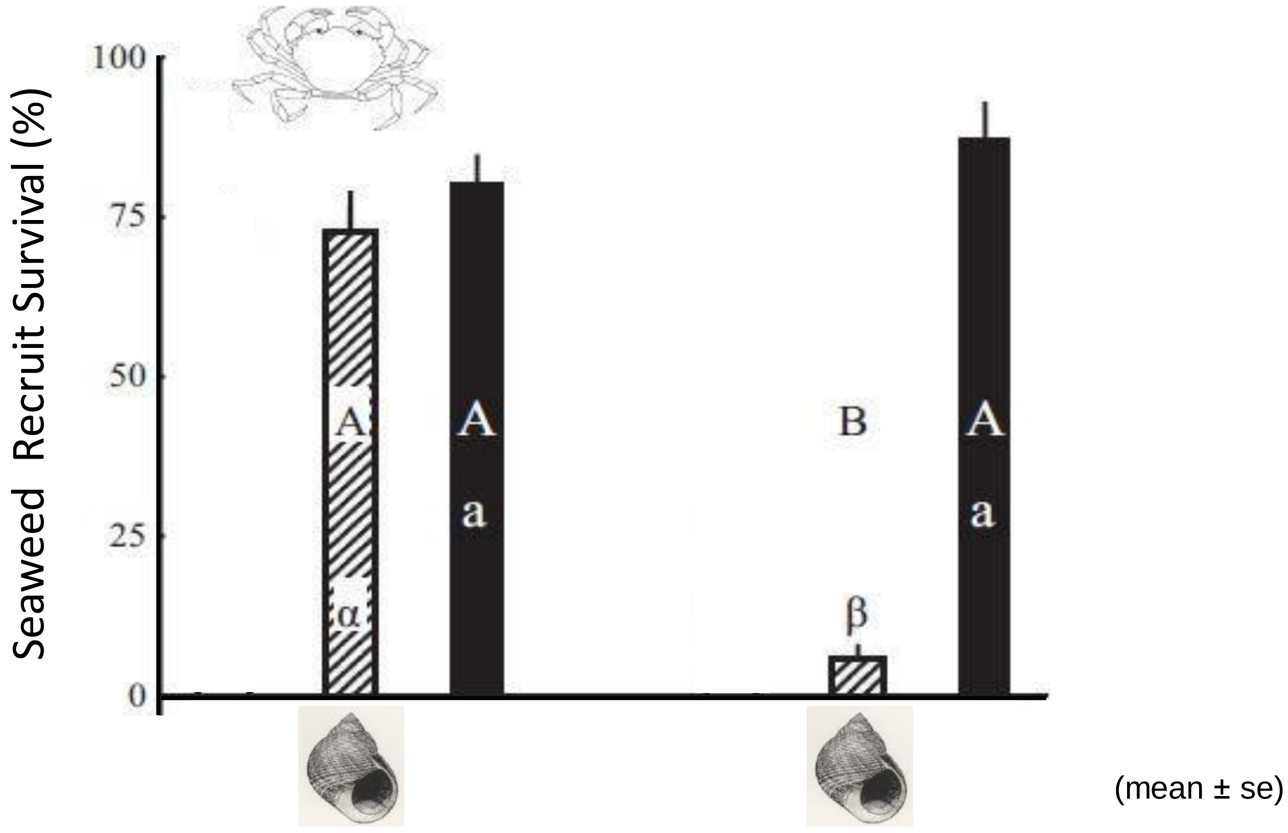
Treatments



10 replicates, summer 2008

Lab Setup, Complete Randomized Design, Summer 2008

Lab Results, Summer 2008

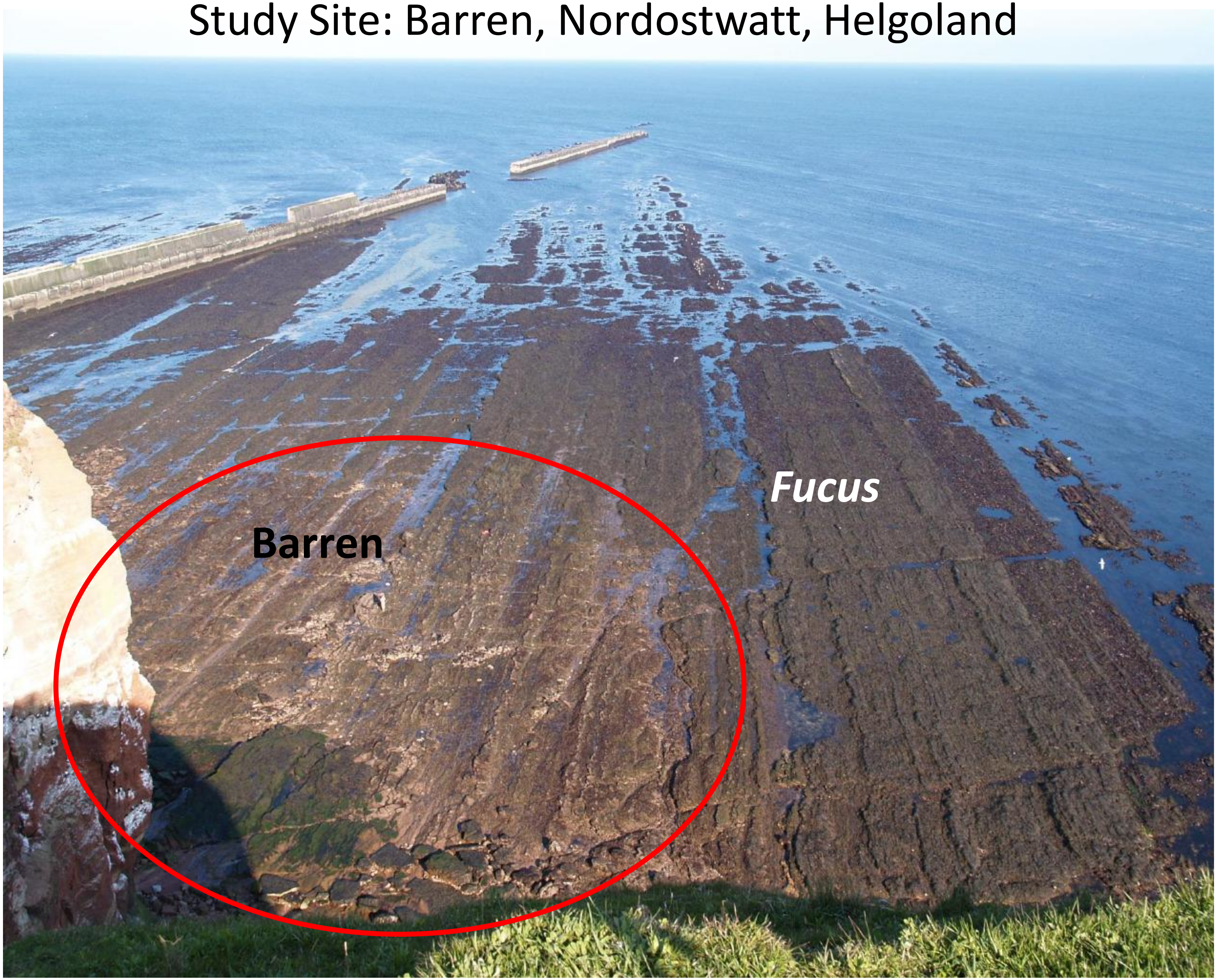


TMII: Predator cues limited consumer feeding activity and, thus, indirectly enhanced seaweed recruit survival.

Molis et al. 2011, Journal of Ecology

Manipulative Field Experiments

Study Site: Barren, Nordostwatt, Helgoland

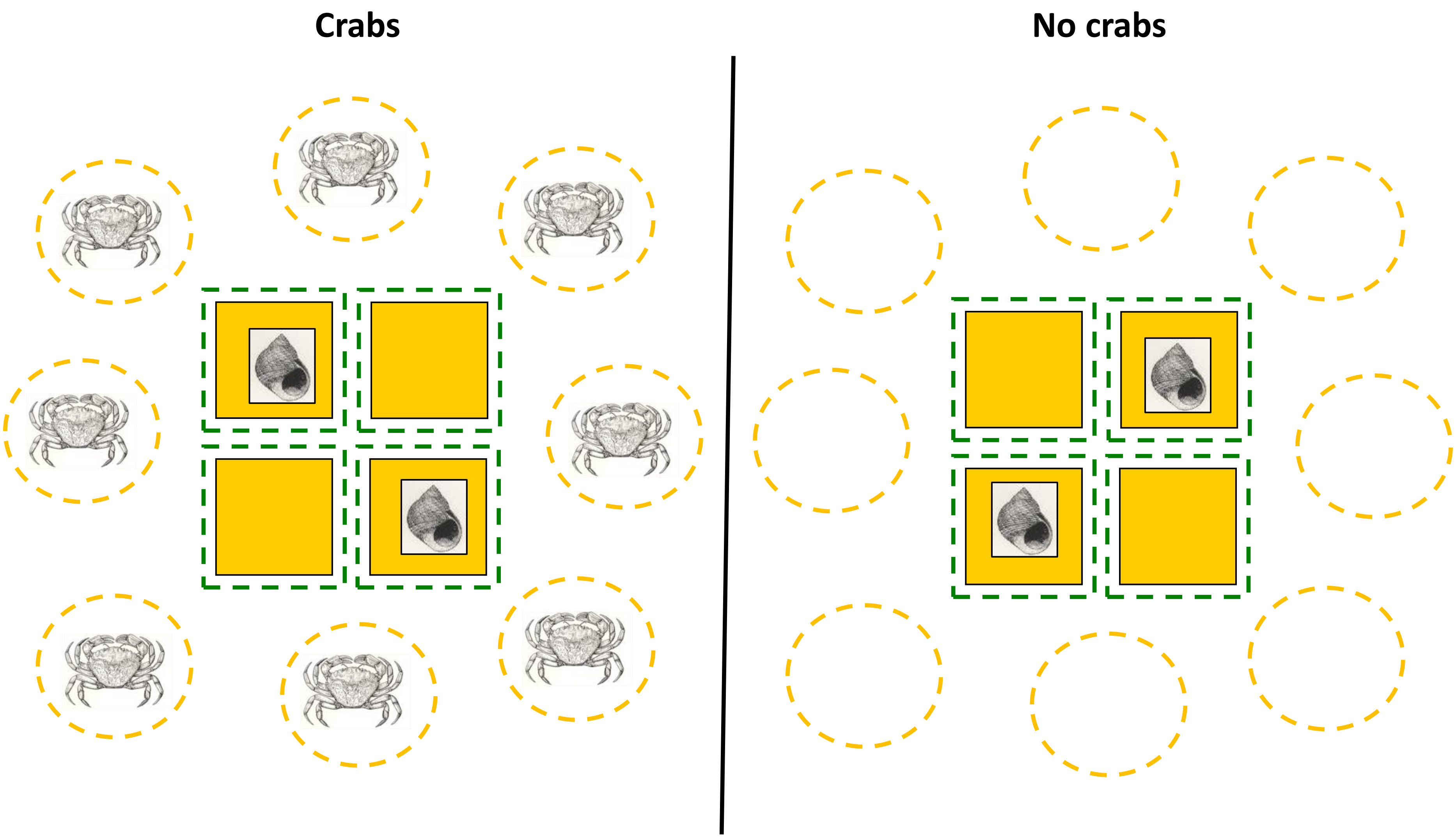


Picture: Andreas Wagner, 2008

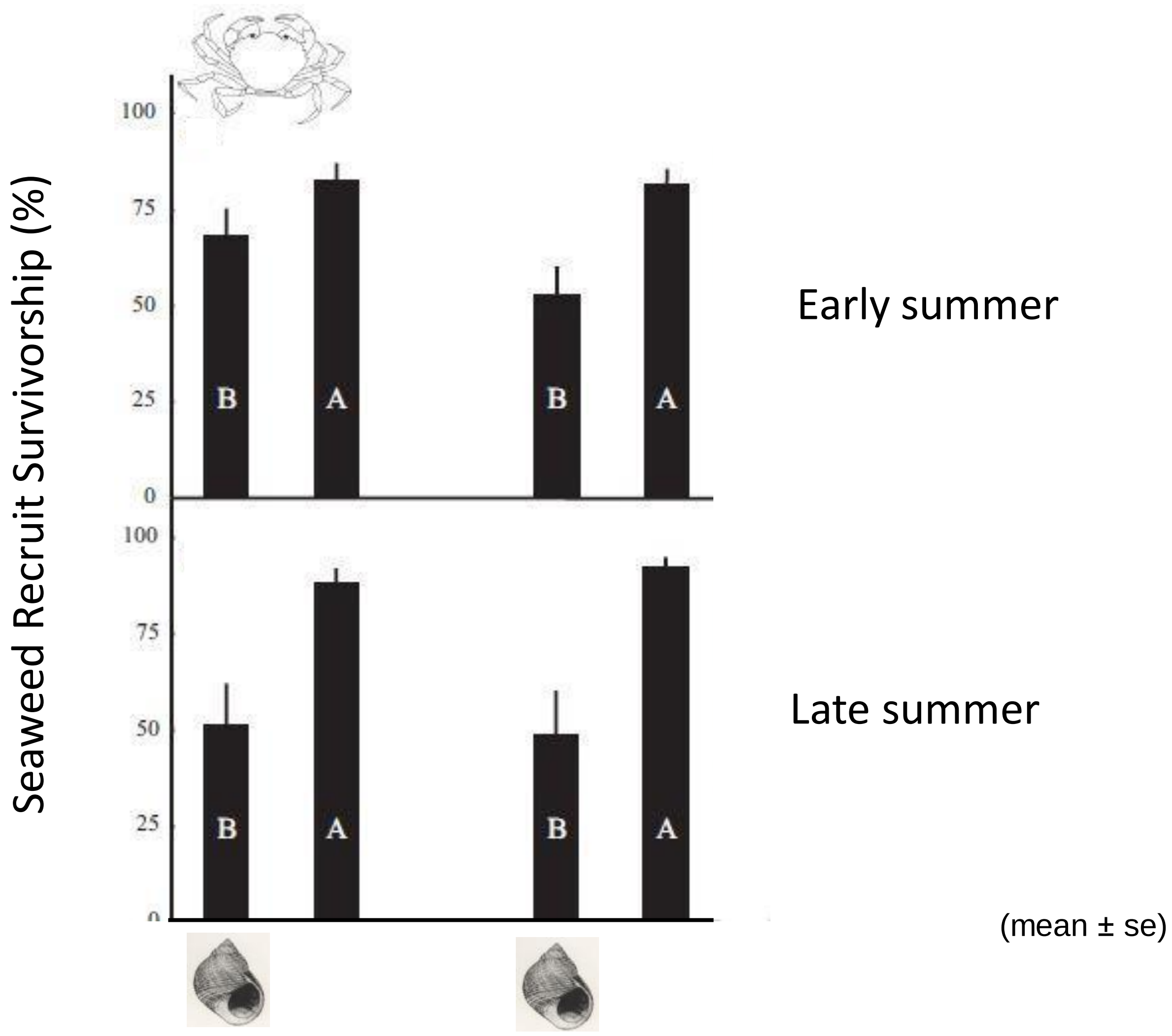
Open Plot Setup, Nested Design, Summer 2008

Picture: Markus Molis, 2008

Predator Presence & Absence



Field Results: Open Plot Setup



No TMII: Predator cues did not limit consumer feeding activity.

Molis et al. 2011, Journal of Ecology

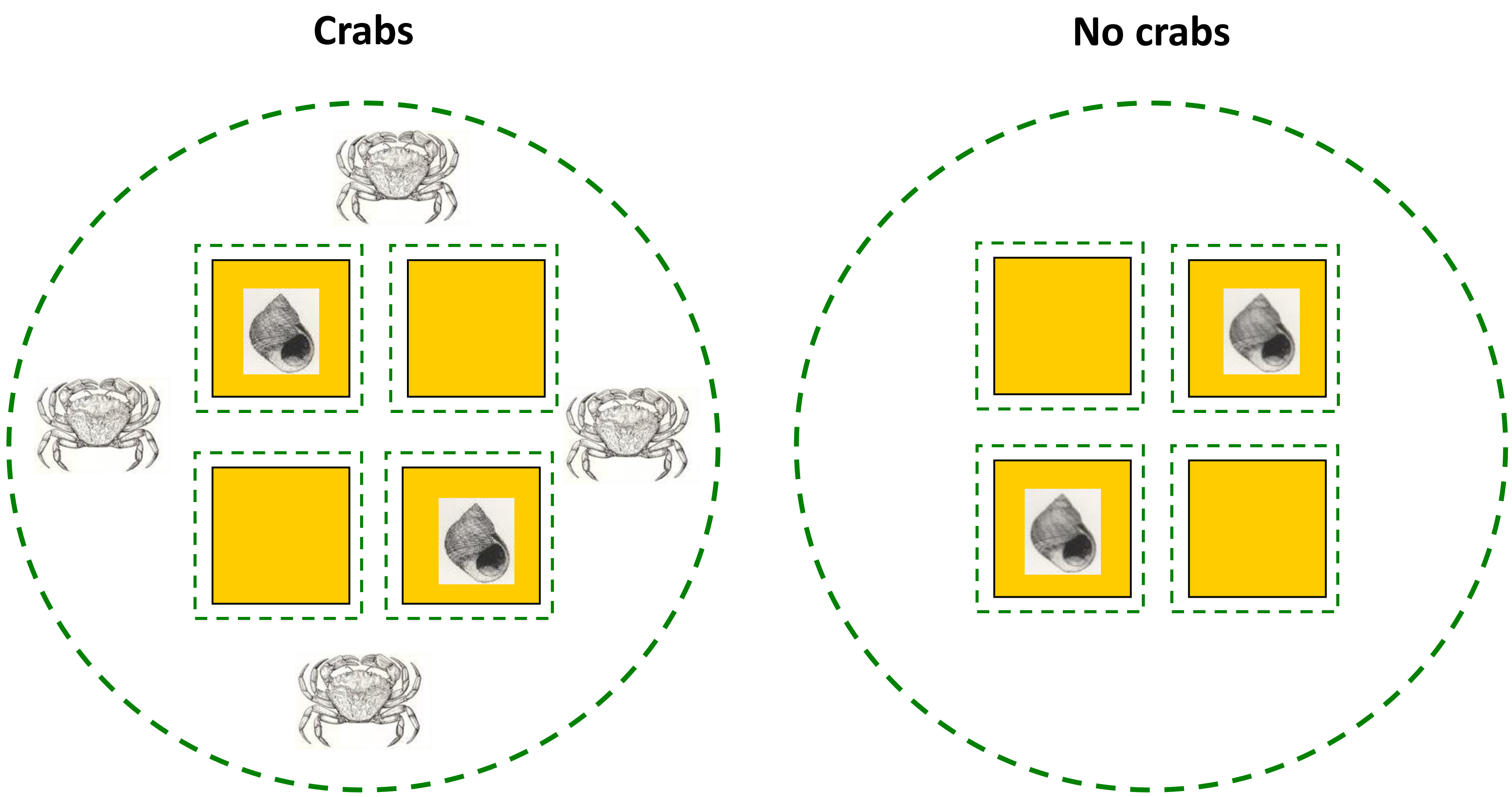
Was the Lack of a TMII Caused by Tresspassing Wild Crabs?

Picture: Markus Molis, 2008

Measurements of Wild Green Crab Activity

On average: 12 green crabs / day

Predator Presence & Absence: Wild Crab Exclusion Plots

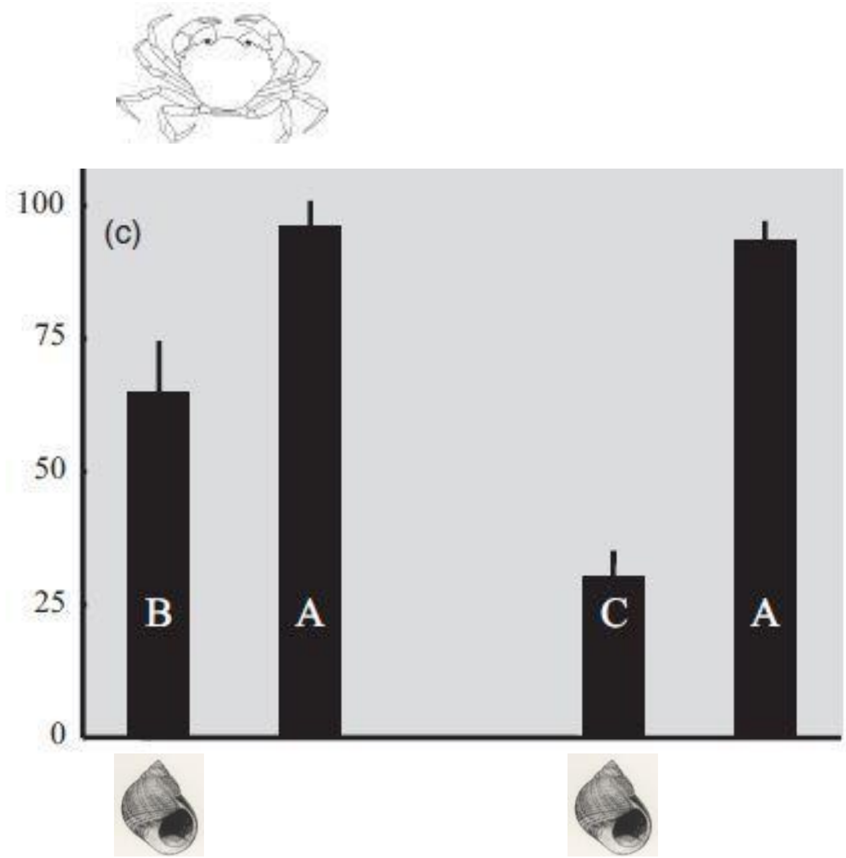


”5 crab plots ” & ” 5 no crab plots ”, summer 2009

Wild Crab Exlusion Plots

Wild Crab Exclusion Plots, Nordostwatt, Helgoland

Field Results: Wild Crab Exclusion Plots



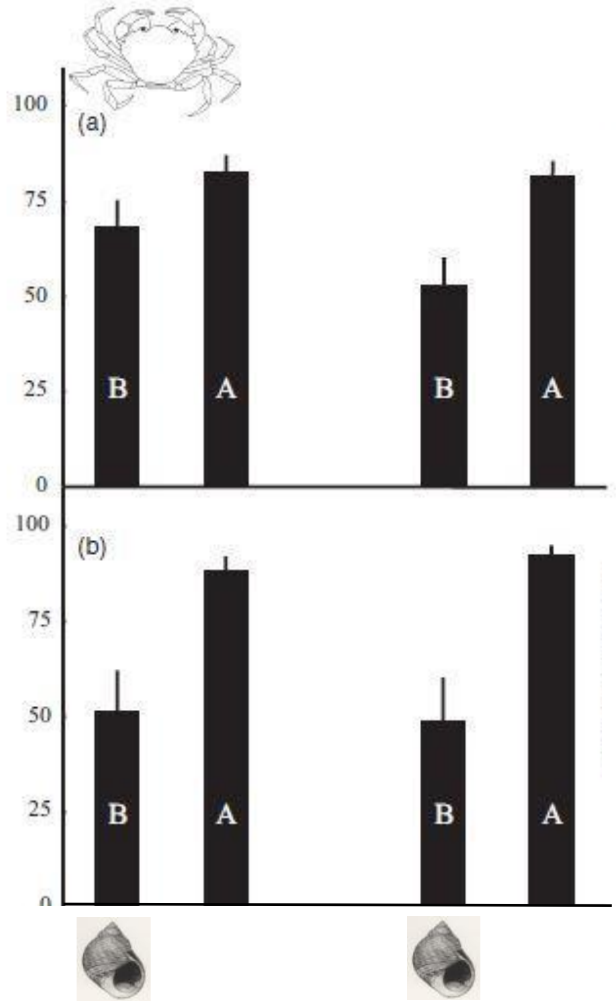
(mean ± se)

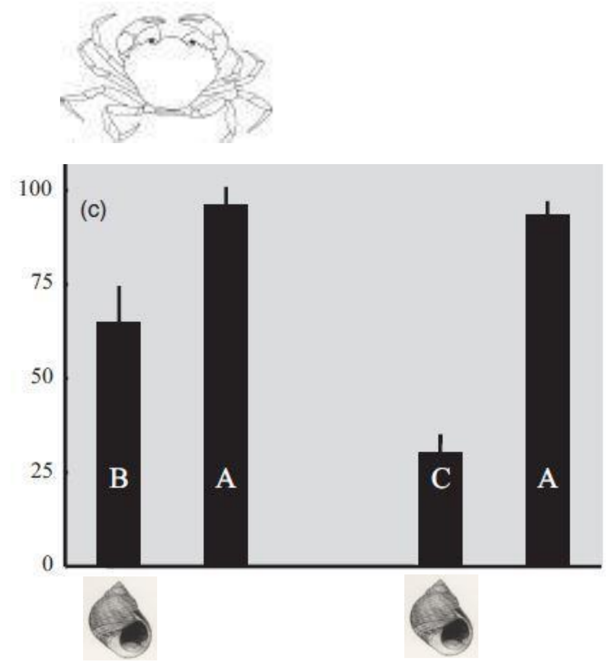
TMII: Predator cues limited consumer feeding activity and, thus, indirectly enhanced seaweed recruit survival.

Molis et al. 2011, Journal of Ecology

Open Plots

Wild Crab
Exclusion Plots





(mean ± se)

Predator cues by trespassing wild green crabs actually limited consumer feeding activity in the open plots setup.

Molis et al. 2011, Journal of Ecology

Summary

- There are two kinds of indirect interactions in food chains: DMIIs & TMIIs.
- DMIIs occur in food chains (tri-trophic interactions), when predators reduce consumer density by killing consumers and, thereby, indirectly affect basal species.
- TMIIs occur, when predator nonconsumptive effects (NCEs) cause trait changes in consumers and, thereby, indirectly affect basal species.
- Indirect effects caused by DMIIs and TMIIs can occur simultaneously.
- TMIIs are stronger than DMIIs, as predator cues can affect multiple consumers simultaneously.

Journal of Ecology

British Ecological Society

Journal of Ecology 2011, **99**, 807–817 doi: 10.1111/j.1365-2745.2011.01800.x

Predation risk indirectly enhances survival of seaweed recruits but not intraspecific competition in an intermediate herbivore species

Markus Molis[1]*, Inken Preuss[2]†, Annika Firmenich[3] and Julius Ellrich[4]‡

Check the course website for this paper.

V. Seaweed Canopies & Adult Barnacles: The Interplay of Positive & Negative Influences on Barnacle Recruitment



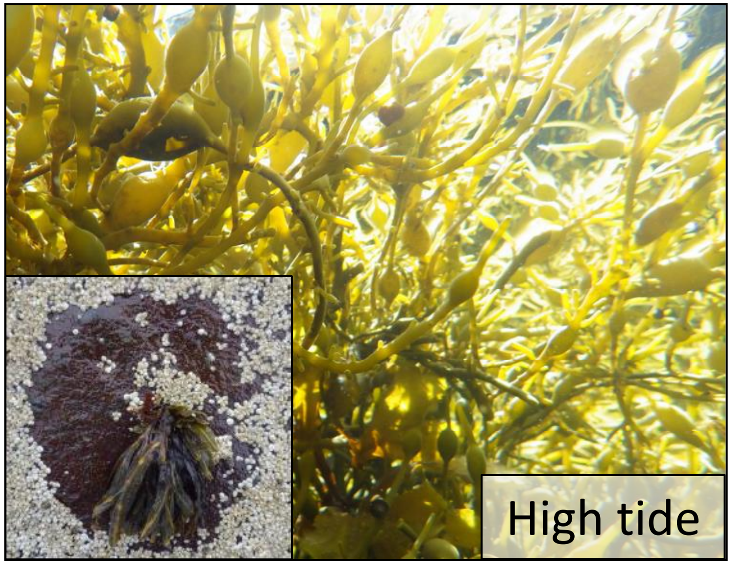

Beermann, A. J., J. A. Ellrich, M. Molis & R. A. Scrosati. 2013. Effects of seaweed canopies and adult barnacles on barnacle recruitment: The interplay of positive and negative influences. Journal of Experimental Marine Biology and Ecology 448: 162-170.

Seaweed, *Ascophyllum nodosum* (L.) Le Jolis, Canopy

Barnacles, *Semibalanus balanoides* (L. 1767)

Suggested Seaweed Canopy Influences on Barnacle Recruitment

\- Whiplash effects by seaweed fronds.



\+ Canopy limitation of temperature and desiccation extremes.

<u>Research Questions:</u>

Do these suggestions apply?

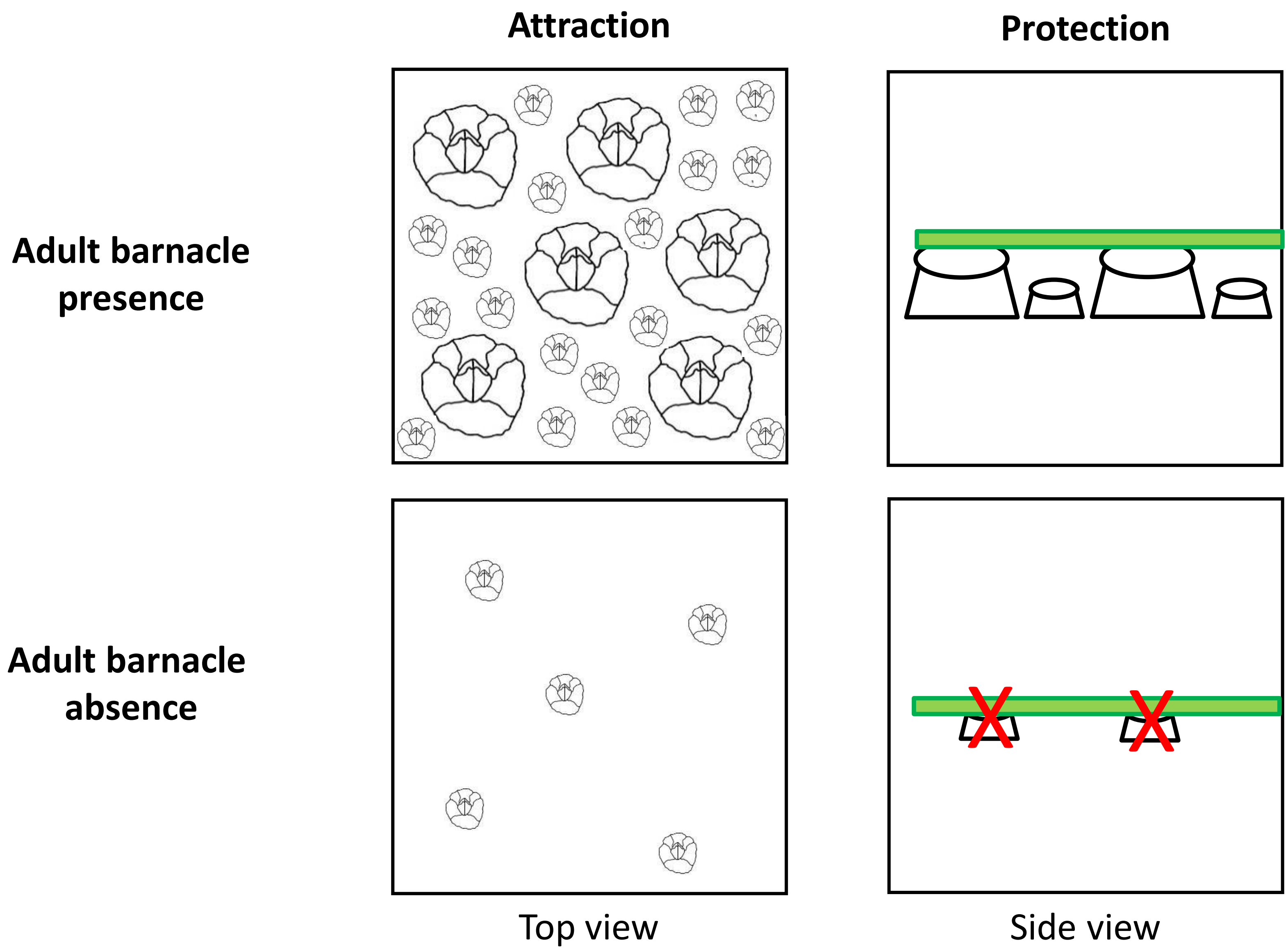
Is there a balance between these influences?

Hypotheses

- Whiplash effects by seaweed fronds limit barnacle recruitment.

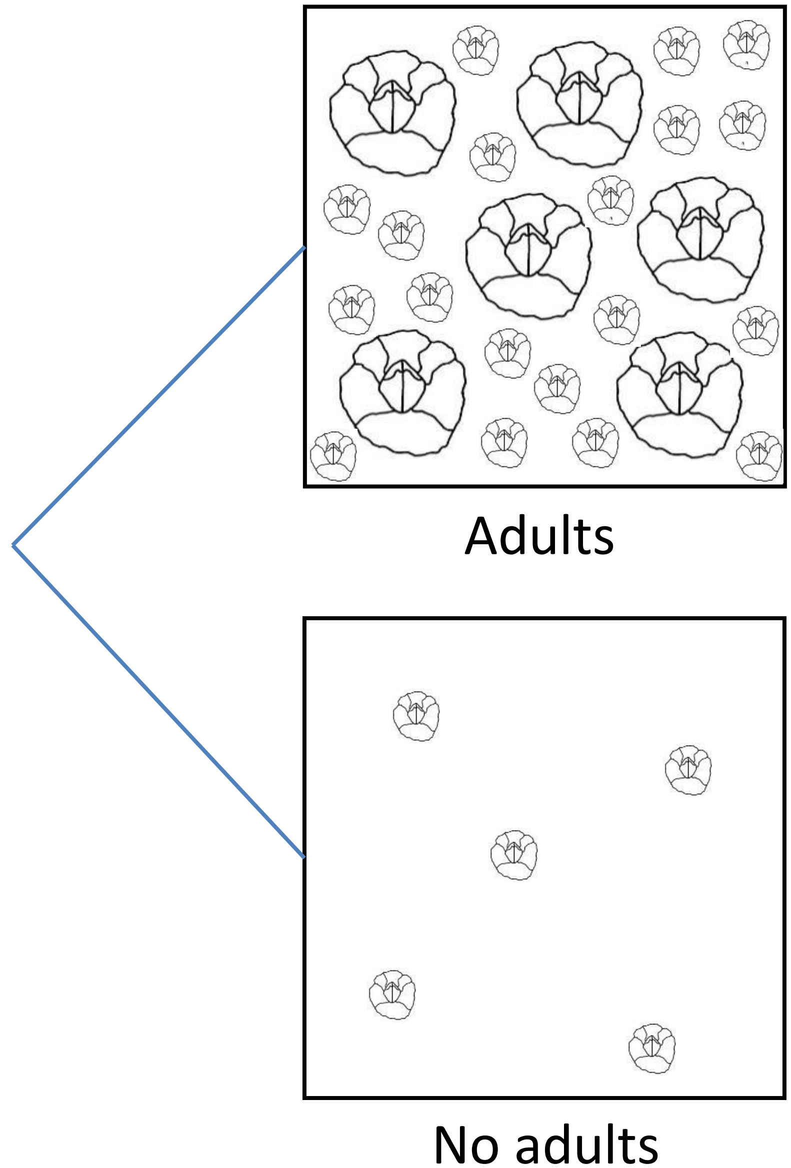
+ Protection from temperature and desiccation extremes enhances barnacle recruitment.

Suggested Adult Barnacle Effects on Barnacle Recruitment

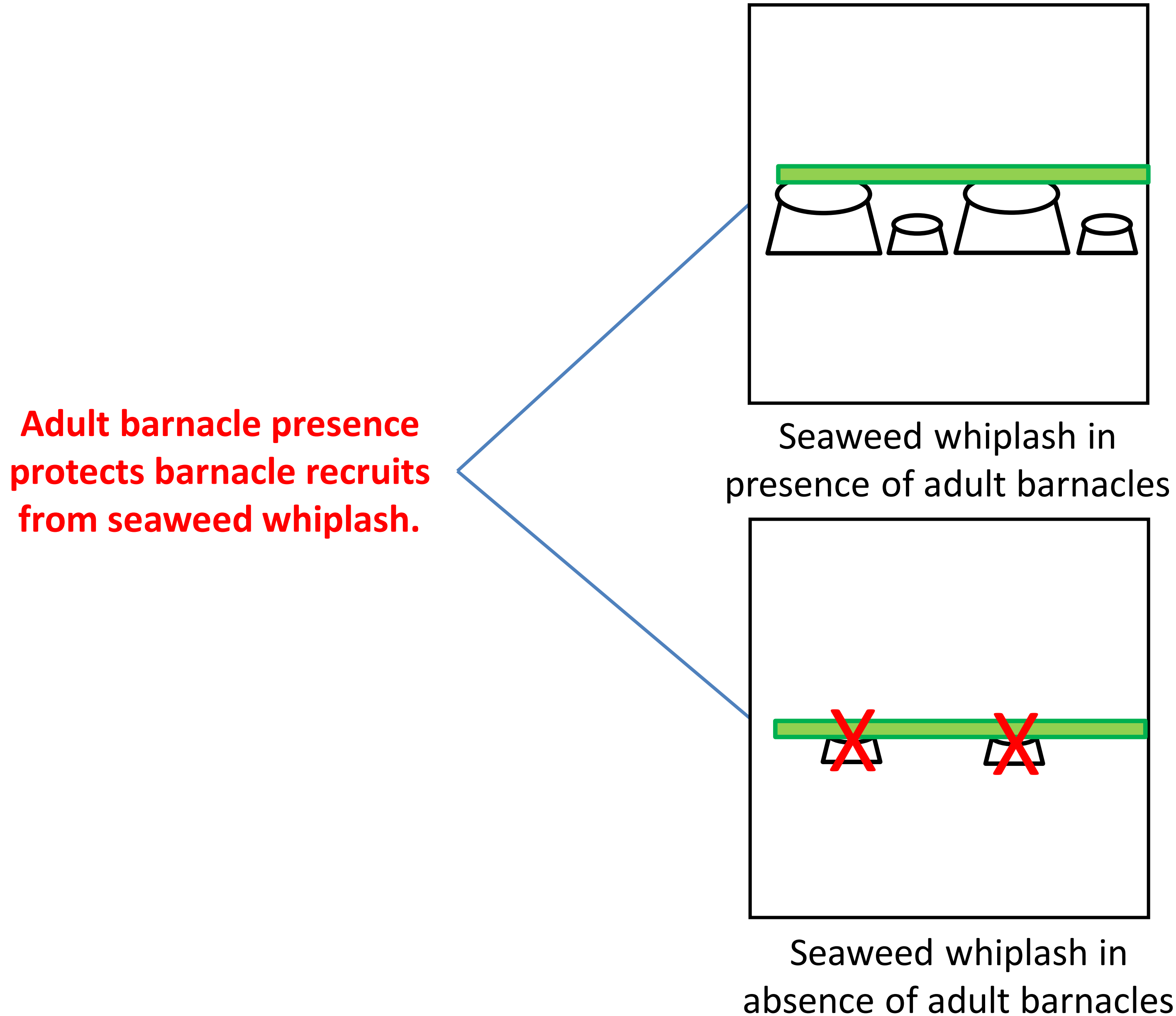


Hypotheses

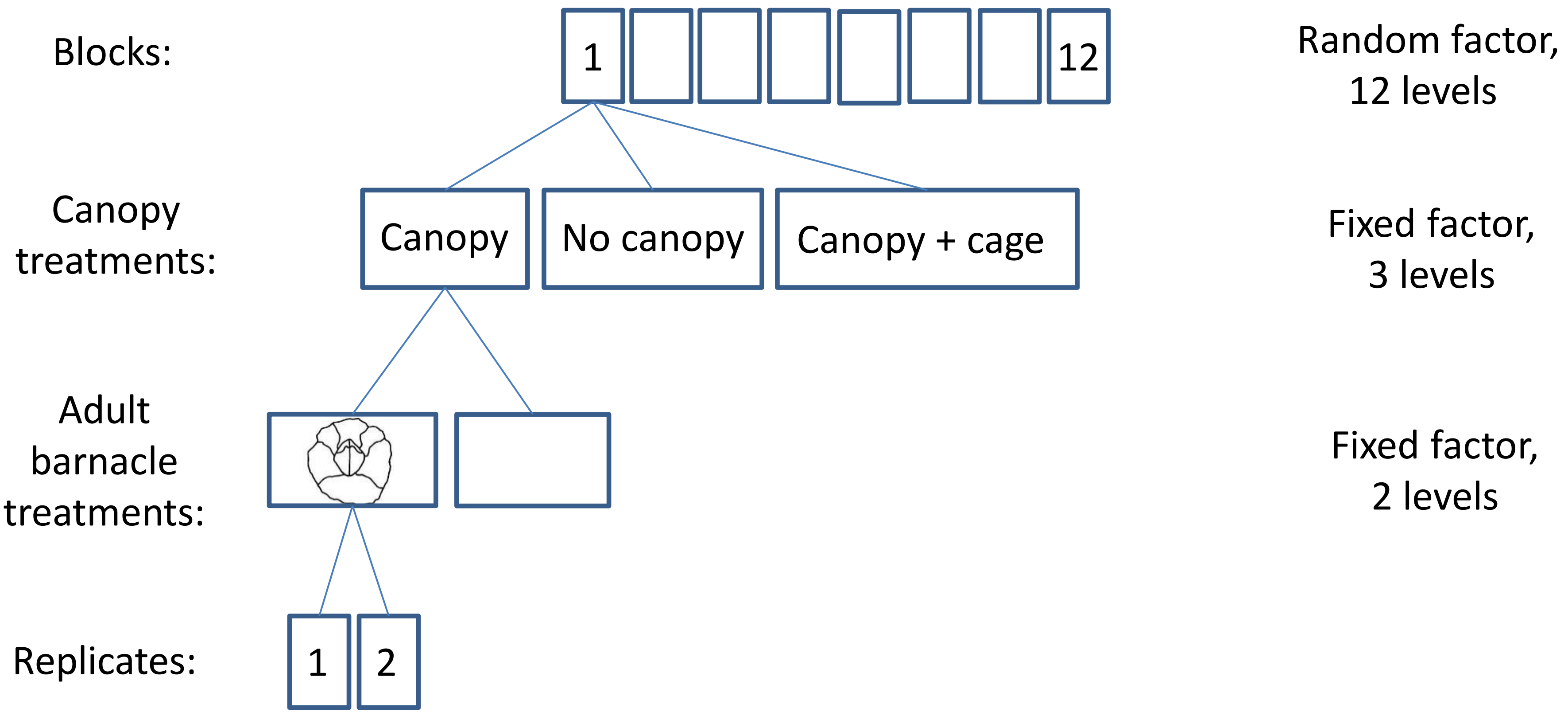
Adult barnacle presence enhances conspecific recruitment.



Hypotheses

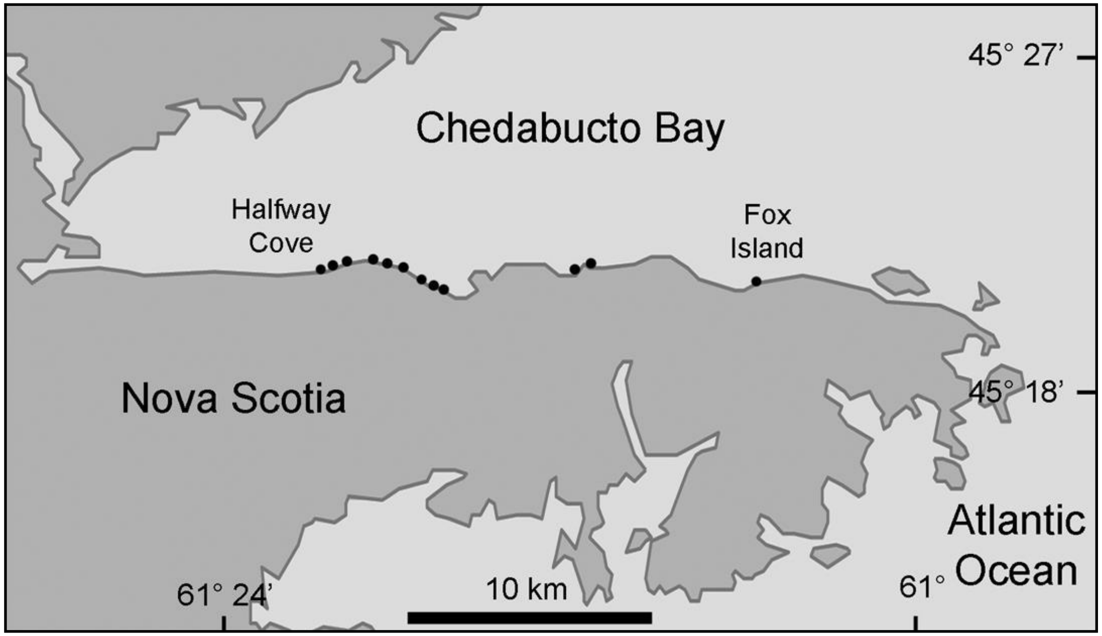

Adult barnacle presence protects barnacle recruits from seaweed whiplash.
Seaweed whiplash in presence of adult barnacles
Seaweed whiplash in absence of adult barnacles

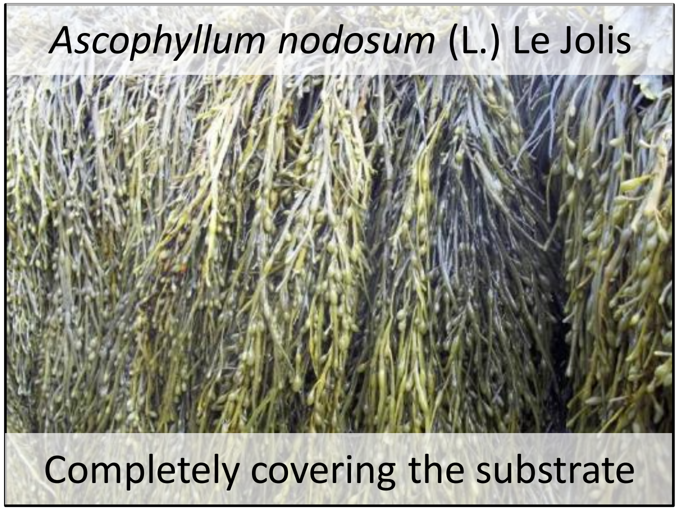
Randomized Block Design



- Response variable: recruit density
- 3-factorial ANOVA, Tukey HSD, Point-biserial correlation coefficient

Study System

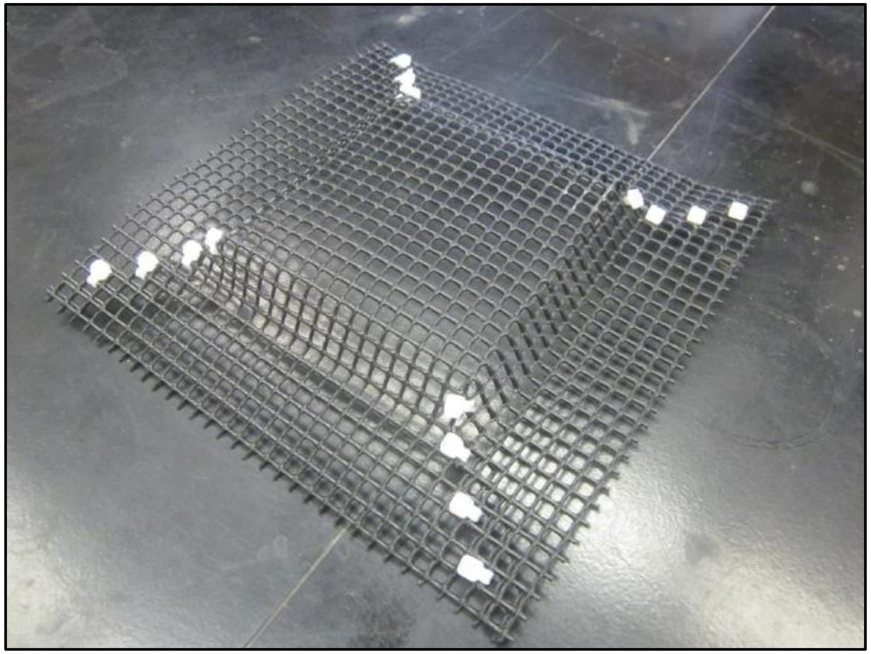




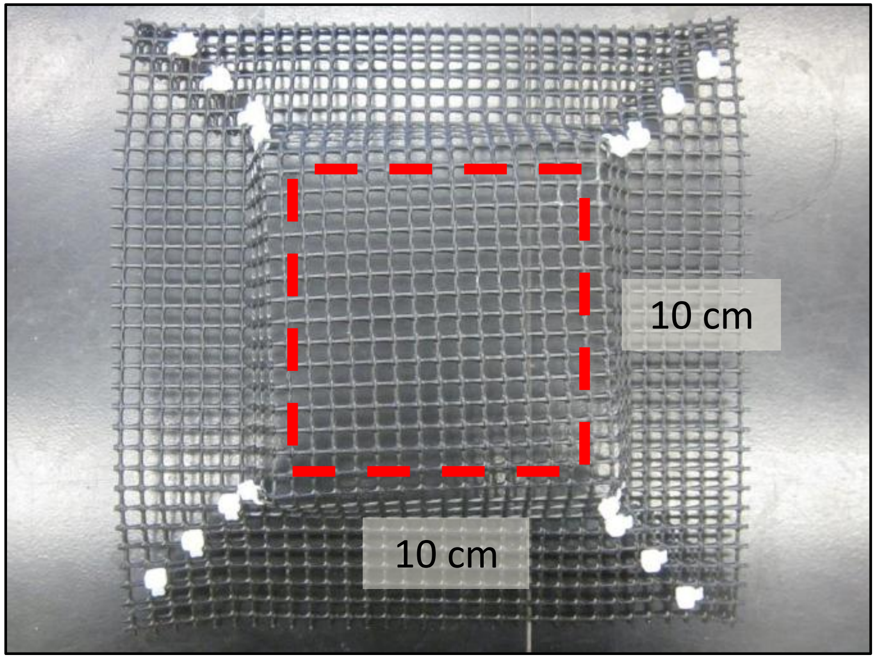
Max. tidal amplitude: 1.8 m
Canopy range: 0.0-1.5 m
Experimental range: 0.3-0.9 m

Cage Design

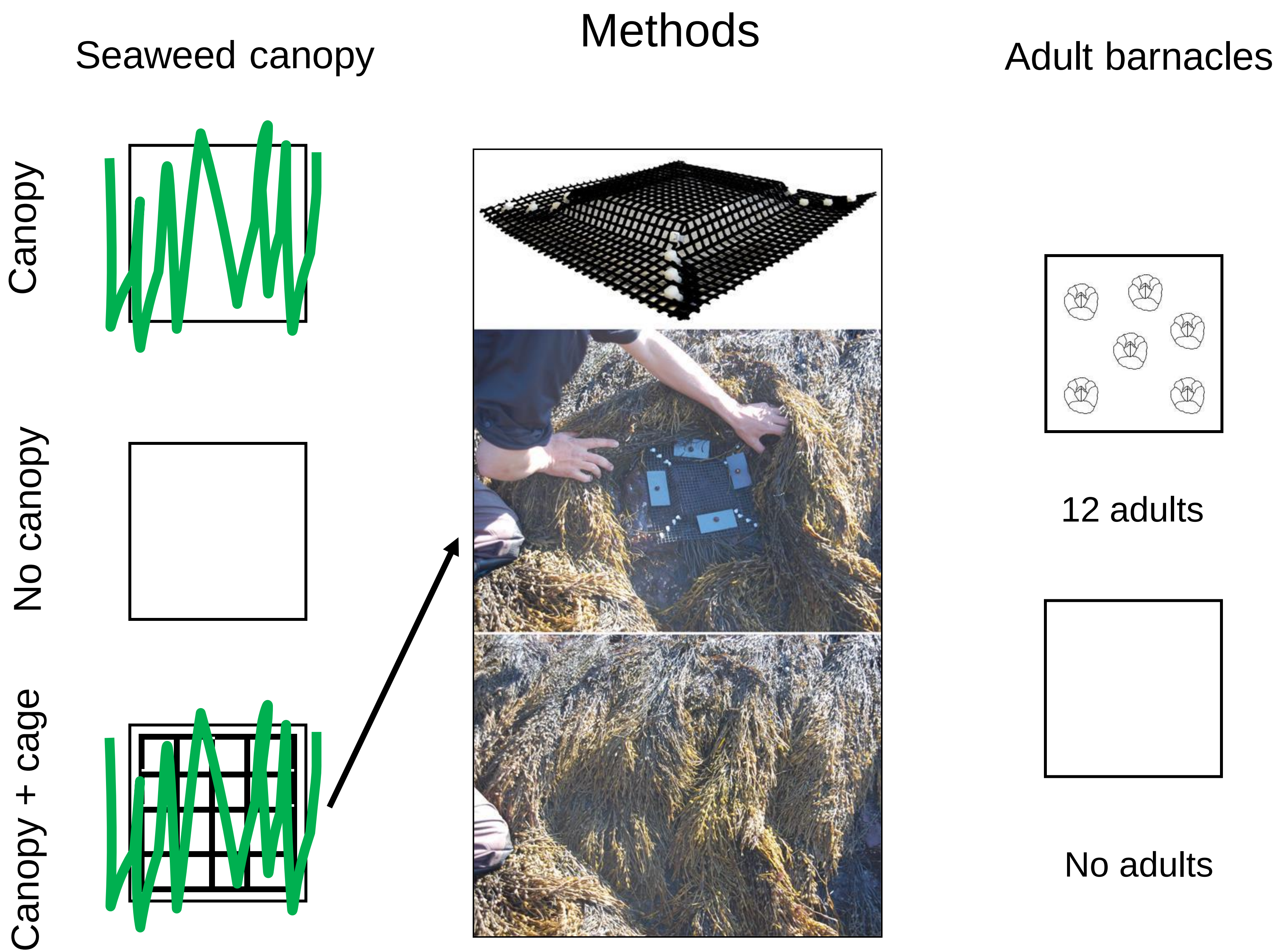
Side view



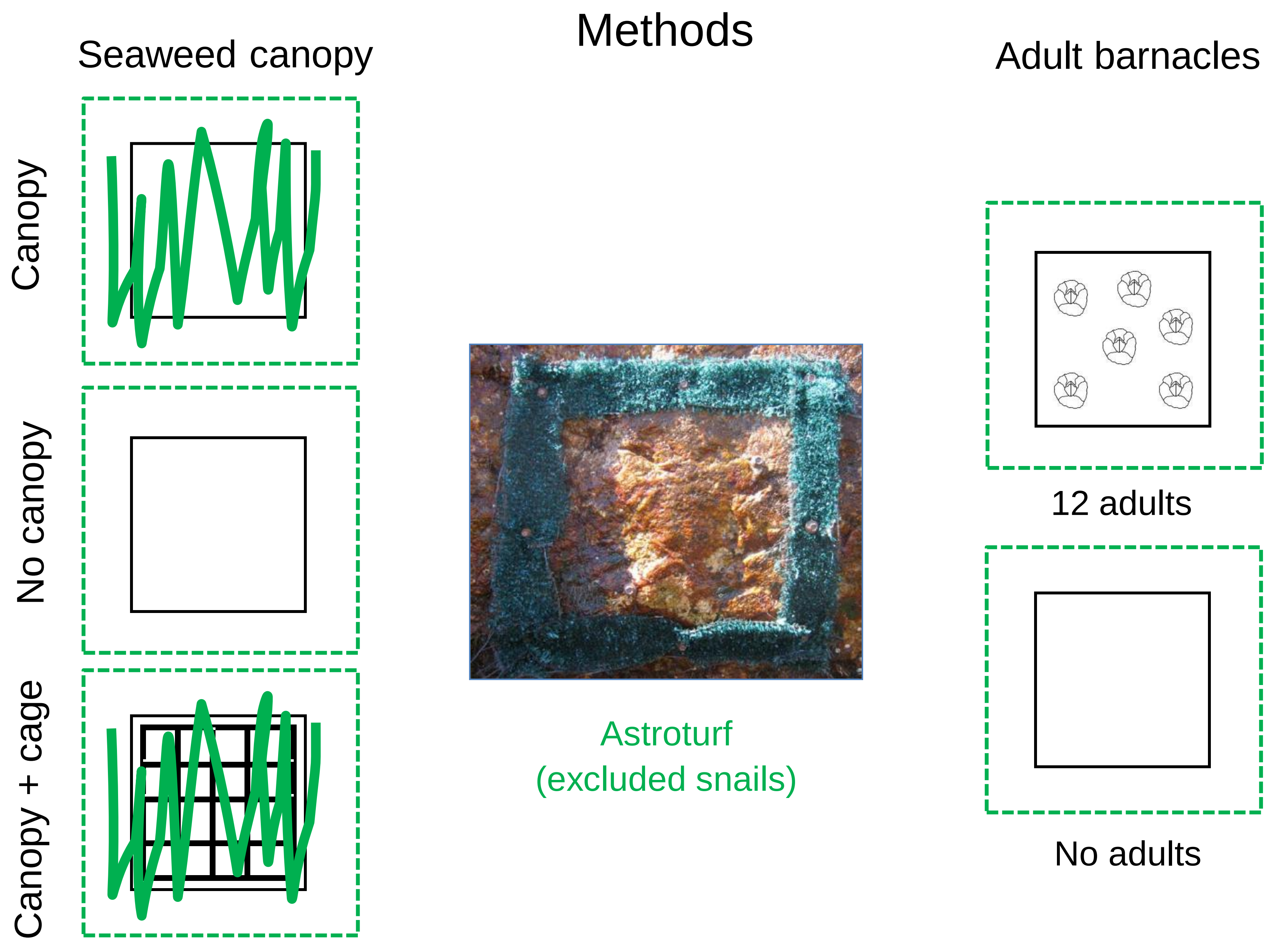
Top view



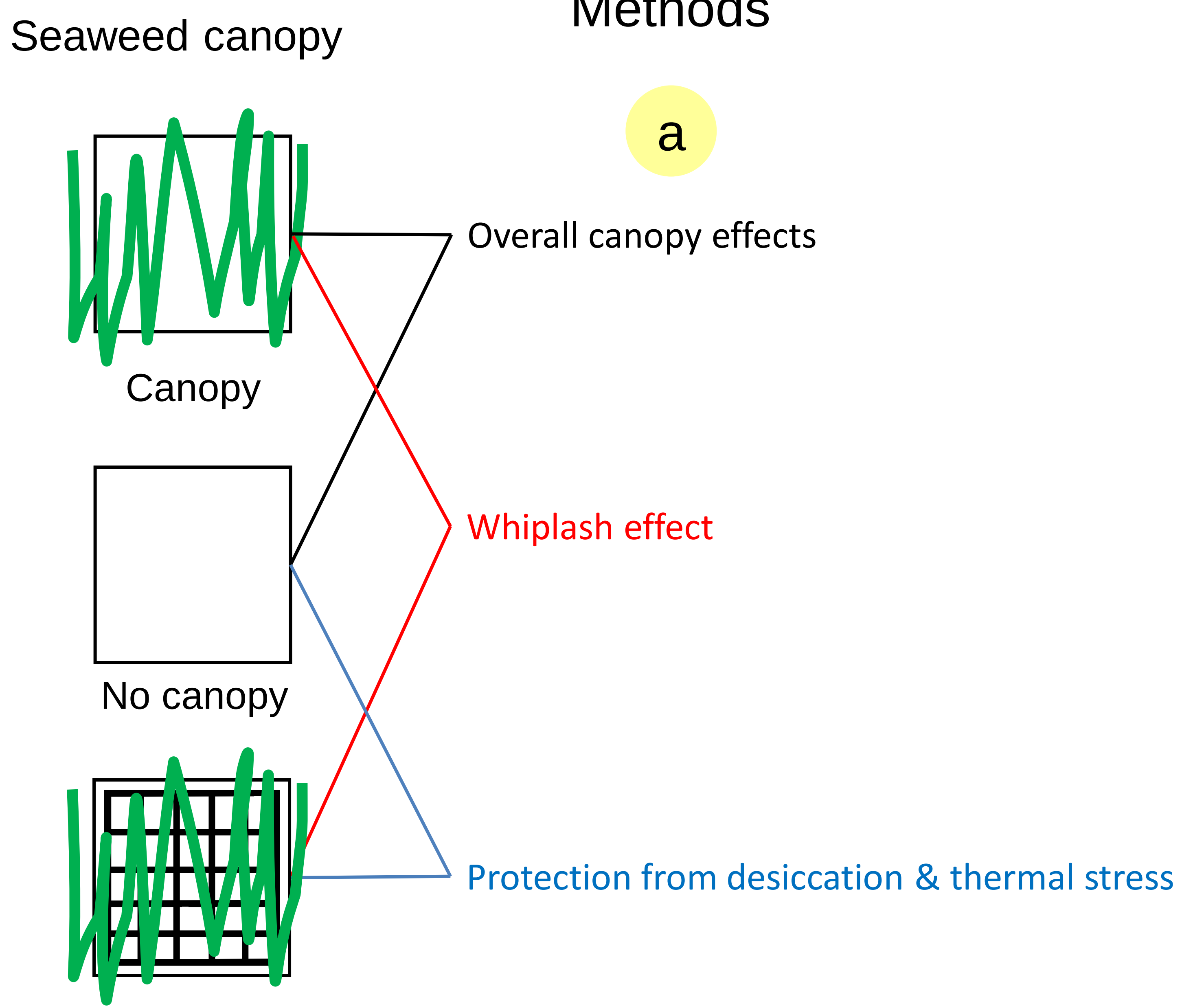
- 48 cages in total
- Cage dimensions: 26 cm x 3 cm x 26 cm
- Covering 1 dm^2 of rocky substrate



Methods
Seaweed canopy
Adult barnacles
Canopy
No canopy
Canopy + cage
12 adults
No adults


Methods
Seaweed canopy
Adult barnacles
Canopy
No canopy
Canopy + cage
Astroturf
(excluded snails)
12 adults
No adults

Methods



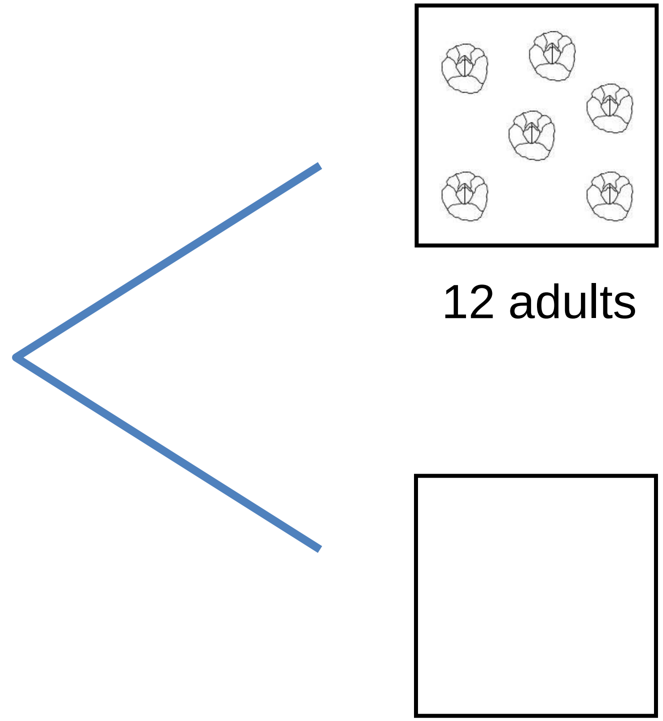
(Tukey HSD)

Methods

Adult barnacles

b

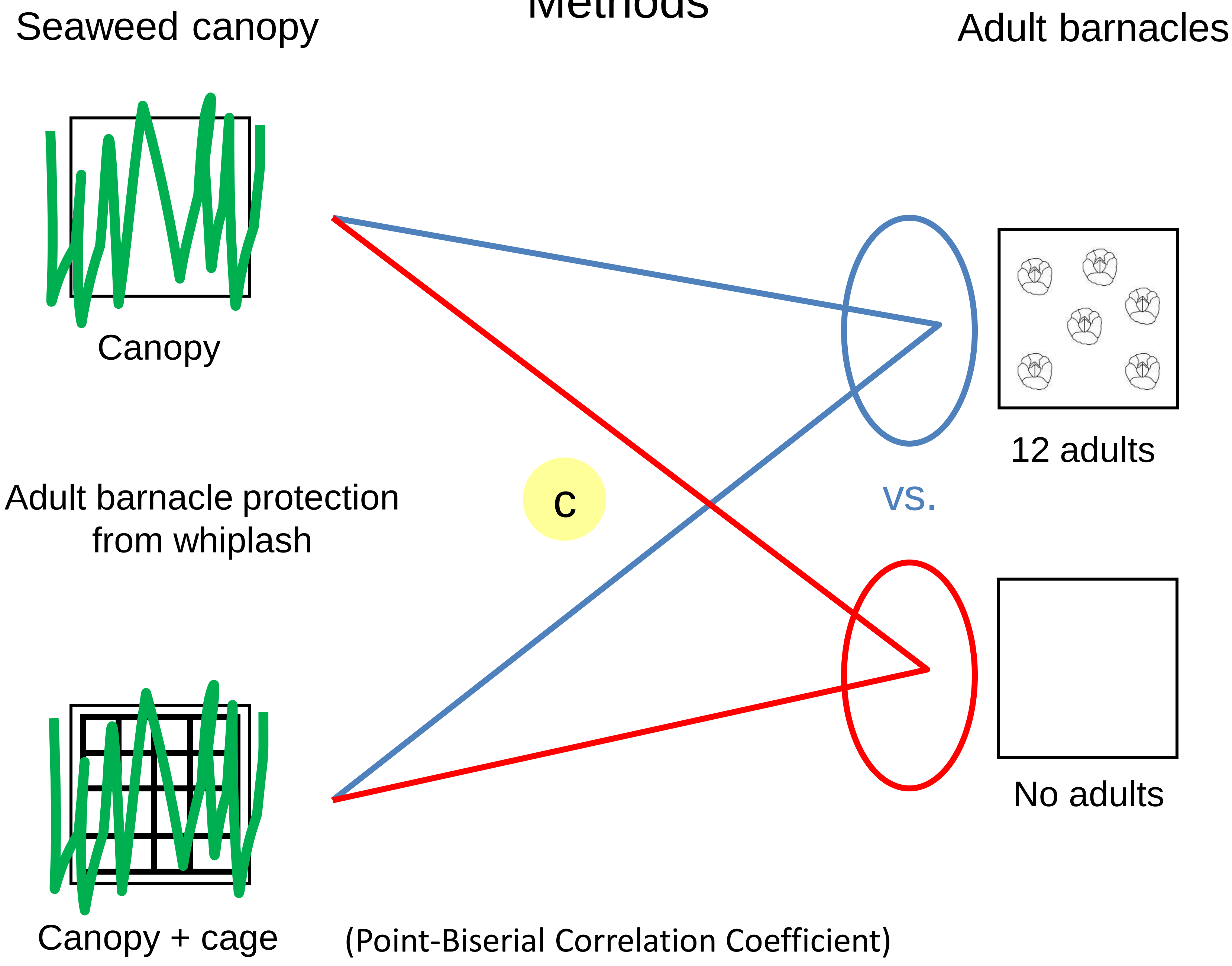
Adult barnacle attraction



No adults

(ANOVA)

Methods



Seaweed canopy
Adult barnacles
Canopy
12 adults
Adult barnacle protection
from whiplash
c
vs.
No adults
Canopy + cage
(Point-Biserial Correlation Coefficient)

Methods

Effects of Each Canopy Treatment

Whiplash

Temperature

Substrate moisture

Water flow

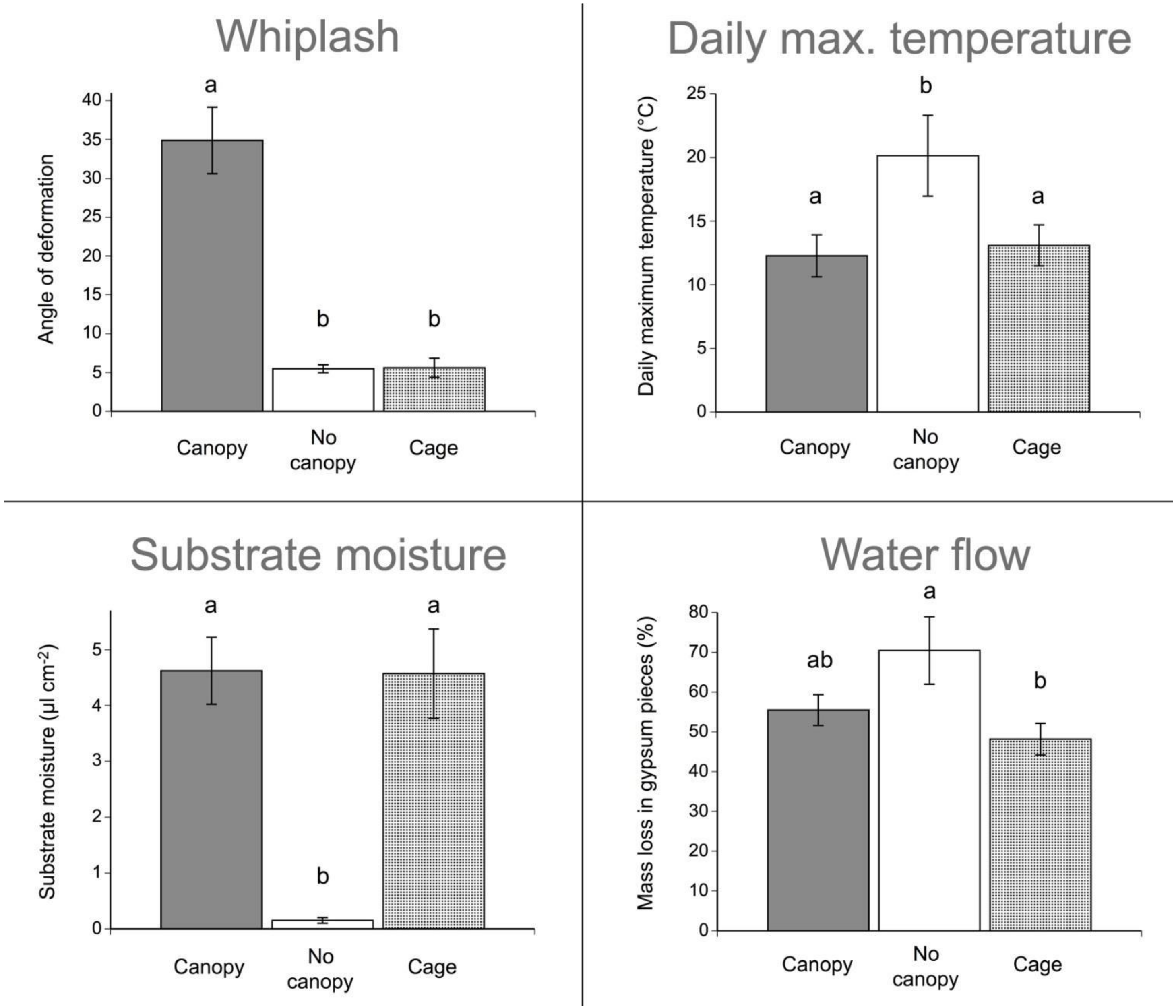
n= sample size per canopy treatment

Video: Wire sensors measuring whiplash by seaweed fronds

https://youtu.be/qZ8XQptwDuY

Results

Effects of Each Canopy Treatment



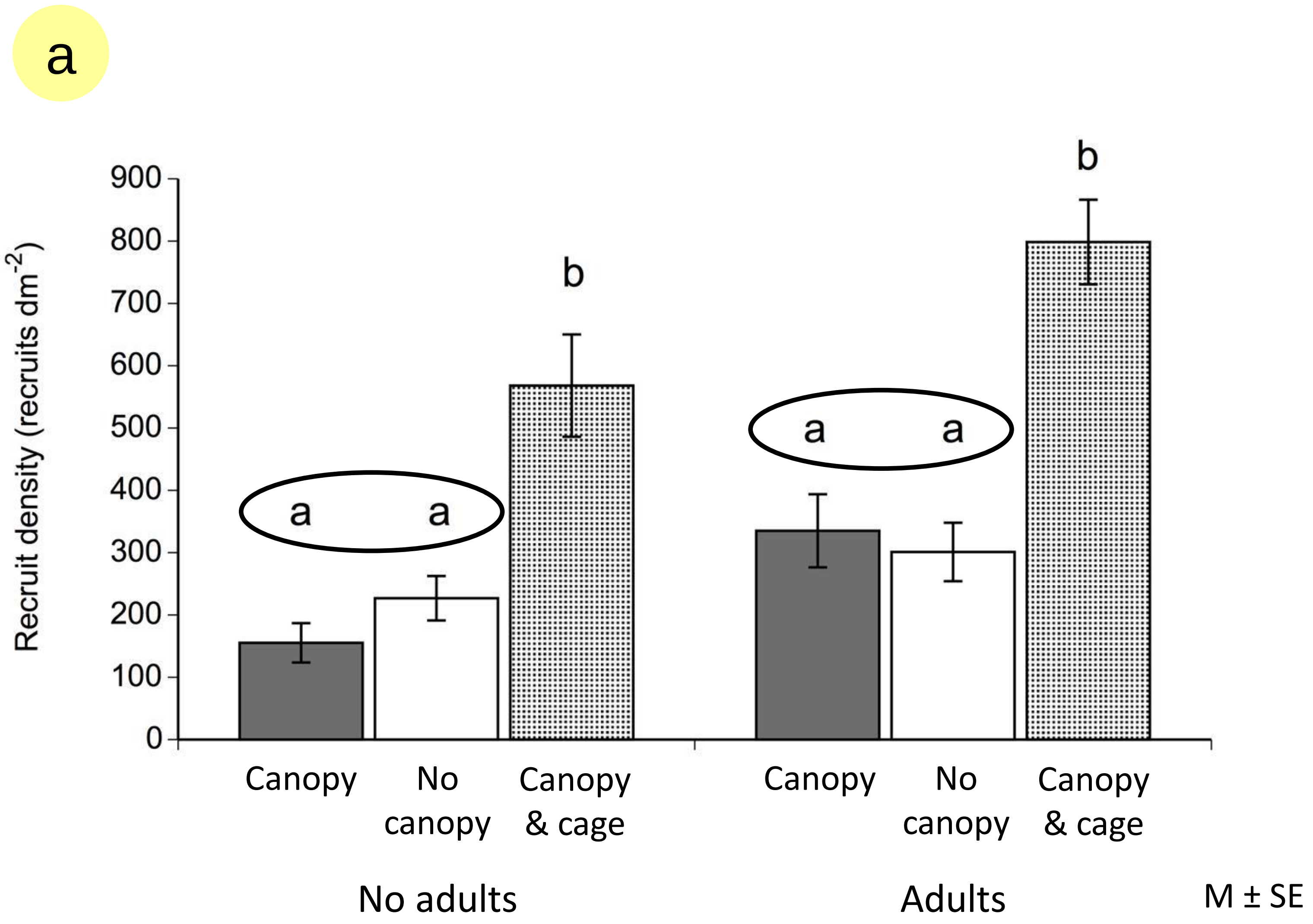
M ± SE

Canopy Influences & Adult Barnacle Effects on Barnacle Recruit Density

ANOVA Table:

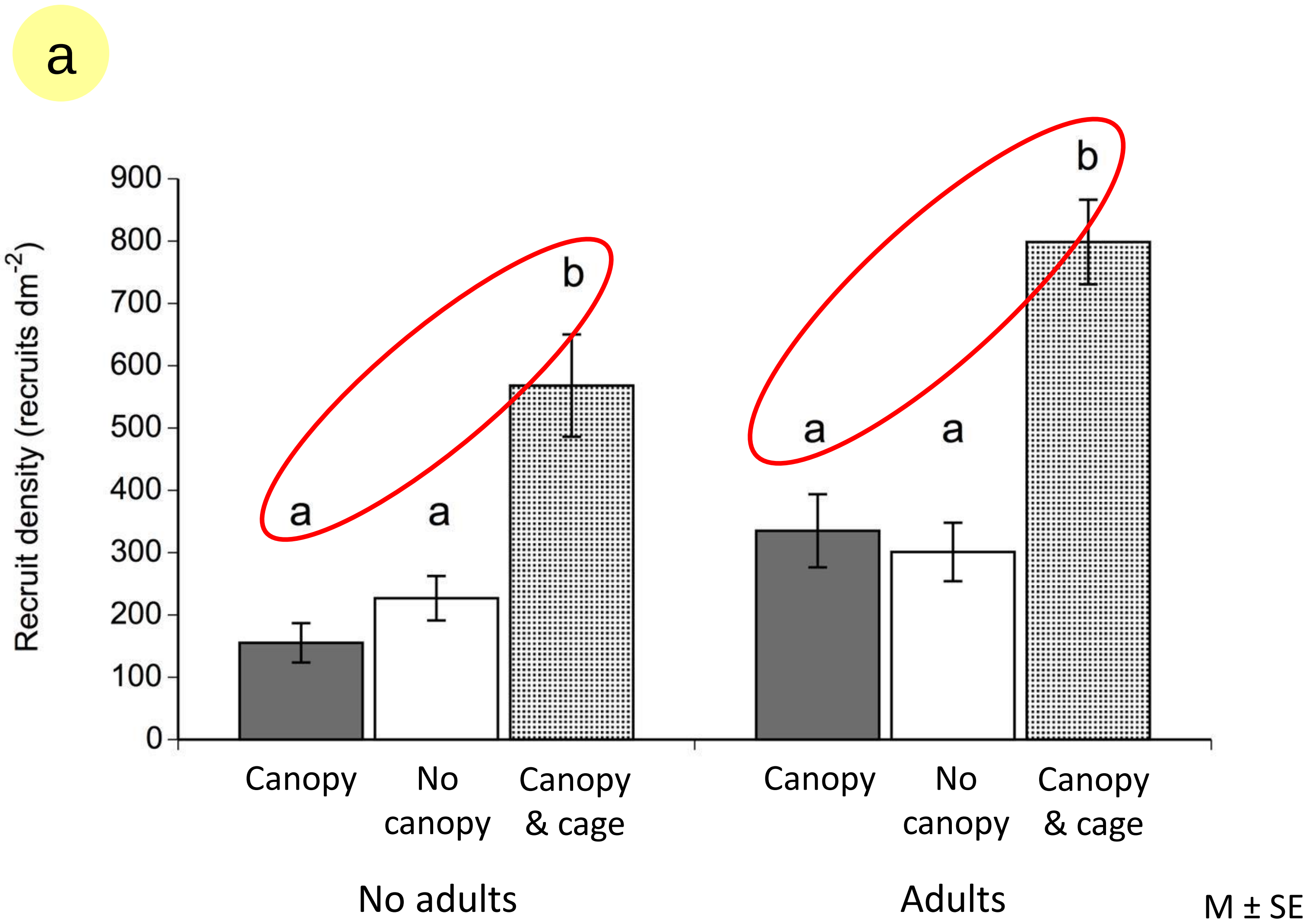
Source of variation	df	SS	MS	F	P	
Canopy	2	3591.88	1795.94	49.88	<0.001	*
Adults	1	715.58	715.58	19.88	<0.001	*
Canopy × Adults	3	82.88	41.44	1.15	0.322	
Blocks	11	2289.87	208.17	5.78	<0.001	*
Blocks × Canopy	22	395.04	17.96	0.50	0.965	
Blocks × Adults	11	323.24	29.39	0.82	0.624	
Blocks × Canopy × Adults	22	525.67	23.89	0.66	0.859	
Error	72	2592.18	36.00			
Total	144	10516.33				

Overall Canopy Effects on Barnacle Recruitment



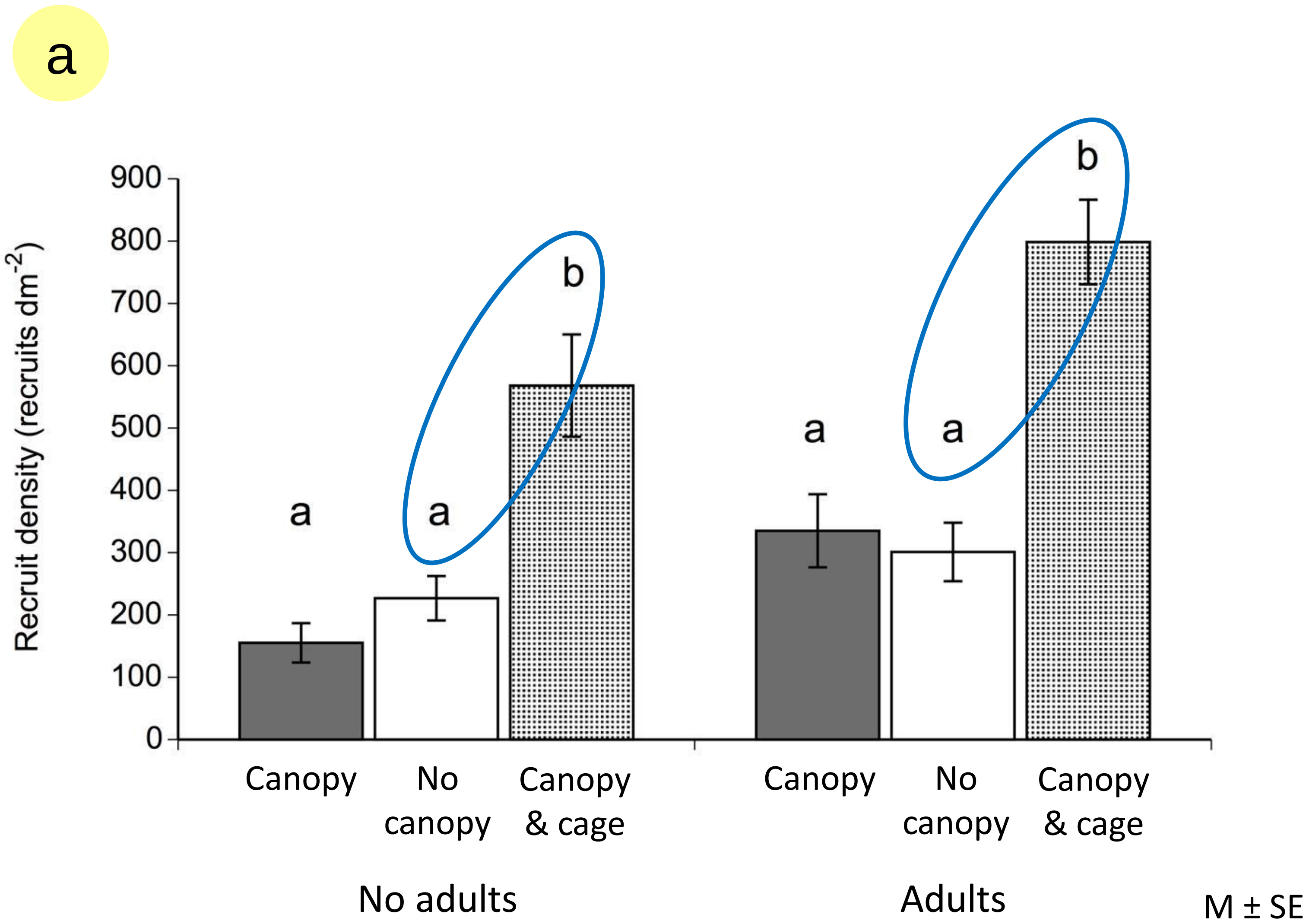
Overall canopy effects on barnacle were neutral.

Negative Whiplash Effects on Barnacle Recruitment



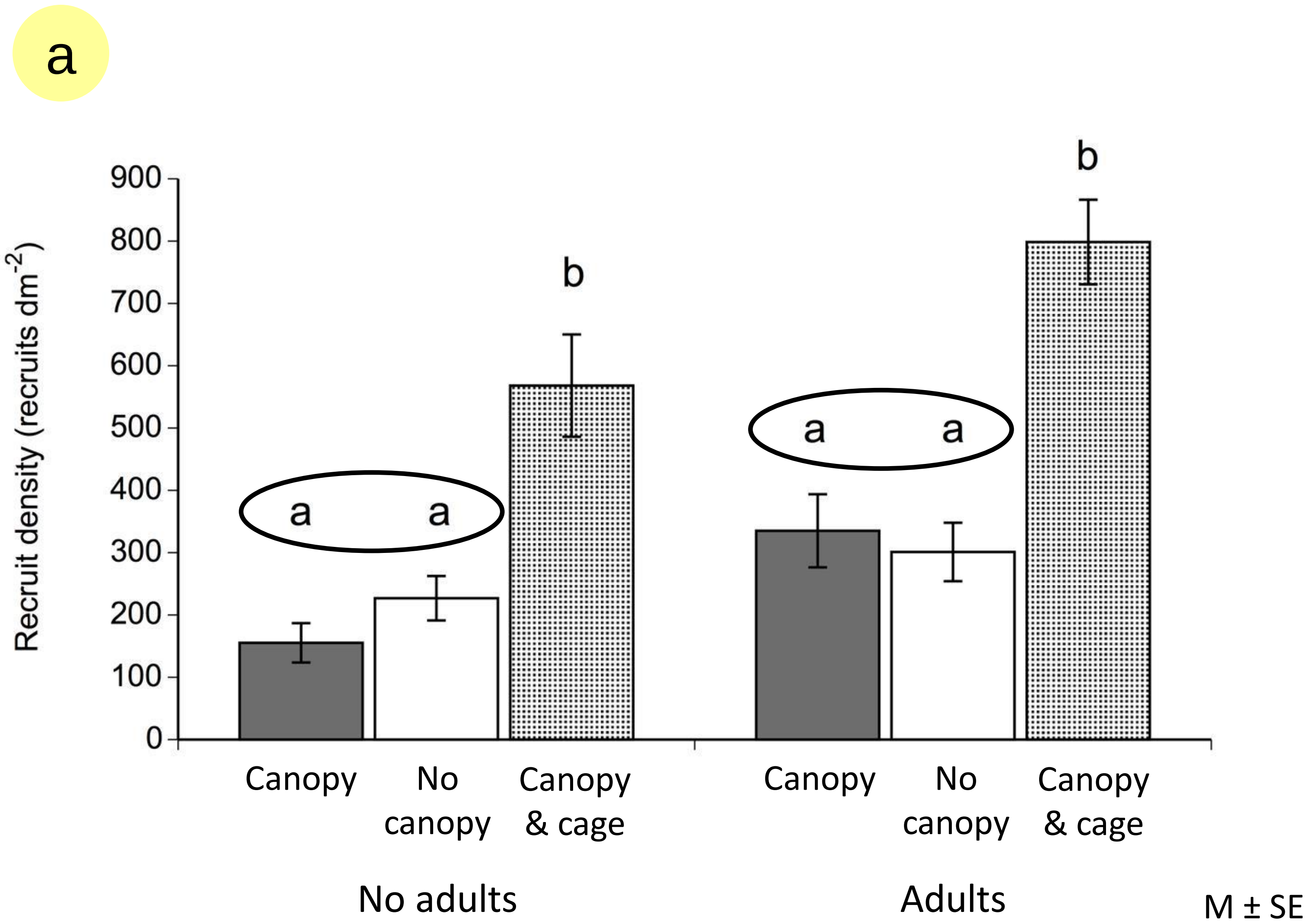
Whiplash limited barnacle recruitment.

Positive Canopy Influences on Barnacle Recruitment



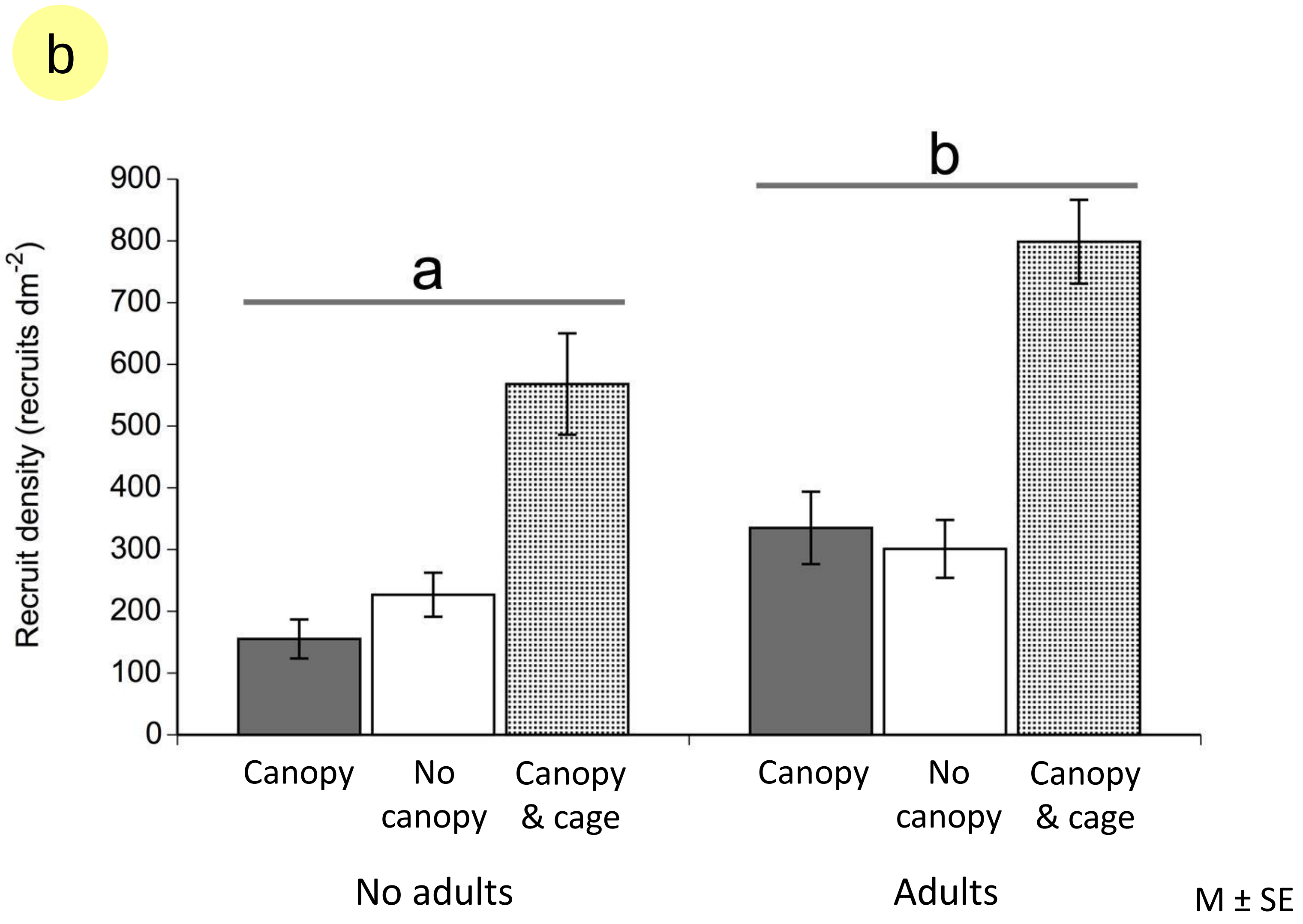
Positive canopy influences enhanced barnacle recruitment.

Overall Neutral Canopy Influences



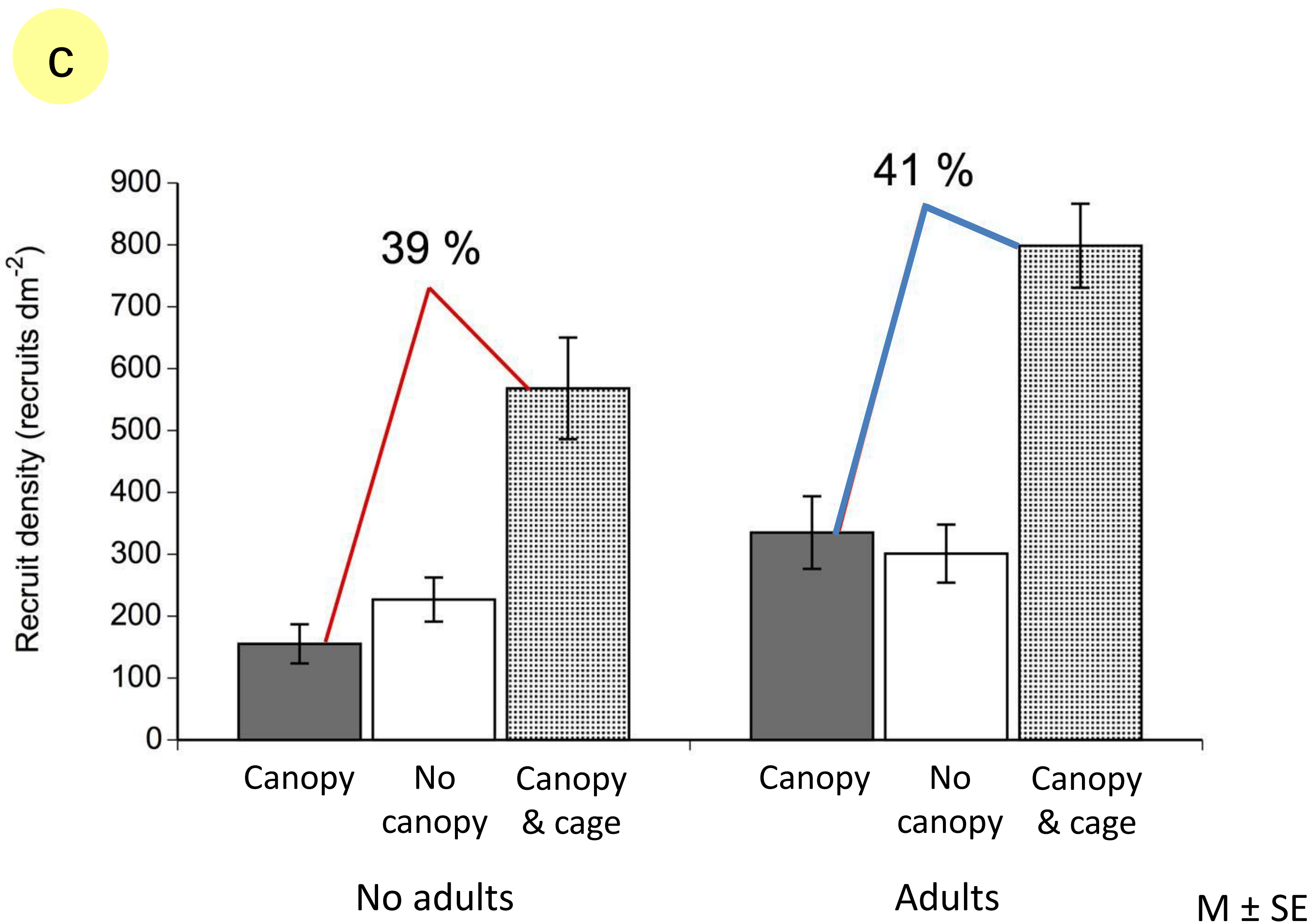
→ Negative & positive canopy influences on barnacle recruitment balanced each other out.

Attractive Adult Barnacle Effects on Barnacle Recruits



→ Adult barnacle presence enhanced barnacle recruitment by 51 % on average.

Adult Barnacle Protection of Recruits From Whiplash



Adult barnacles did not protect barnacle recruits from whiplash.

Conclusions

Seaweed Canopy Influences

- Negative & positive canopy influences on barnacle recruitment were explained by canopy treatment effects.

Whiplash

Daily max. temperature

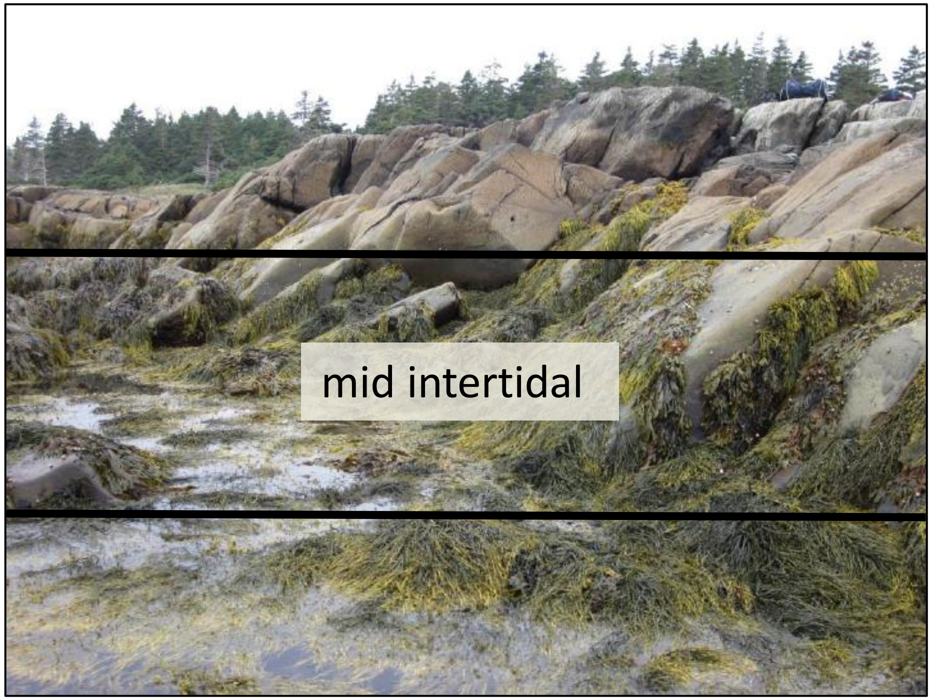
Substrate moisture

- The lack of canopy effects on water flow may result from the relatively slender *A. modosum* fronds.

Seaweed Canopy Influences

- **Overall canopy influences are neutral**

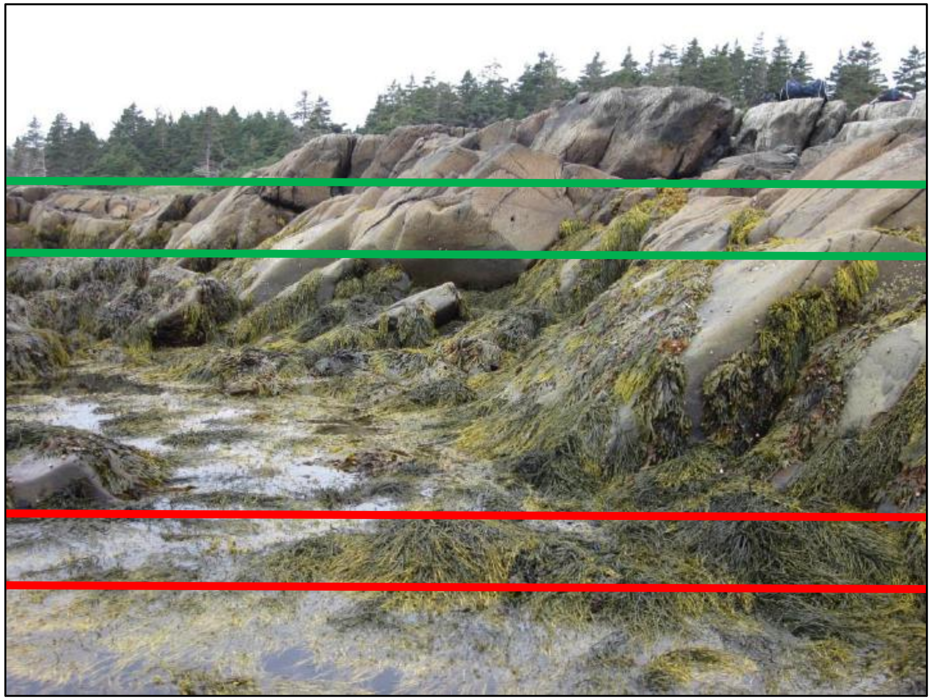
  - Negative & positive canopy influences balanced each other out.



Seaweed Canopy Influences

- ***Positive*** *canopy effects may prevail under high physiological stress but low physical stress.*

- ***Negative*** *canopy effects may prevail under low physiological stress but high physical stress.*



Future research could address these hypotheses through field experiments that compare seaweed canopy influences on barnacle recruitment at high, mid and low intertidal elevations.

Adult Barnacle Effects

- **Adult barnacles enhance barnacle recruitment:**

- *likely through chemical cues*
  (Crisp & Meadows 1962, Clare 2011)

- *confirming findings in canopy-free habitats*
  (Bertness 1991, Scrosati & Ellrich 2017)

- **Adult barnacles do not protect recruits from whiplash:**

- *may result from low adult density and/or small adult size*
  (Jenkins et al. 1999)

Summary

- For the first time, suggested positive and negative influences of seaweed canopies on barnacle recruitment were confirmed through *in-situ* field measurements of temperature, substrate moisture and whiplash.
- Positive canopy influences enhanced barnacle recruitment.
- Negative whiplash effects limited barnacle recruitment.
- Overall canopy effects were neutral, as positive influences and negative effects balanced each other out.
- The presence of adult barnacles enhanced barnacle recruitment, but did not protect barnacle recruits from whiplash.

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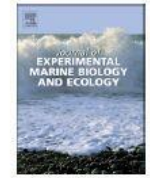

Effects of seaweed canopies and adult barnacles on barnacle recruitment: The interplay of positive and negative influences

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Thank You