Bottom-up and top-down regulation of *Noctiluca scintillans*

Hongbin Liu

The Hong Kong University of Science and Technology

6ZPS, Bergen, Norway

2016-5-13

Outline

1. Introduction
2. Bottom-up regulation
3. Top-down regulation
4. Conclusion

1. Introduction

珠海出现蓝色荧光海滩 被确认为夜光藻赤潮

2015年01月13日 14:22 来源：珠海特区报 参与互动(0)

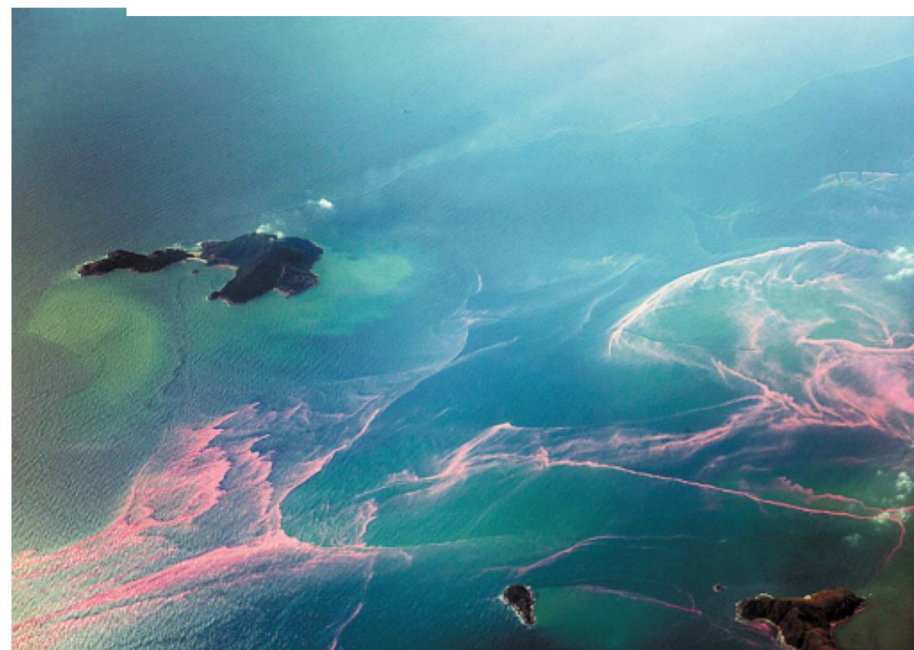
NEWS › HONG KONG

Hong Kong in bloom: stunning photos of 'Sea Sparkle' on city's shores

Long-exposure pictures taken by the Associated Press show a mesmerising luminescence from the marine plankton Noctiluca scintillans, triggered by wat pollution along Hong Kong's seashore

Staff Reporters

PUBLISHED : Friday, 23 January, 2015,
UPDATED : Friday, 23 January, 2015,



11月25日，深圳大梅沙海域赤潮 新华社发

Noctiluca in Hong Kong

>28%

紅潮種類在不同水質管制區的分佈狀況(1980 – 2014)

種類	發生次數										
	吐露港及赤門	大鵬灣	東部緩衝區	牛尾海	將軍澳	維多利亞港	南區	西北部	西部緩衝區	后海灣	總數
Noctiluca scintillans	68	69		62			59	6	9		273
Skeletonema costatum	23	3		1	3	9	13	3	10	2	67
Mesodinium rubrum	8	9		11	1		18	7	3	2	59
Gonyaulax polygramma	23	8		16			6	1			54
Prorocentrum minimum	45	1							1		47
總數 : 95種	413	152	1	143	7	14	155	31	31	13	960

註: 一次紅潮可由多個種類引發

數據來源: 漁農自然護理署及環境保護署

(HKEPD, 2014)

Map of the distribution of *Noctiluca* blooms recorded in Hong Kong waters from 1980 to present (AFCD, HK; https://www.afcd.gov.hk/eindex.html)

● : the occurrence of *Noctilcua* bloom

Noctiluca blooms in the world :

Fig.2 Map of the global distribution of red *Noctiluca scintillans* derived from Table 1

Fig.3 Map of the global distribution of green *Noctiluca scintillans* derived from Table 2

(Harrison et al., 2011)

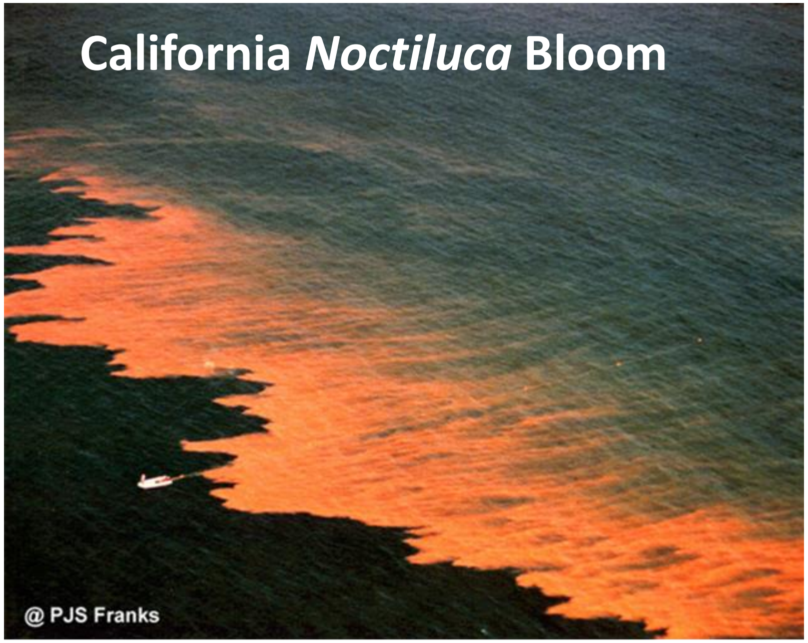
Environmental impacts :

- Discoloration of water

- Oxygen depletion

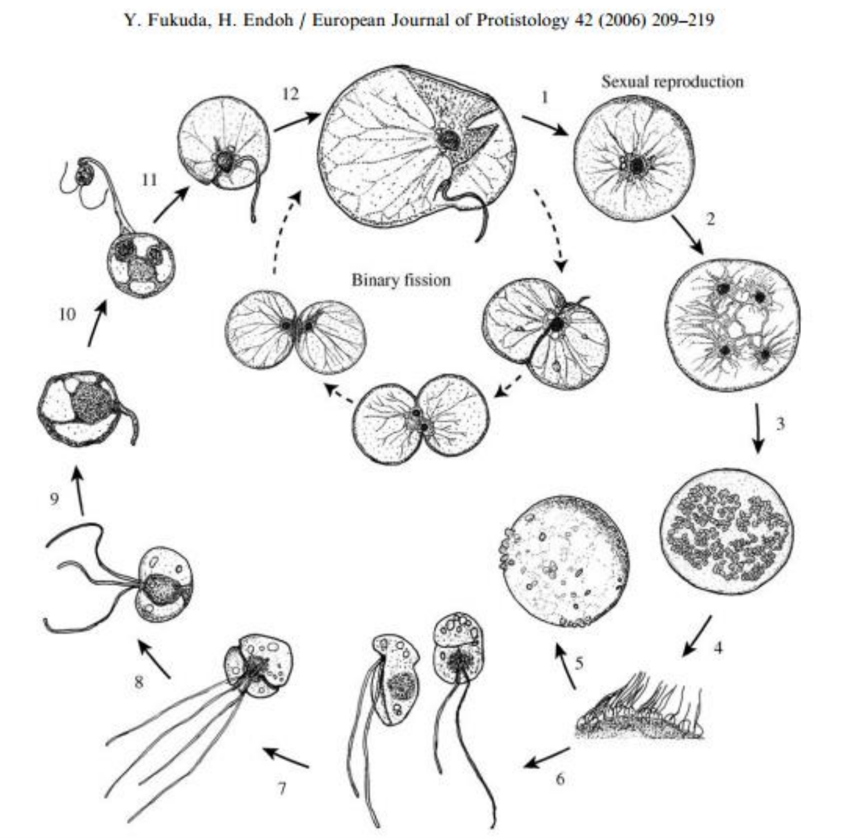
- Potential ammonium toxicity

- Interrupt regular food web structure



Characteristics:

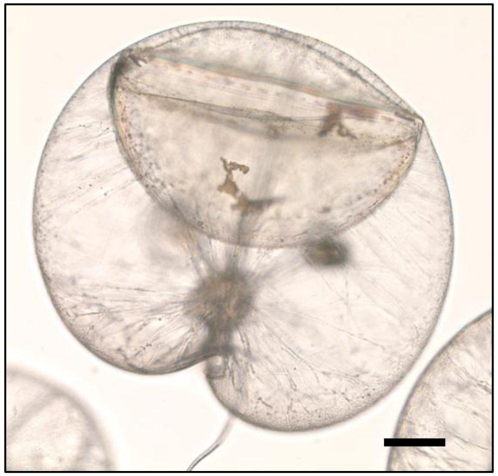
1. Large size (100-2000 μm)
2. Positively buoyance
3. Diploid
4. Two kinds of reproduction
5. Two kinds of feeding behavior
6. High feeding flexibility



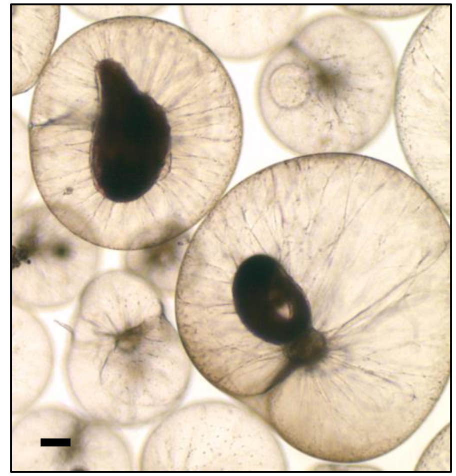
Noctiluca as a predator

Small diatom

Large diatom



***Trichodesmium* sp.**

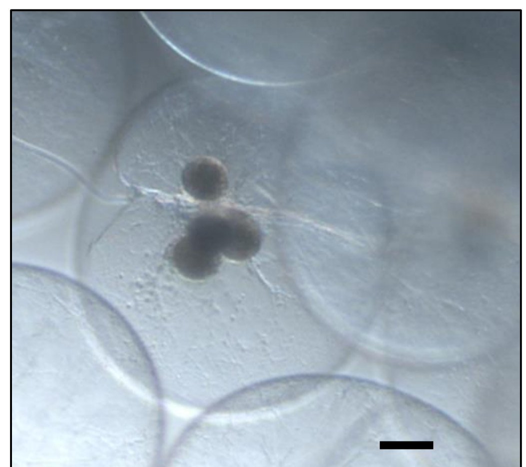


Detritus

Tintinnid

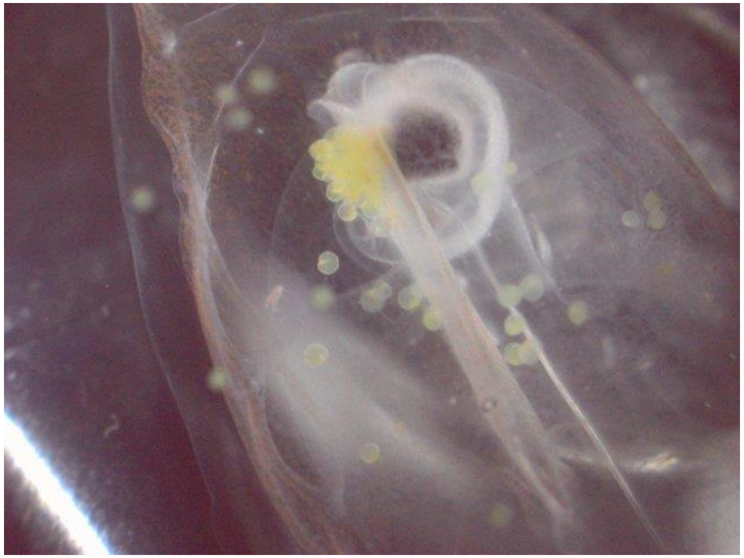
Copepod

Copepod egg



Copepod fecal pellet

Noctiluca as a prey



The salp *Pegea confoederata* feeding on a dense *Noctiluca* bloom (http://vimeo.com/104527669)

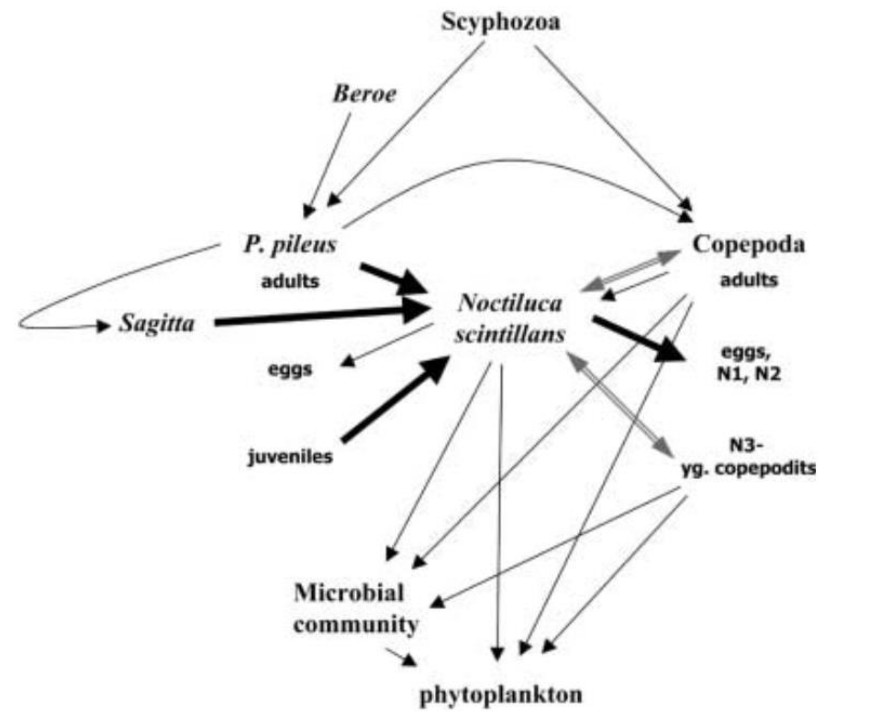


Fig. 10 Hypothetical food web related to *Noctiluca scintillans* (*single-pointed arrows* feeding relationships; *double-pointed arrows* potential competition; *bold arrows* potential interactions described in the "Discussion"). For copepods, eggs and early naupliar stages are summarised into one category, although only naupliar stages were investigated. Exemplary references for *thin arrows*: microbial community–*Noctiluca* (Kirchner et al. 1996) microbial community–copepods (Hansen et al. 1993; Nakamura and Turner 1997), phytoplankton–*Noctiluca* (Enomoto 1956; Kiørboe and Titelman 1998), *Pleurobrachia*–*Beroe* (Greve 1981), ctenophores–scyphozoa (Feigenbaum and Kelly 1984; Kopacz 1994), copepods–scyphozoa (Lucas et al. 1997)

(Fock et al., 2002)

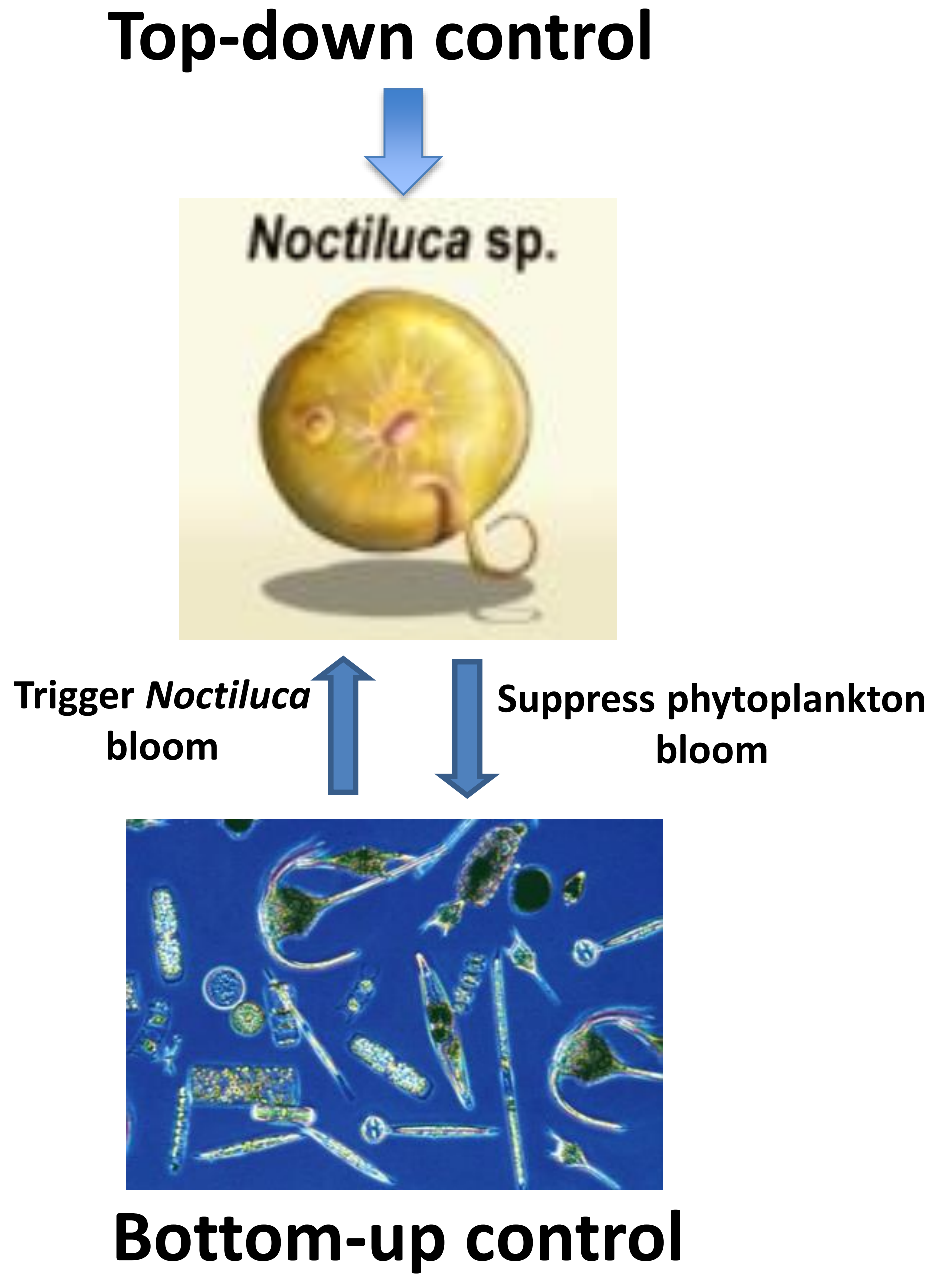
Possible blooming/succession mechanisms:

✧ **Bottom-up control**

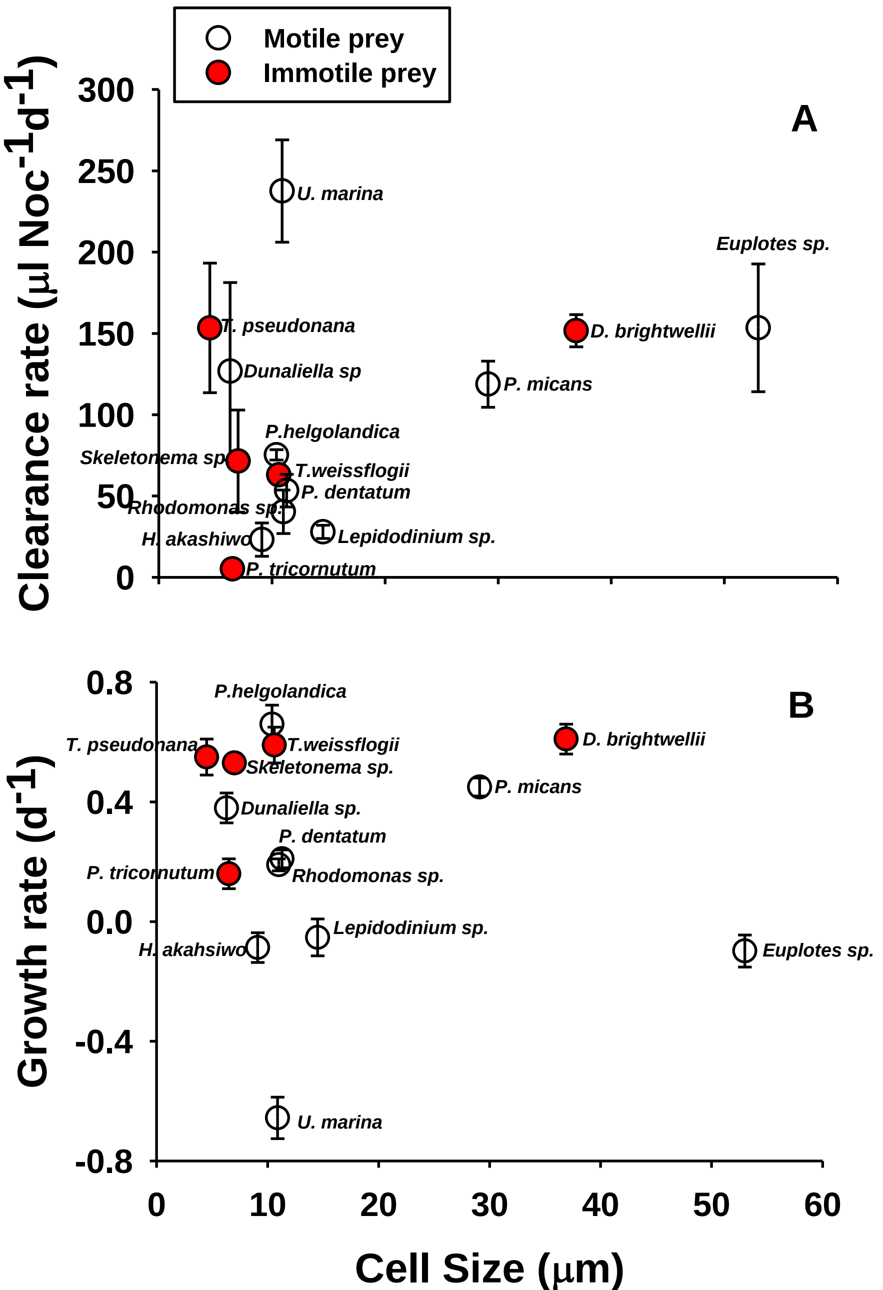
- prey spectrum
- prey quantity and quality
- prey composition

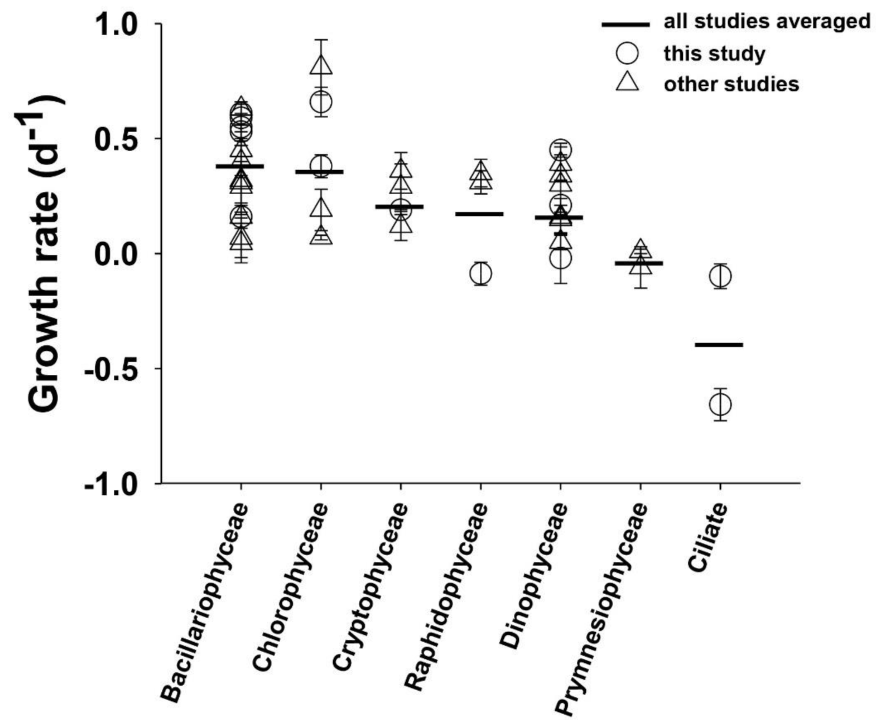
✧ **Top-down control**

✧ **Sexual reproduction**



2.1 Prey of different size and motility

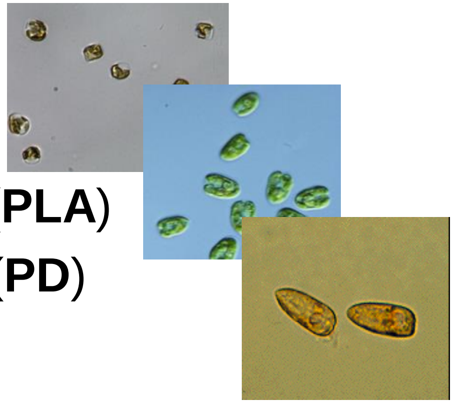




- Feeding without size limitation
- Cell size and motility cannot explain the suitability of the organisms as a prey for *Noctiluca*
- Higher growth rates on diatoms and chlorophytes

2.2 Prey of different quantity and quality

- ❑ Monospecific diets with gradient concentrations of prey items (3 species X 3 nutrient status)



Taxonomic difference

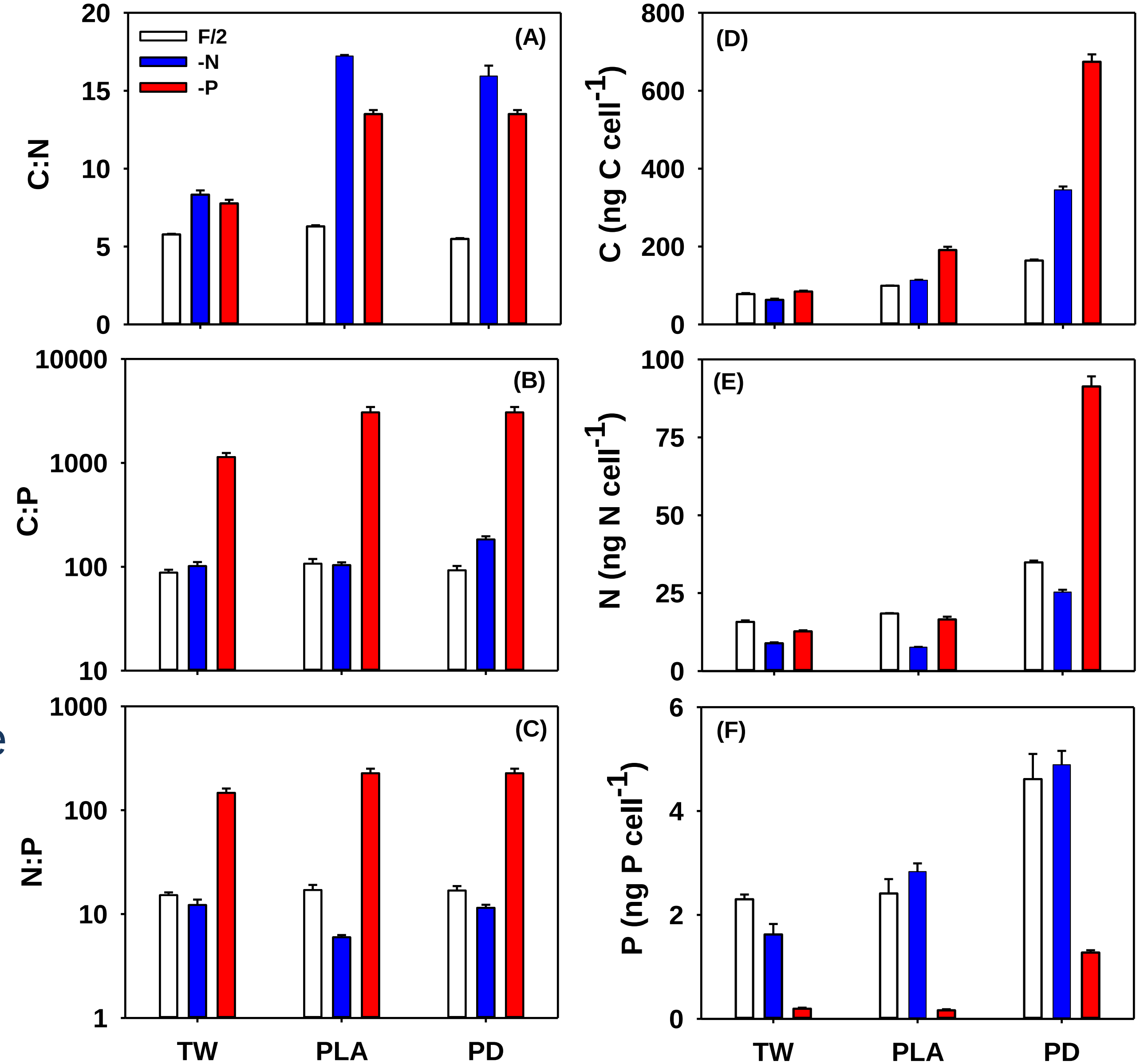
- Diatom – *Thalassiosira weissflogii* (**TW**)
- Chrolophyte – *Platymonas helgolandica* (**PLA**)
- Dinoflagellate – *Prorocentrum dentatum* (**PD**)

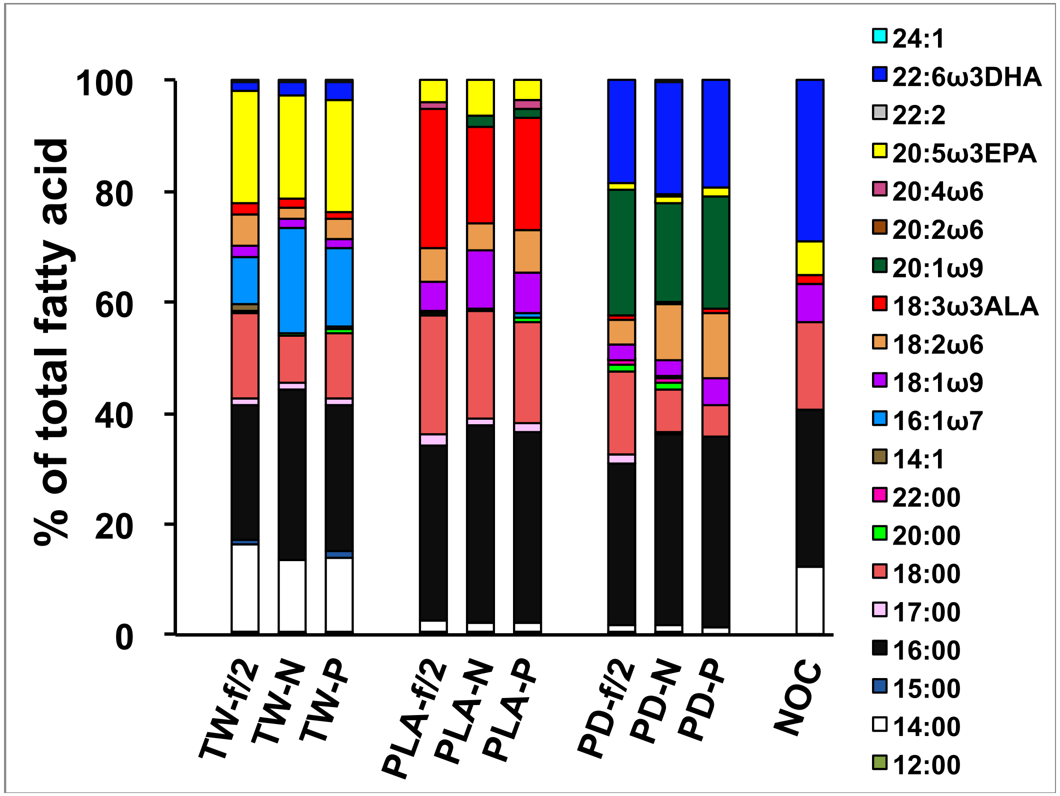
Nutritional status

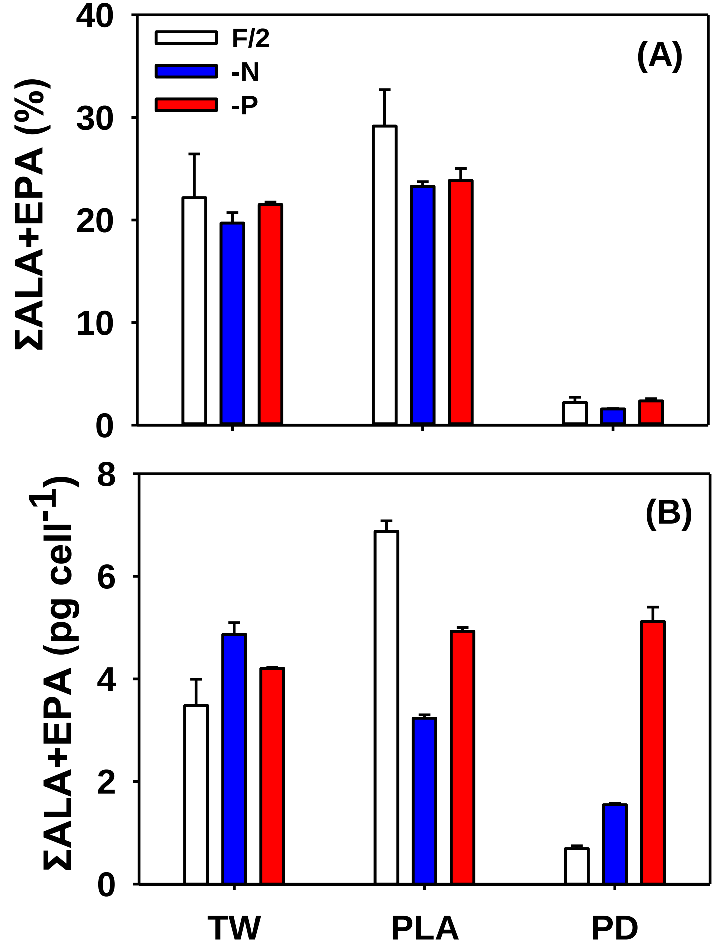
- Nutrient replete (f/2 medium)
- N-depleted (f/2 medium without N)
- P-depleted (f/2 medium without P)

- ❖ Phytoplankton cells grown in N- or P-depleted conditions correspondingly contained lower amounts of N or P content in cell

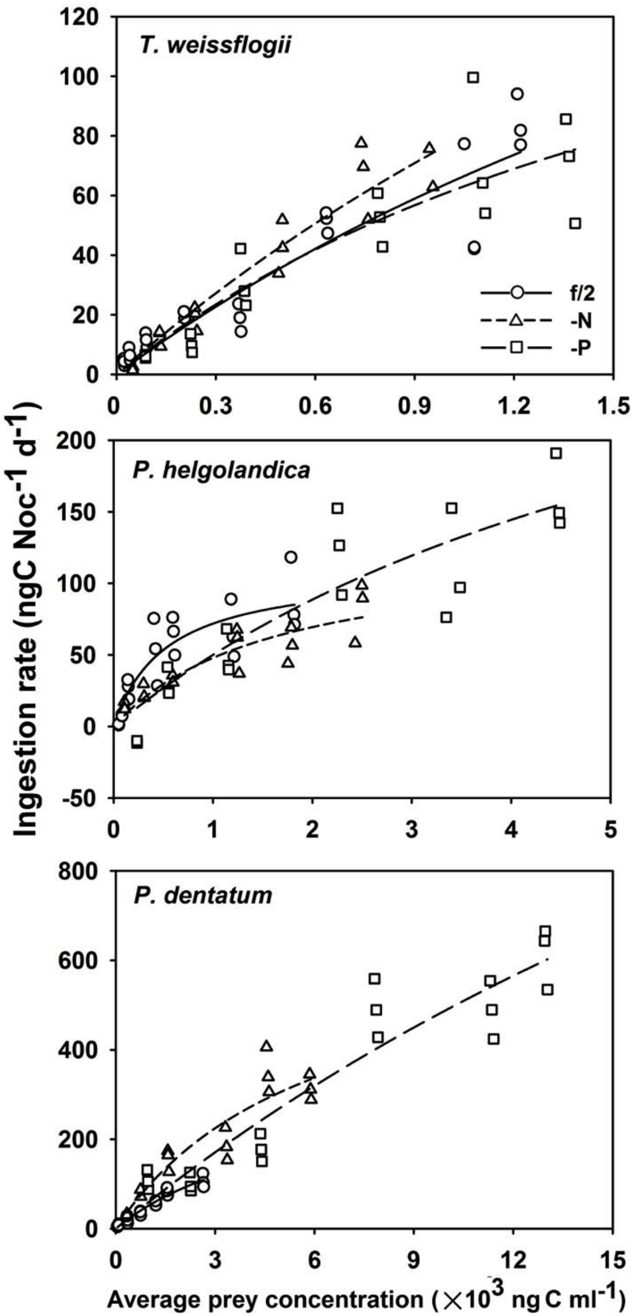
- ❖ Elemental ratios were generally more variable within than between algal groups







- ❖ Fatty acid composition were much less variable within than between algal taxonomic classes
- ❖ Diatoms were rich in EPA (~20%), dinoflagellates were rich in DHA (~18%), while in green algae, DHA was absent but ALA was substantially high (~26%)



Type Ⅱ functional curve

$$I=I_{max}\bullet C/(K_S+C)$$

I – ingestion rate (ng C Noc^{-1} d^{-1})
I_{max} – maximum ingestion rate (ng C Noc^{-1} d^{-1})
C – averaged prey concentration (ng C ml^{-1})
K_S – a half saturation concentration (ng C ml^{-1})

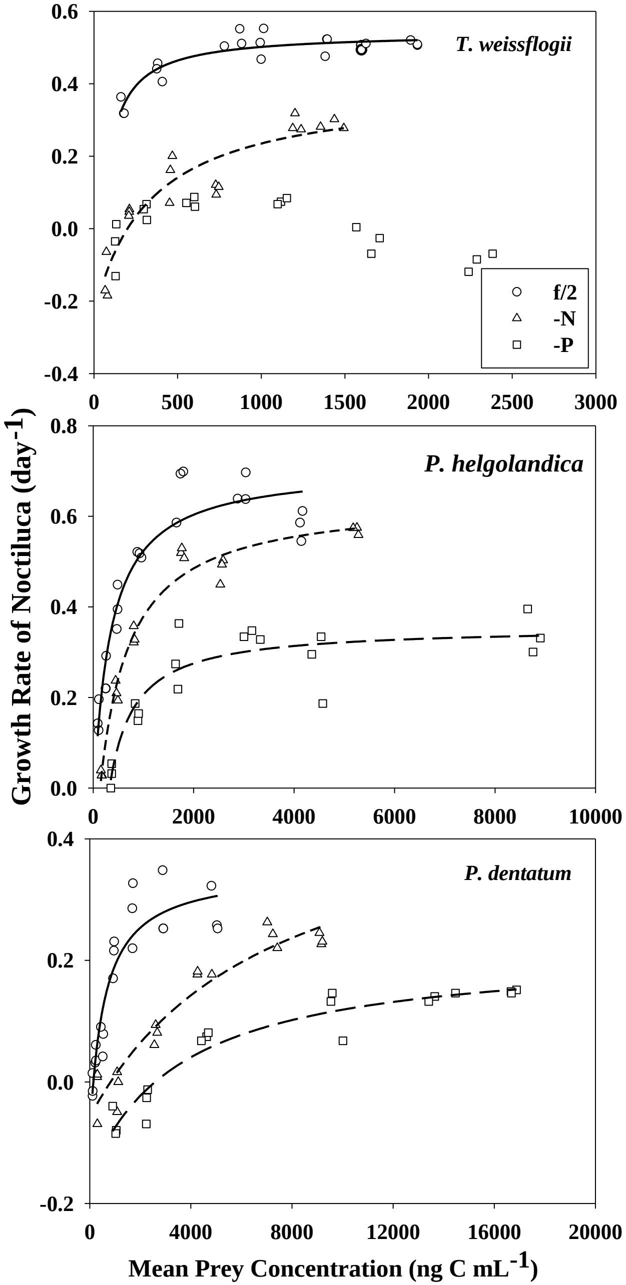
Prey	Treatment	I_{max} (ng C Noc^{-1} d^{-1})	K_S (ng C ml^{-1})	R^2	*p*
TW	f/2	293	3580	0.86	<0.0001
	-N	355	3615	0.93	<0.0001
	-P	196	2205	0.81	<0.0001
PLA	f/2	110	525	0.80	<0.0001
	-N	126	1629	0.79	<0.0001
	-P	389	6778	0.82	<0.0001
PD	f/2	331	5383	0.95	<0.0001
	-N	340	3038	0.87	<0.0001
	-P	710	11617	0.89	<0.0001

- I_{max} was generally higher on nutrient depleted prey
- Enhanced consumption did not occur at low food level

Modified type Ⅱ numerical curve

$$\mu = \mu_{max} \cdot (C-S')/[K_S+(C-S')]$$

- μ – growth rate (d^{-1})
- μ_{max} – maximum growth rate (d^{-1})
- C – averaged prey concentration (ng C $cell^{-1}$)
- S' – growth threshold (ng C ml^{-1})
- K_M – a half saturation concentration (ng C ml^{-1})



Experiment	Treatment	μ_{max} (d^{-1})	S' (ng C ml^{-1})	K_M (ng C ml^{-1})	R^2	*p*
TW	f/2	0.54	51	74	0.85	<0.0001
	-N	0.39	201	532	0.94	<0.0001
	-P	-	-	-	-	--
PLA	f/2	0.71	22	348	0.92	<0.0001
	-N	0.64	138	598	0.97	<0.0001
	-P	0.36	326	488	0.83	<0.0001
PD	f/2	0.35	145	707	0.89	<0.0001
	-N	0.50	830	7941	0.94	<0.0001
	-P	0.22	2591	6187	0.92	<0.0001

- Nutrient-depleted prey generally yielded lower μ_{max} (except PD-N), and higher K_M and S' for *Noctiluca*
- P-depleted prey reduced the growth of *Noctiluca* more significantly than N-depleted prey
- Impact of food quality was evident even at low food level
- PLA supported the highest μ_{max} and required lowest S', while TW yielded μ_{max} with the lowest prey concentration

Model Fits based on C, N, P and various fatty acids

Model fits based on **P content**

Independent variable	Formula	R^2	p-value	AIC
TW	$\mu = \frac{0.74\times(x-1.46)}{25.17+(x-1.46)}$	0.67	< 0.0001	-61.65
PLA	$\mu = \frac{0.69\times(x+3.06)}{14.43+(x+3.06)}$	0.74	< 0.0001	-95.80
PD	$\mu = \frac{0.33\times(x-5.49)}{28.52+(x-5.49)}$	0.80	< 0.0001	-168.66
Total (9 prey types combined)	$\mu = \frac{0.50\times(x+0.60)}{16.93+(x+0.60)}$	0.40	< 0.0001	-129.30

- Overall, P content is the best indicator to explain the growth of *Noctiluca*
- Model fits are better for each algal group individually than in combination

Model fits using **nutrient rich prey**

Independent variable	Formula	R^2	p-value	AIC
C	$\mu = \frac{0.52\times(x-59.27)}{227.17+(x-59.27)}$	0.42	< 0.0001	-52.30
N	$\mu = \frac{0.51\times(x-11.09)}{43.16+(x-11.09)}$	0.39	< 0.0001	-49.42
P	$\mu = \frac{0.51\times(x-1.52)}{6.03+(x-1.52)}$	0.40	< 0.0001	-51.03
ΣALA+EPA	$\mu = \frac{\mathbf{0.65\times(x+0.36)}}{\mathbf{15.6+(x+0.36)}}$	**0.89**	**< 0.0001**	**-155.35**
ΣPUFA	$\mu = \frac{0.55\times(x-3.44)}{19.4+(x-3.44)}$	0.52	< 0.0001	-65.04
ΣFA	$\mu = \frac{0.53\times(x-12.78)}{51.68+(x-12.78)}$	0.45	<0.0001	-56.30

- ΣALA +EPA is also important in determining the food quality for *Noctiluca*

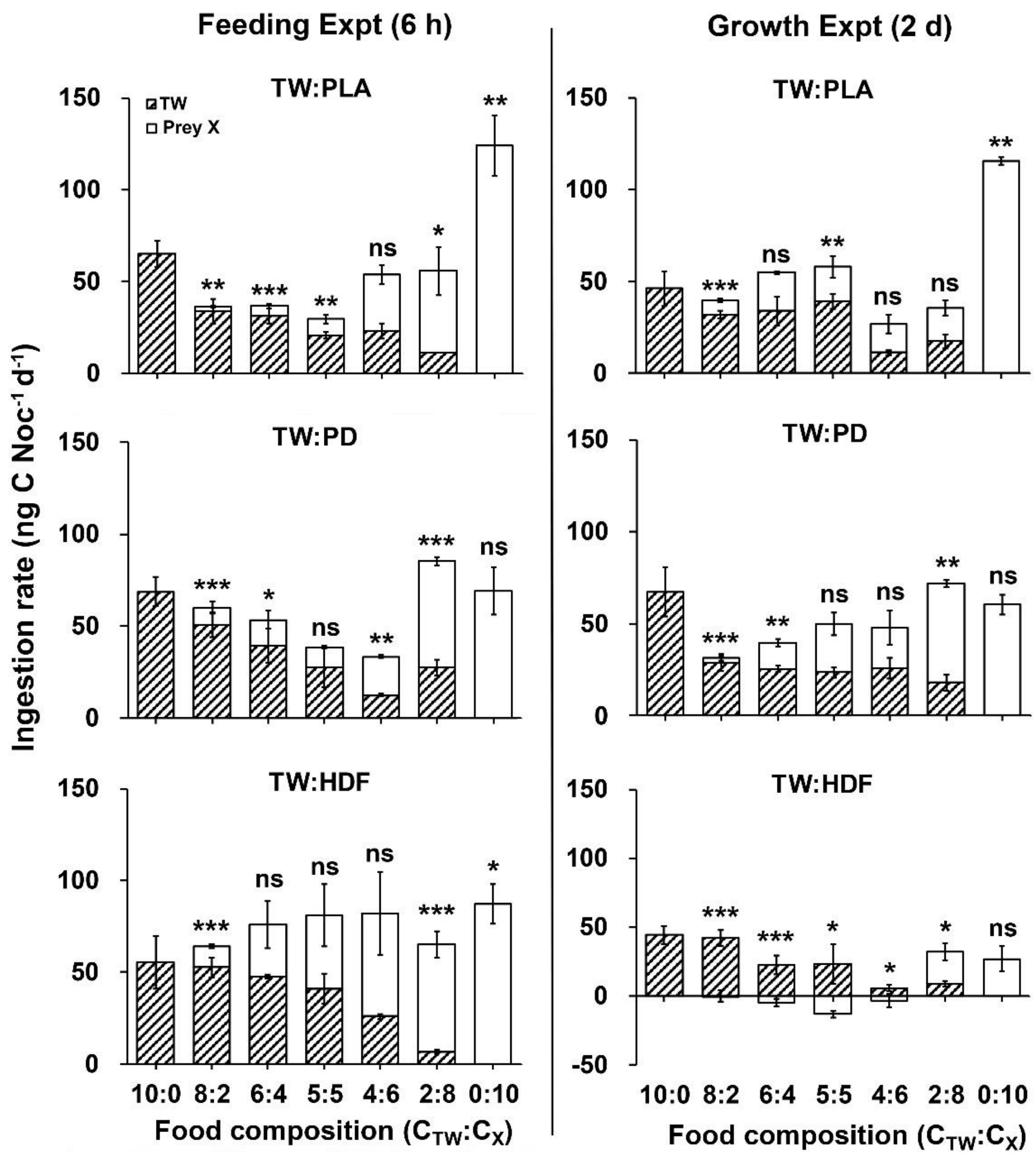
3.3 Prey of different combinations

- Mixed diets (3 food pairings)

		Prey paired		
	T. weissflogii (TW)	*P. helgolandica* (PLA)	*P. dentatum* (PD)	*Lepidodinium sp.* (HDF)
Quality		Superior	inferior	poor
Trophic type	autotrophic	autotrophic	autotrophic	heterotrophic
Class	Bacillariophyceae	Chlorophyceae	Dinophyceae	Dinophyceae

Total prey conc. is **CONSTANT** (1 mg C l^{-1})

C_{TW}:C_X =10:0, 2:8, 4:6, 5:5, 6:4, 8:2 and 0:10



- Ingestion showed no significant difference on the **single food treatments** (C_{TW}:C_x = 10:0 and 0:10) between two incubation periods, except that on HDF
- Ingestion on the **mixed diet treatments** differed among prey treatments, and also varied between the two incubation periods

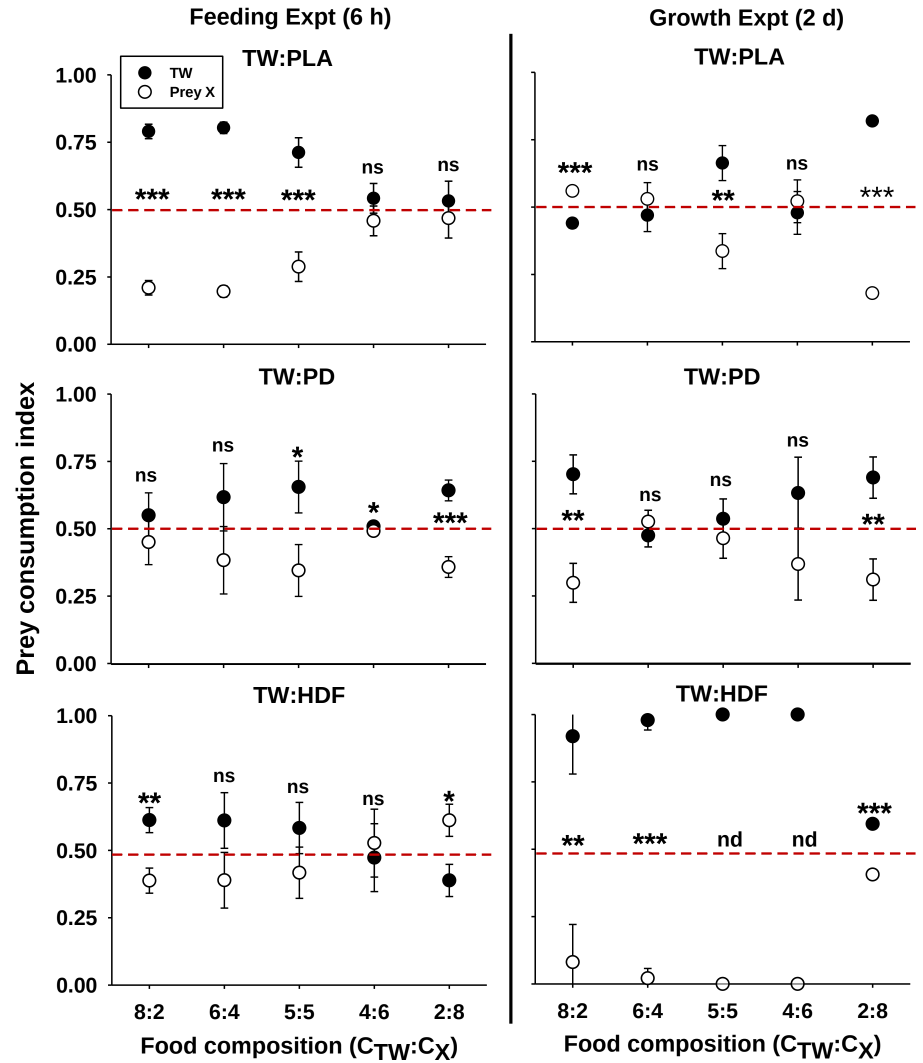
The difference between two prey species in the same food treatment is * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns: not significant.

Prey consumption & Prey abundance

Food pairings	Initial prey concentration (Cx)	Ingestion rate	Clearance rate	Prey consumption index
6 h Expt				
TW+PLA	C_{TW}	0.932***	0.317	0.791***
	C_{PLA}	0.906***	0.895***	0.782***
TW+PD	C_{TW}	0.831***	-0.45	-0.25
	C_{PD}	0.922***	0.628**	-0.24
TW+HDF	C_{TW}	0.892***	0.323	0.715**
	C_{HDF}	0.923***	0.41	0.653**
2 d Expt				
TW+PLA	C_{TW}	0.676**	-0.622**	-0.848***
	C_{PLA}	0.764***	0.409	-0.862***
TW+PD	C_{TW}	0.776***	-0.621**	-0.078
	C_{PD}	0.958***	0.795***	-0.162
TW +HDF	C_{TW}	0.864***	0.536*	0.513
	C_{HDF}	0.686**	0.699**	0.311

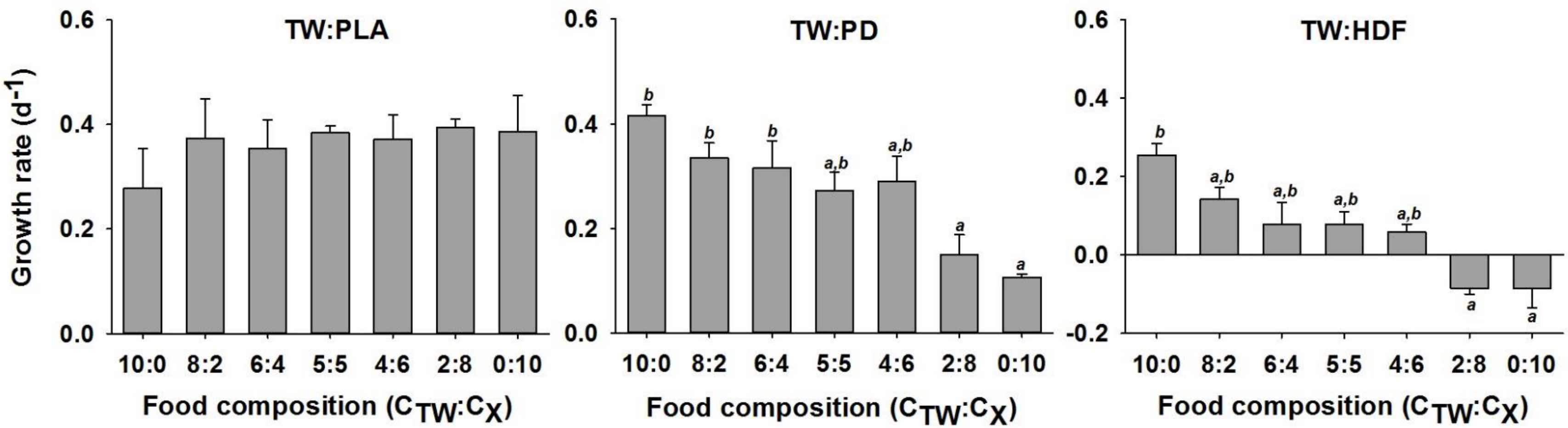
Note: Levels of significance for correlations are * $p<0.05$, ** $p<0.01$, *** $p<0.001$

- In short incubations (6 h), *Noctiluca*'s ingestion and feeding preference depended on the prey abundance
- In the longer time incubation (2 d), *Noctiluca* increased its feeding preference on superior prey



The difference between two prey species in the same food treatment is * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns: not significant, nd: not determined.

Noctiluca's growth & Prey abundance and ingestion

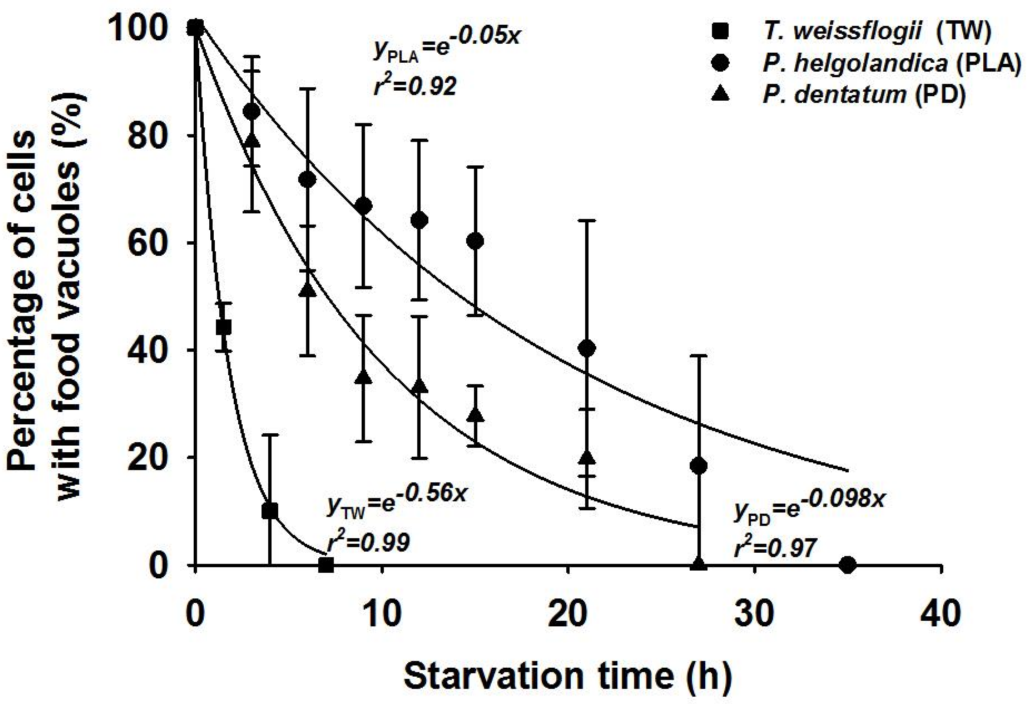


Growth rate	C_{TW}	C_X	I_{TW}	I_X
μ_{TW+PLA}	-0.551*	0.175	-0.455	-0.245
μ_{TW+PD}	0.874***	-0.900***	0.678**	-0.896***
μ_{TW+HDF}	0.937***	-0.819***	0.715**	-0.779***

Note: Levels of significance for correlations are * $p<0.05$, ** $p<0.01$, ***. $p<0.001$

- Nutritional value of the prey was important in governing *Noctiluca*'s growth
- The energetic cost in handling two different prey seemed outweigh the synergetic nutritional advantage of consuming these prey

- The handling time on **TW is 0.38 min prey^{-1}, PD is 0.71 min prey^{-1} and PLA is 1.31 min prey^{-1}** based on the functional response models ($T_{handling}=1/I_{max}$)



❖ It is energetically efficient for *Noctiluca* to feed preferentially on TW when mixed with a refractory prey

❖ *Noctiluca*'s ultimate dietary choice seems a result of the trade-off between maximizing food/nutrient intake and minimizing the energy cost of handling food, or specifically food digestion

Bottom-up forcing:

1) Species-specific nutritional properties rather than prey size or motility constrain *Noctiluca*' feeding preference and growth.

2) Growth and grazing of *Noctiluca* generally respond numerically to food supply.

3) P limitation had stronger negative effects on *Noctiluca* than N limitation.

4) P and ΣALA +EPA are good indicators of the food quality for *Noctiluca*, but the importance of their influence depends on the prey nutritional status.

5) It is energetically and efficiently for *Noctiluca* to feed preferentially on diatom, which should have great implication for the formation and succession of *Noctiluca* blooms and food web dynamics during its bloom.

3. Top-down control – as a prey for meso- or metazoan

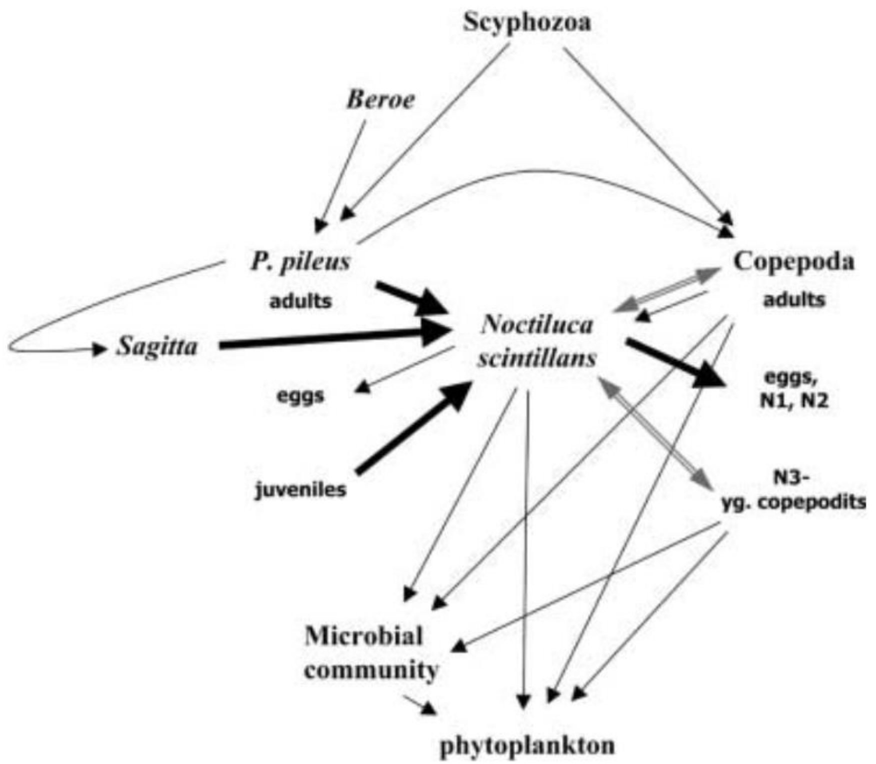
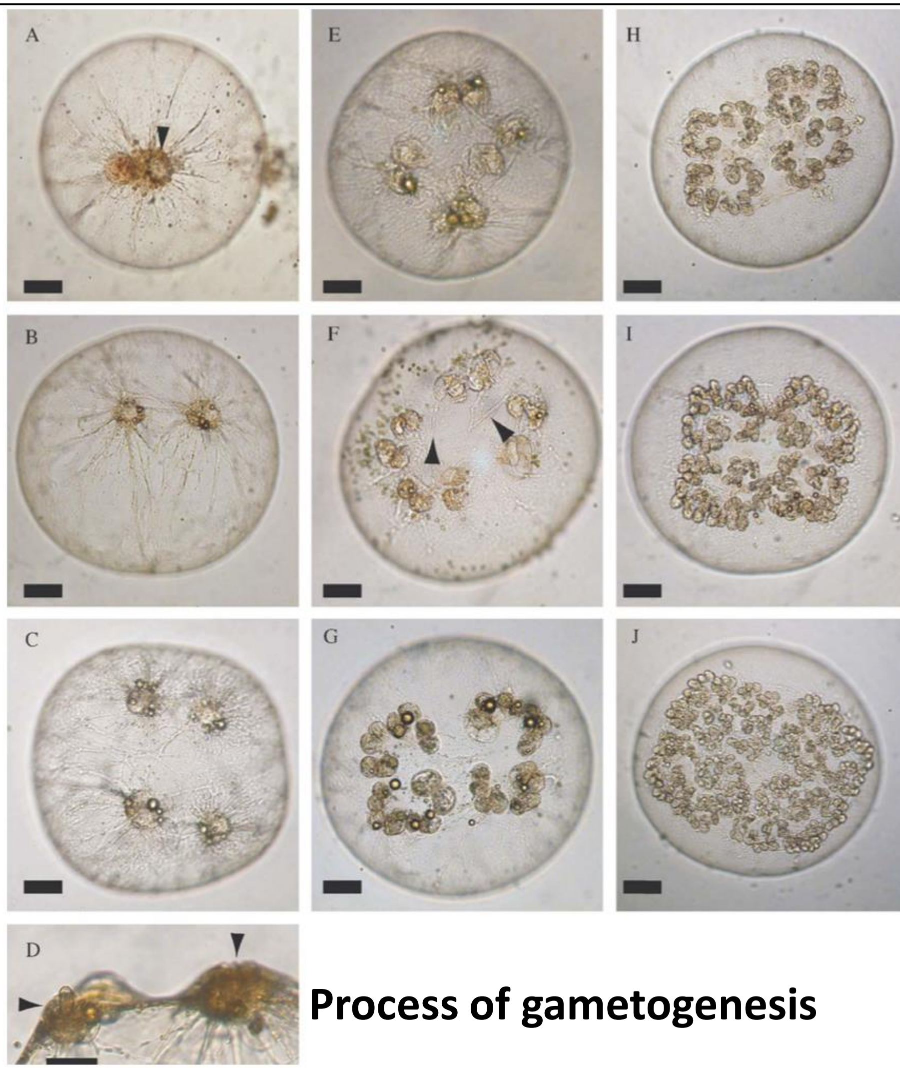


Fig. 10 Hypothetical food web related to *Noctiluca scintillans* (*single-pointed arrows* feeding relationships; *double-pointed arrows* potential competition; *bold arrows* potential interactions described in the "Discussion"). For copepods, eggs and early naupliar stages are summarised into one category, although only naupliar stages were investigated. Exemplary references for *thin arrows*: microbial community–*Noctiluca* (Kirchner et al. 1996) microbial community–copepods (Hansen et al. 1993; Nakamura and Turner 1997), phytoplankton–*Noctiluca* (Enomoto 1956; Kiørboe and Titelman 1998), *Pleurobrachia*–*Beroe* (Greve 1981), ctenophores–scyphozoa (Feigenbaum and Kelly 1984; Kopacz 1994), copepods–scyphozoa (Lucas et al. 1997)

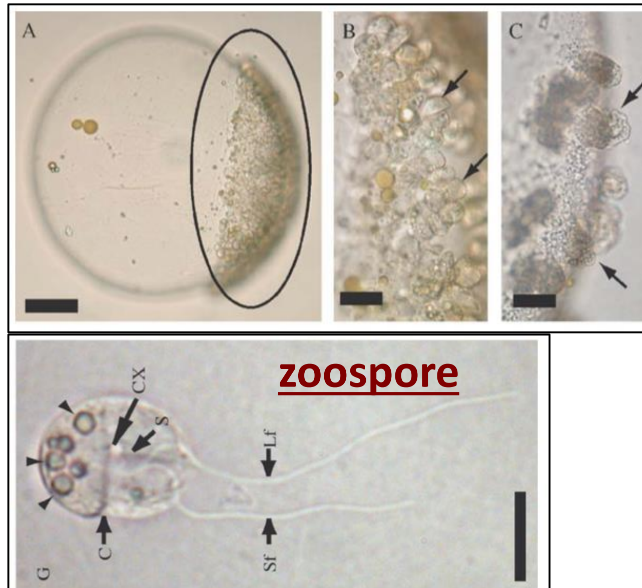
(Fock et al. 2002)

As an untypical “prey” for ciliate

Process of *Noctiluca’s* sexual reproduction



Process of gametogenesis



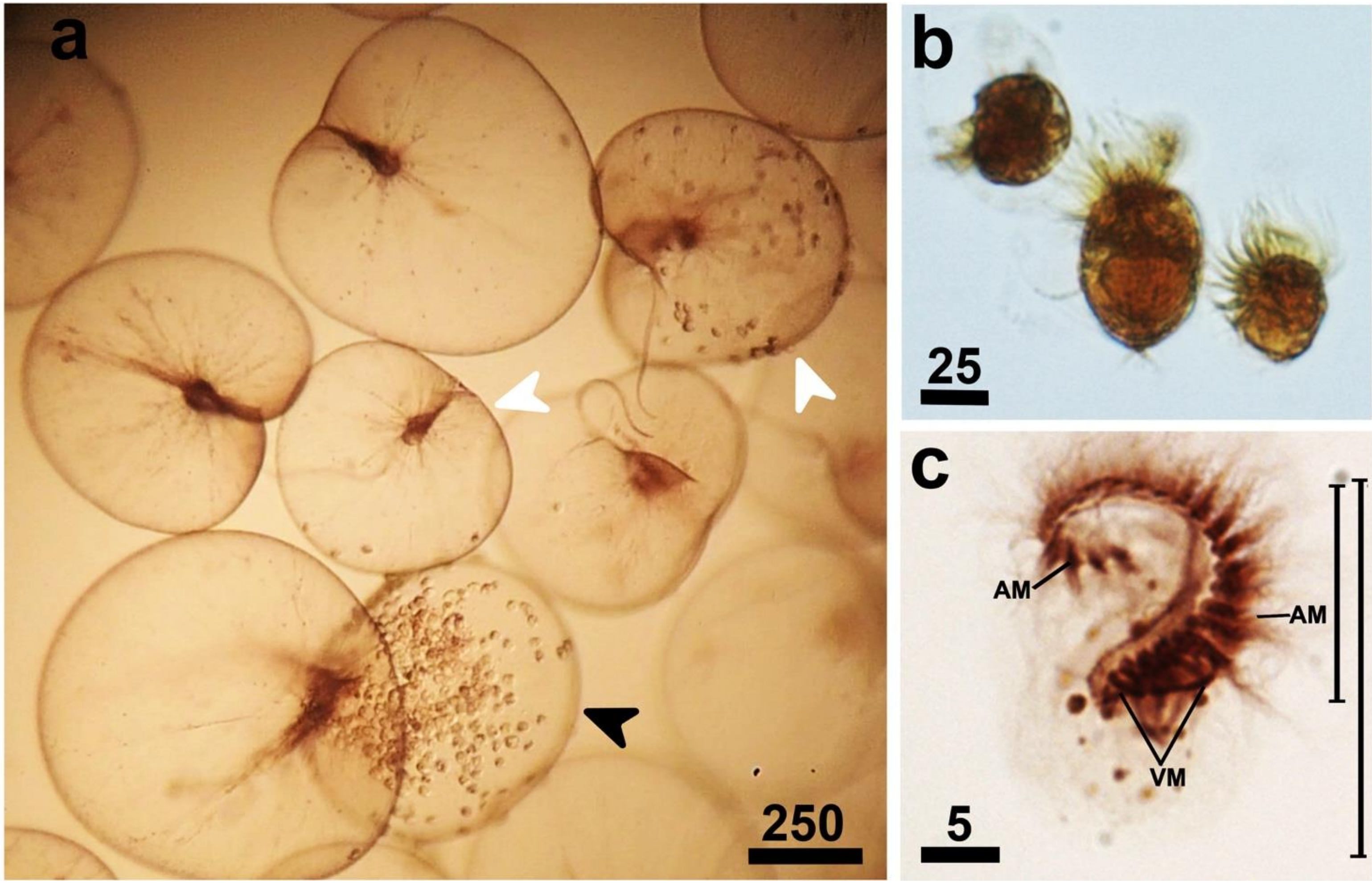
Maturation of gametes

(Fukuda, 2006)

Repeated *Noctiluca* blooms in Port Shelter

December 2014

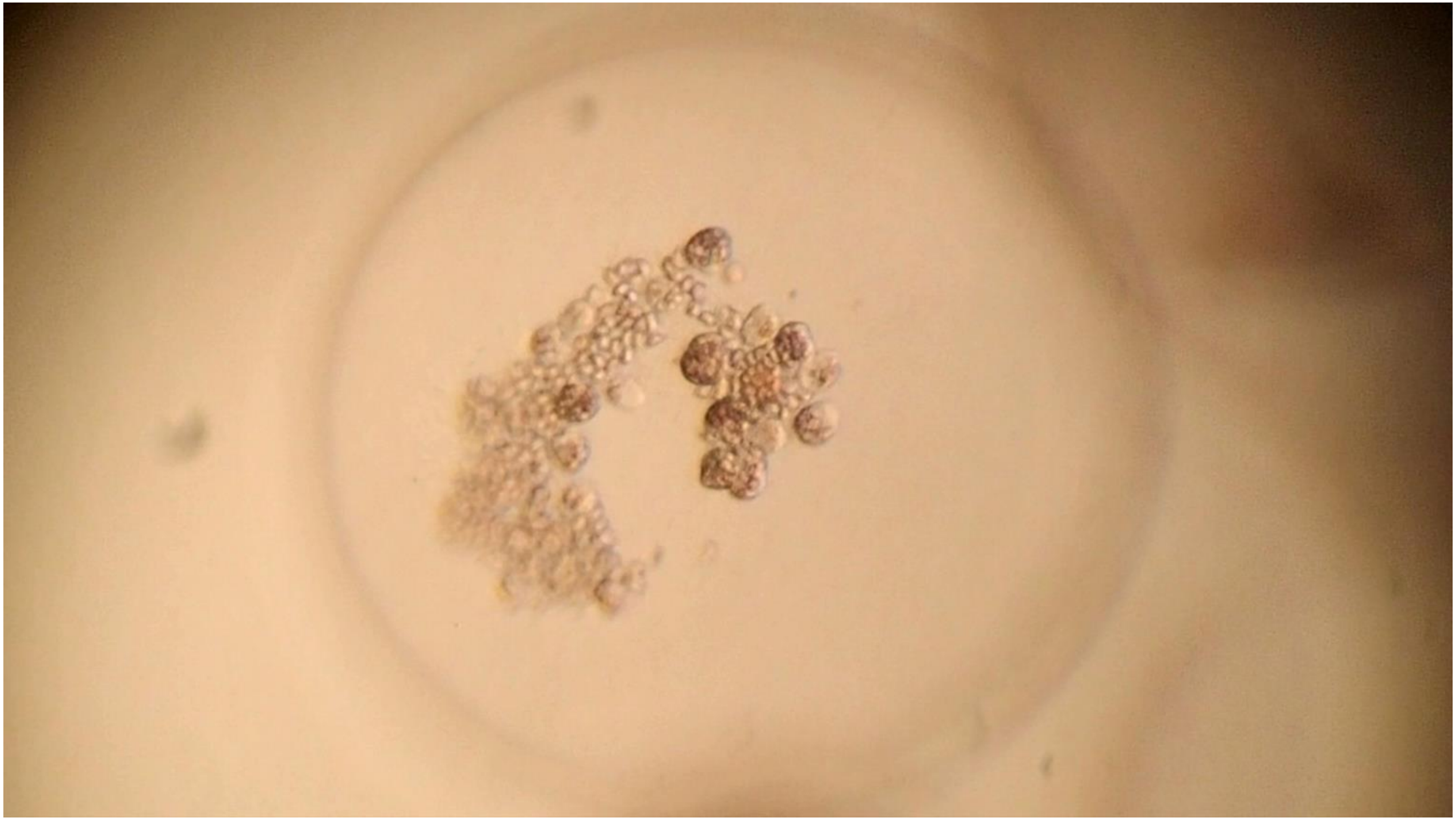
Noctiluca & swimming organisms



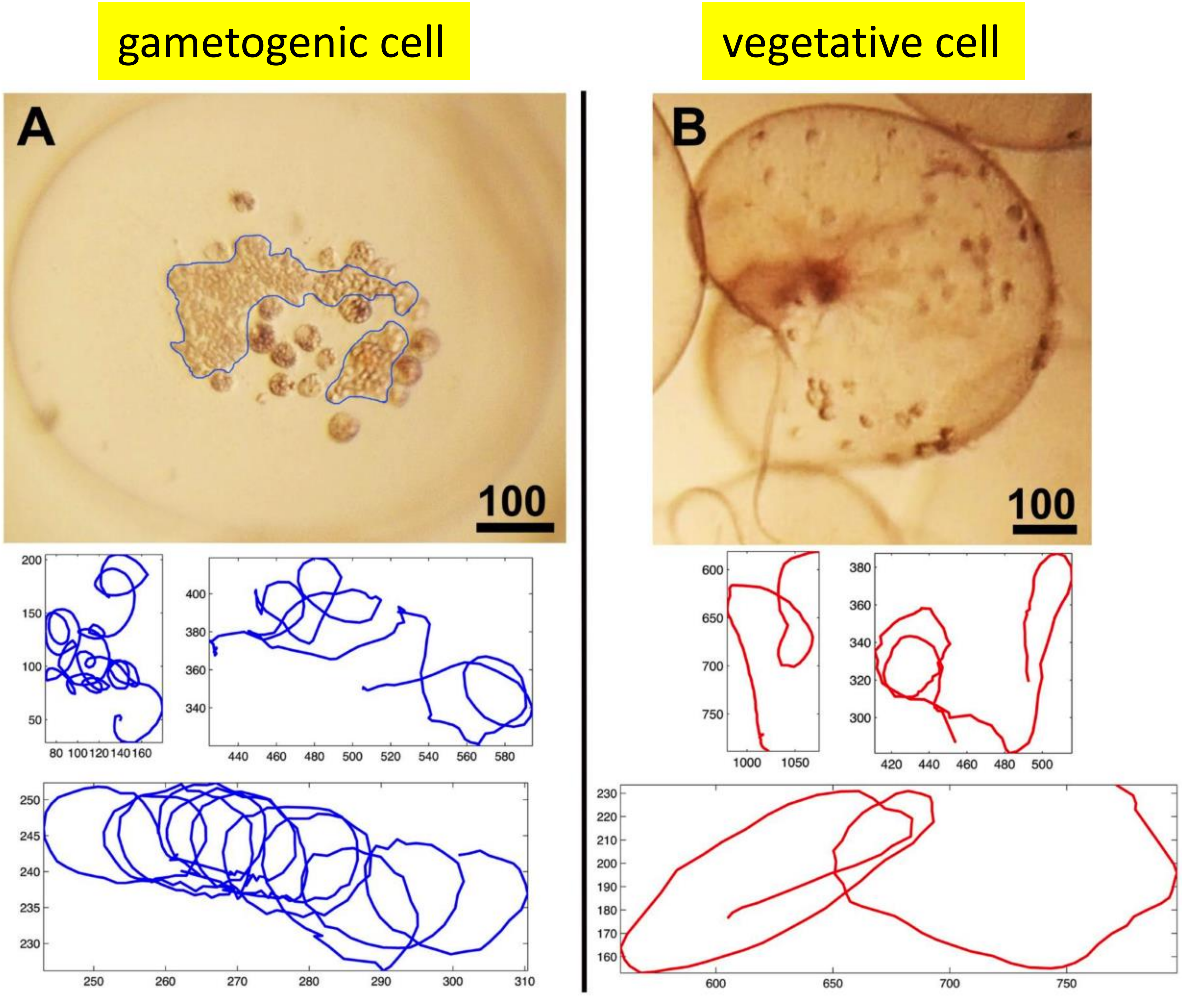
Strombidium hongkongense swarming on or around gametogenic (black arrow) and vegetative (white arrows) *Noctiluca* cells

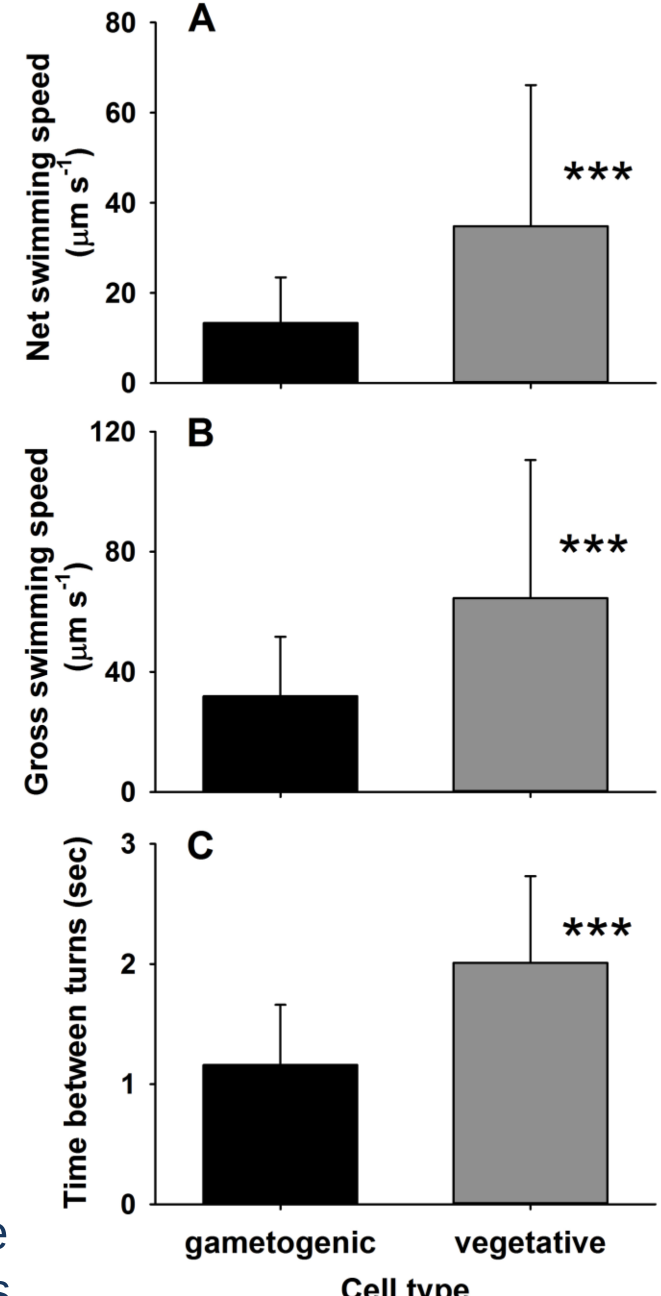
- The ciliate is a new species belonging to the *Strombidium* group, and tentatively named *S. hongkongense*
- *S. hongkongense* has deep and prominent buccal cavity, and short but strong adoral zone of membranelles that are used as walking or crawling appendages

Ciliate feed on progametes of *Noctiluca*



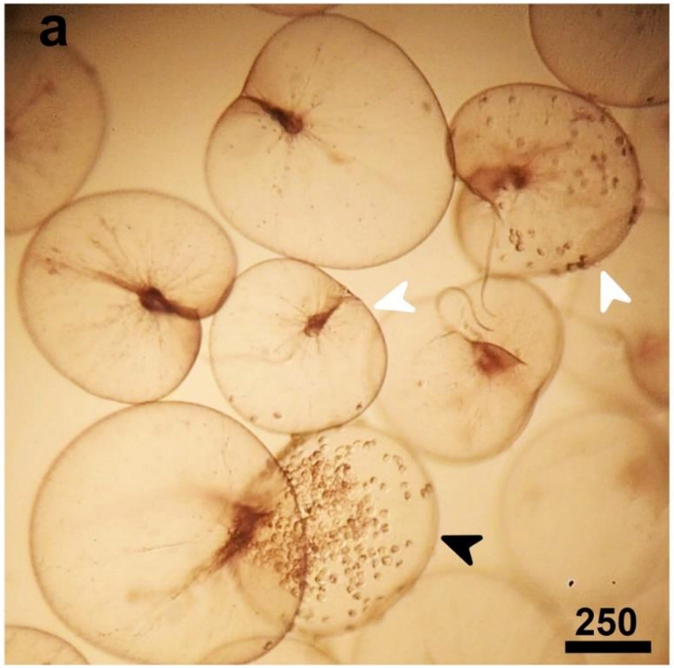
Swimming behavior of *S. hongkongense*

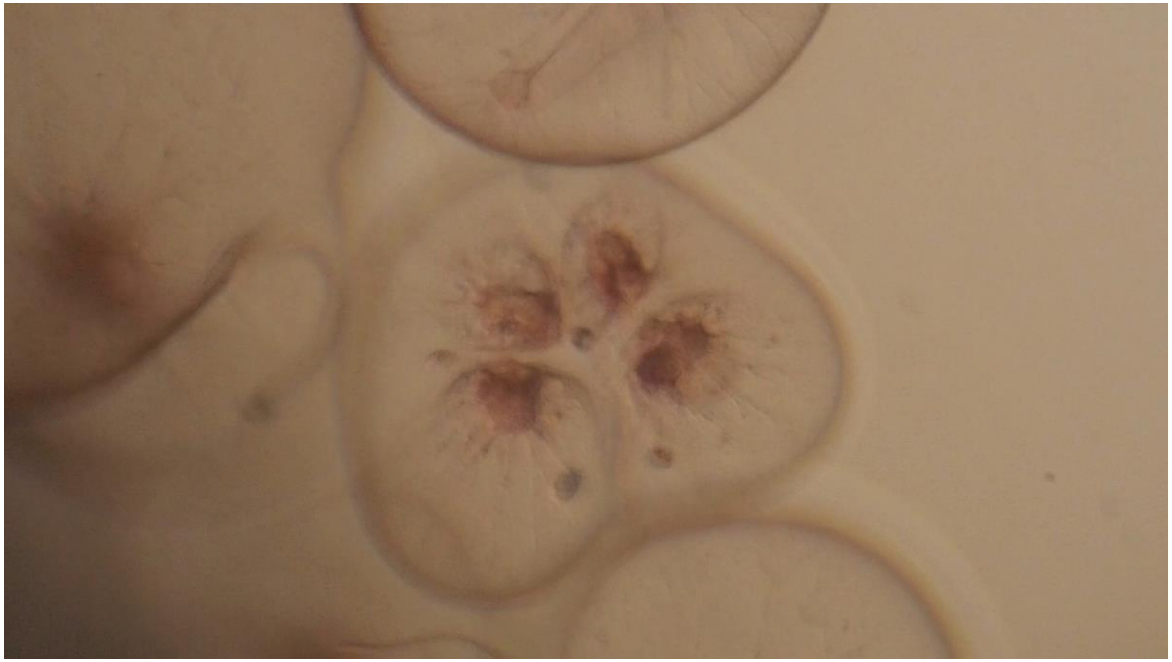




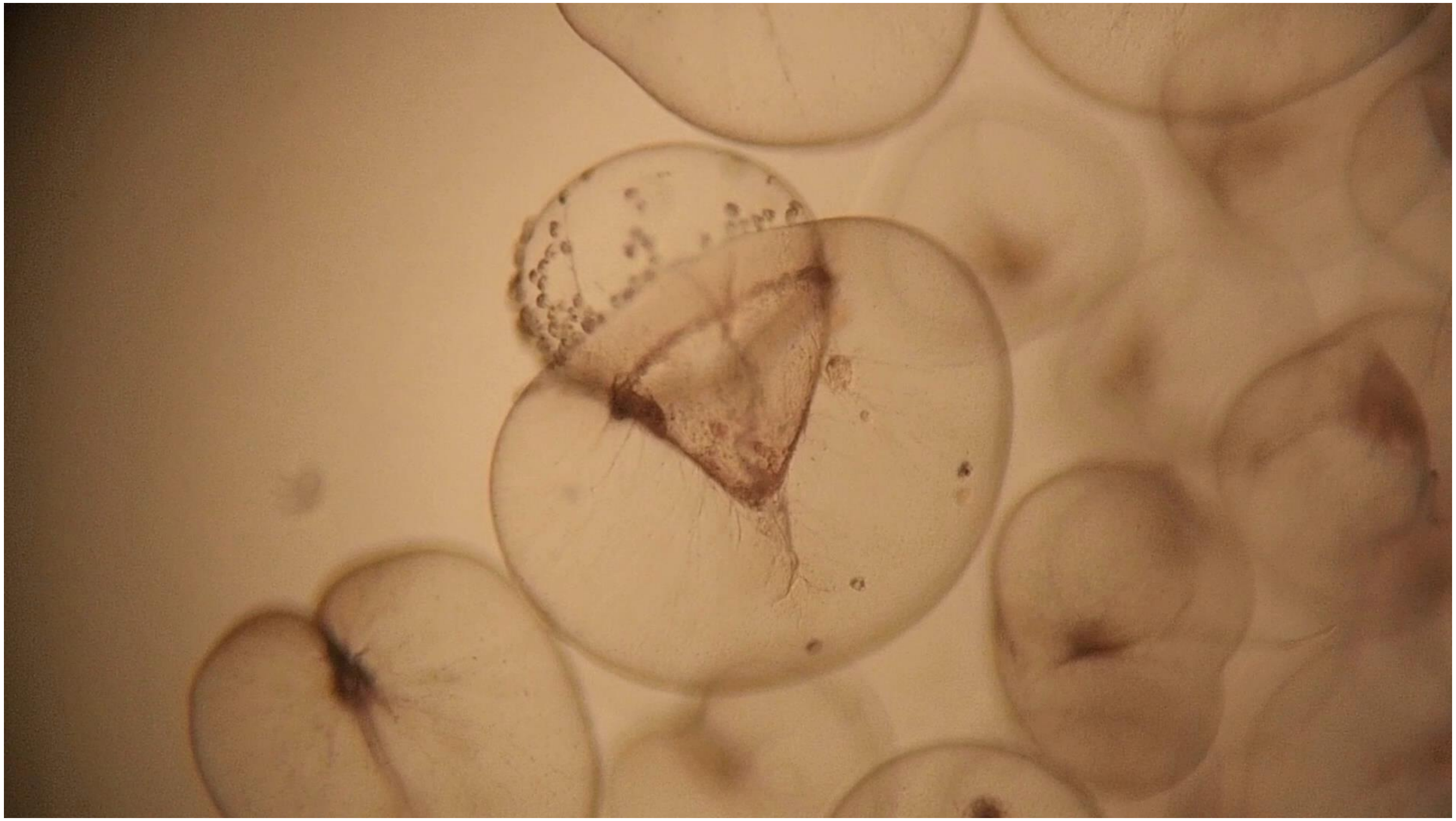
- ❖ Ciliates associated with gametogenic cells had significantly lower speed and changed direction more frequently than those associated with vegetative cells

Localization & Chemosensory?

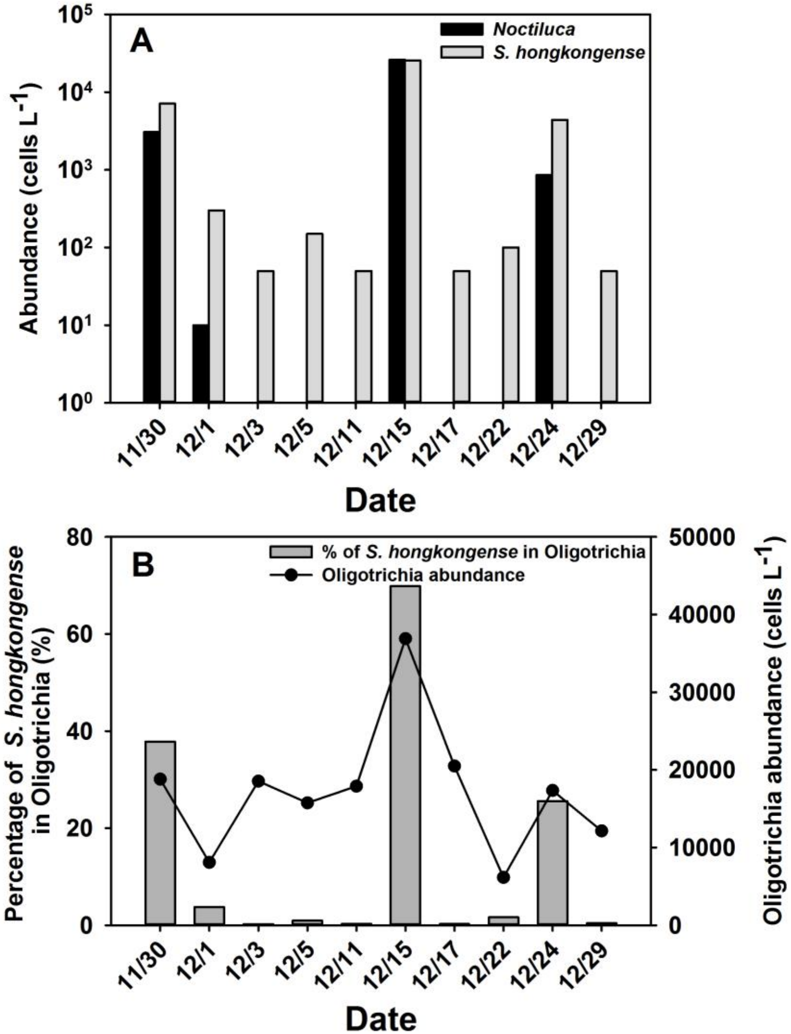




Noctiluca did not to feed the ciliate



- A vegetative *Noctiluca* cell cannibalizing a ghost gametogenic cell that had just been cleared of progametes by *S. hongkongense*

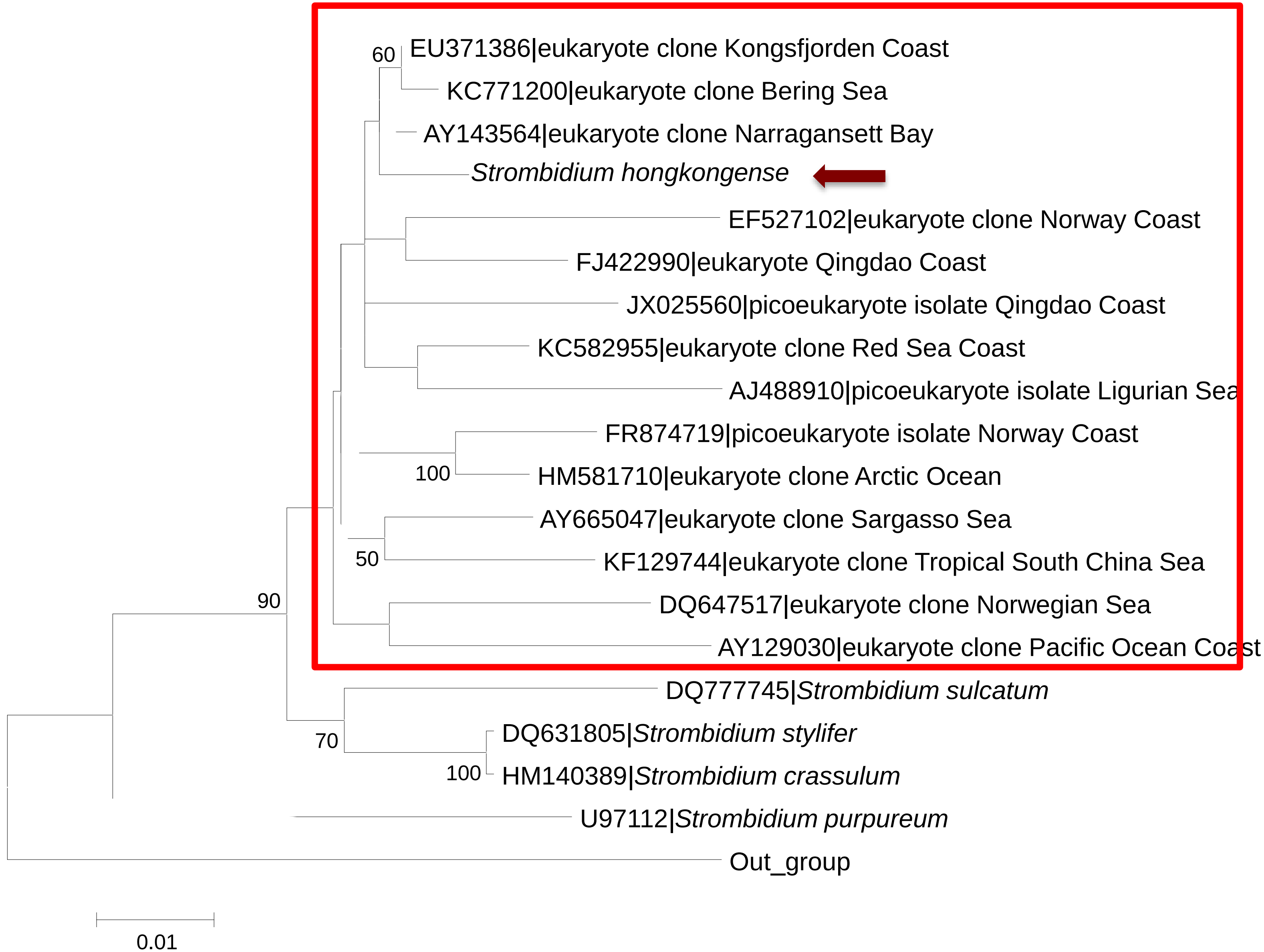


- The ingestion potential of *S. hongkongense* was 0.5~13 progametes ciliate^{-1} h^{-1}, depending on the division stage of progametes (i.e. the cell size)

❖ *S. hongkongense* reached maximum abundance of 25,700 cells L^{-1} when *Noctiluca* bloomed (26,100 cells L^{-1}) on 15 December

❖ Assuming 5% of *Noctiluca* cells on 15 December were at 1024-progamet stage, the seeding stock of *S. hongkongense* would remove the progametes of all gametogenic cells as short as 4h

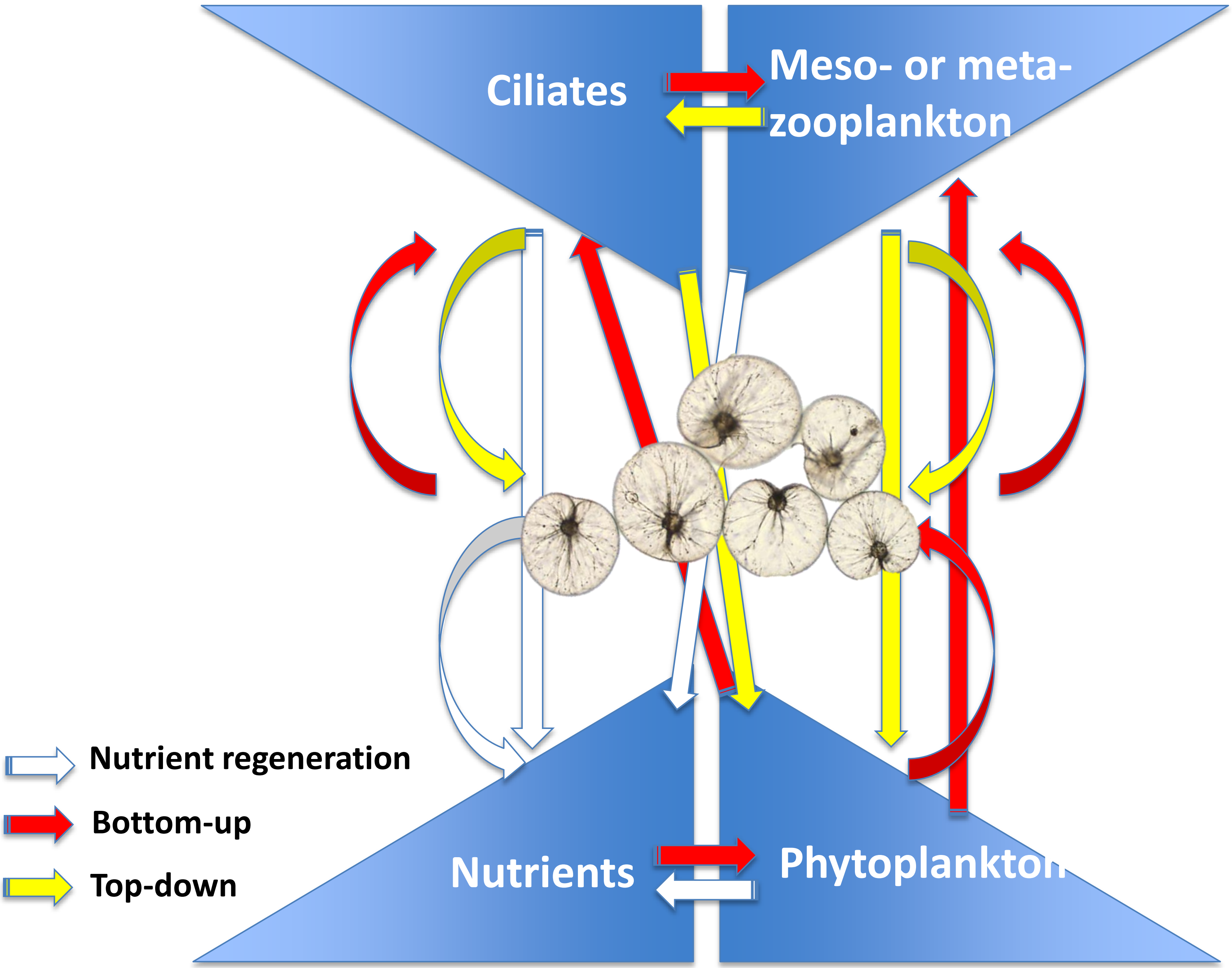
Probably not only a regional occurrence !!



Top-down forcing:

1) Predation by *S. hongkongense* reduces the effectiveness of sexual reproduction as a survival or blooming strategy for *Noctiluca*, potentially shortening the durations of *Noctiluca* blooms and altering food web structure and energy flows during bloom conditions

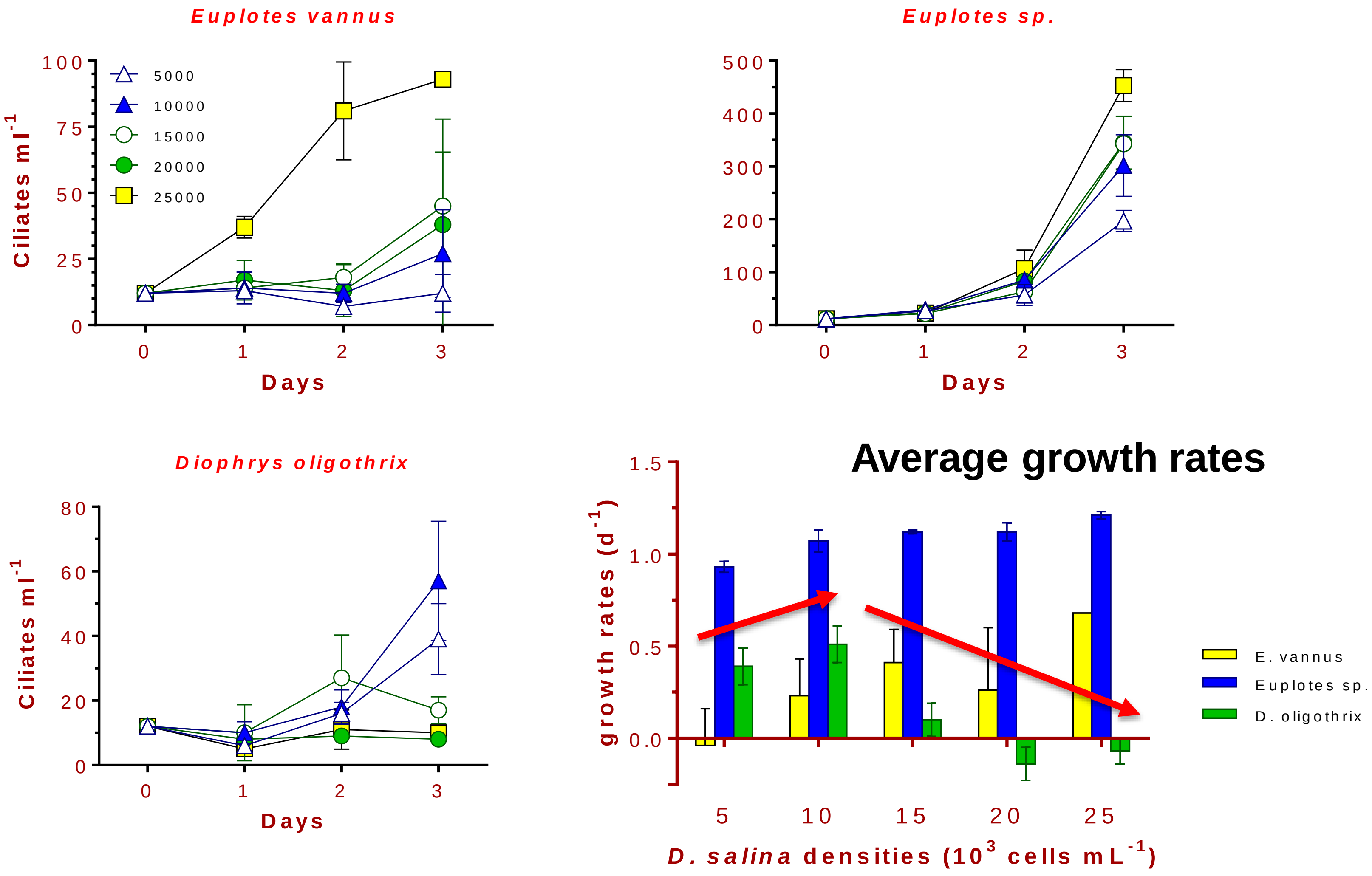
2) Such unique trophic interaction between *S. hongkongense* and *Noctiluca* is likely more than a regional occurrence or occasional event, but possibly a common phenomenon in marine ecosystems worldwide.


Ciliates
Meso- or meta-zooplankton
Nutrients
Phytoplankton
Nutrient regeneration
Bottom-up
Top-down

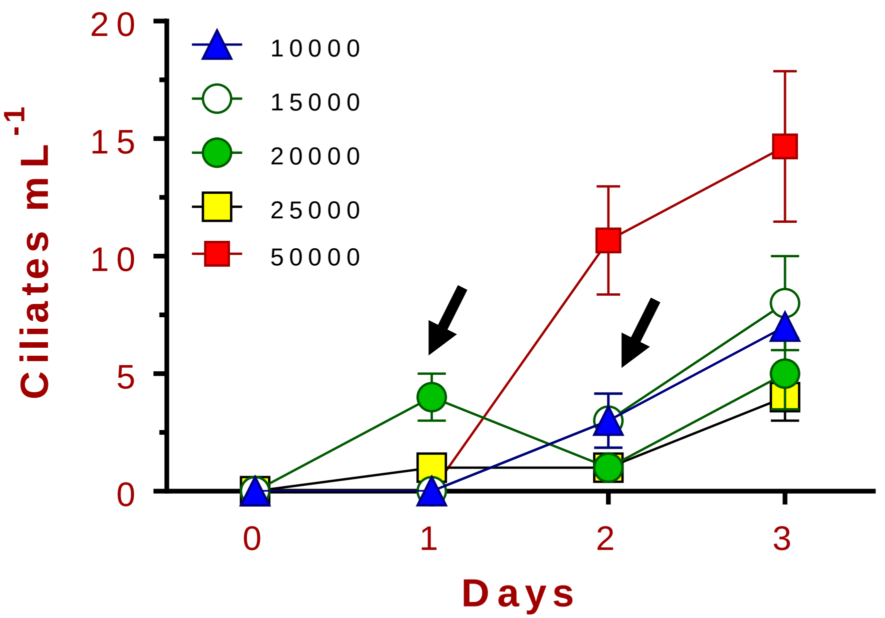
Other reversal trophic links?

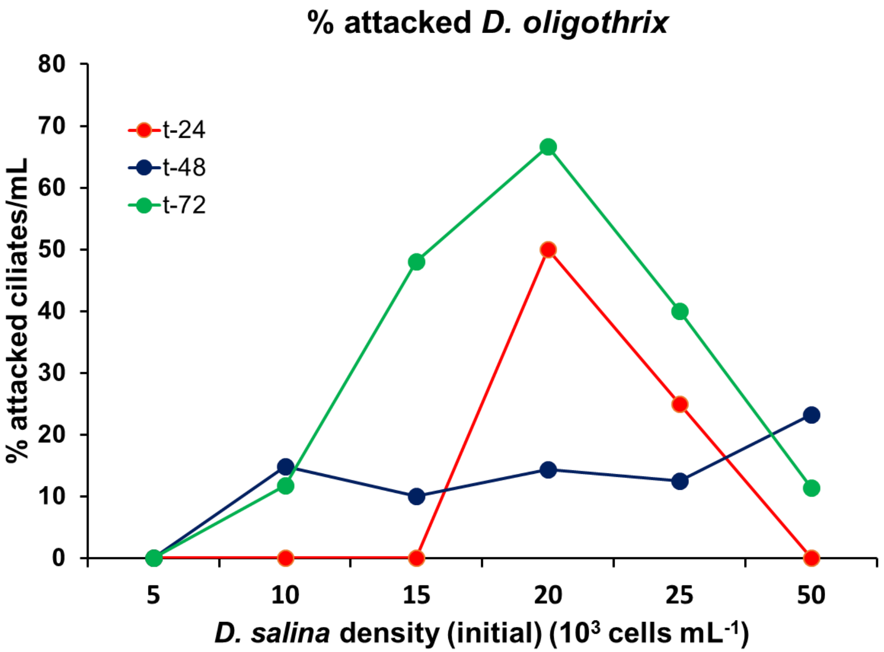
Dunaliella salina attacking *Diophrys oligothrix*

Growth of ciliates on D. salina



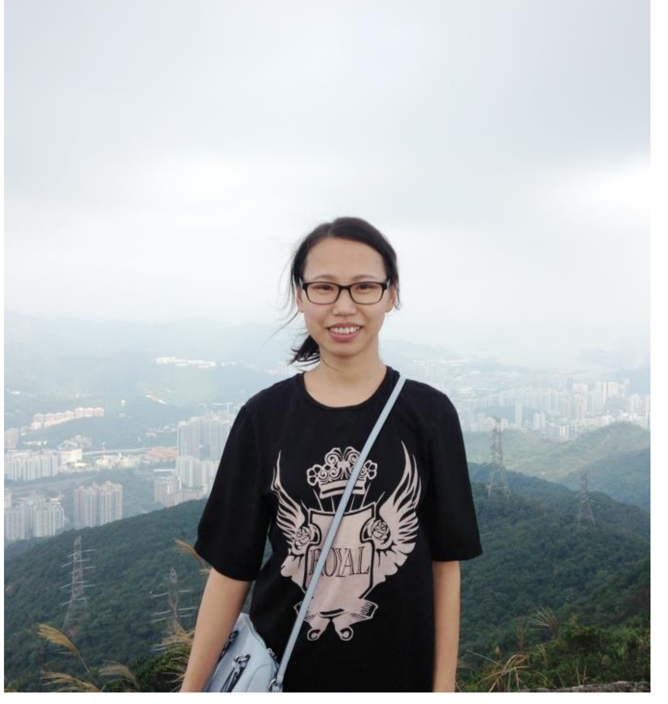
Number of *D. oligothrix* ‘attacked’ by *D. salina*





Acknowledgements

- Shuwen Zhang for carrying out most of the studies
- Michael Landry (SIO) and Karen Chan (HKUST) for helpful discussion and comments
- Research Grants Council of Hong Kong for financial support



THANK YOU