
Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

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Abstract :

While theoretical food web studies highlight the importance of alternative energy pathways in shaping community response to bottom-up and top-down forcing, empirical insight on the relevance of the predicted patterns is largely lacking. In marine plankton food webs differences in food size spectra between ciliates and copepods lead to alternative energy pathways, one expanding from small phytoplankton over ciliates to copepods, the other from large edible phytoplankton directly to copepods. Correspondingly, predation pressure by copepods leads to an increase of small phytoplankton through top-down control of copepods on ciliates, but to a decrease of large phytoplankton through direct predation by copepods. Hence, food web theory predicts a shift from the dominance of large to small algae along an enrichment gradient. This prediction clearly deviates from the general assumption of a shift from small fast growing to larger slow-growing phytoplankton taxa with increasing nutrient availability. However, if copepods themselves are under top-down control by strong predation through planktivores such as fish or jellyfish, dominance of large algae is expected throughout the enrichment gradient. We tested these predictions by analyzing the phytoplankton composition from numerous marine lakes and lagoon sites located on the archipelago of Palau covering a wide range of nutrient levels, comparing sites lacking large numbers of higher trophic levels with sites harboring high densities of jellyfish. The observed patterns strongly support that higher trophic levels influence the phytoplankton size distribution along a nutrient enrichment gradient, highlighting the importance of alternate energy pathways in food webs for community responses.

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22

44 **Introduction**

45 The interplay between bottom-up and top-down control in shaping community composition has
46 been under debate for decades (Hairston et al. 1960, Hunter and Price 1992, Hessen and
47 Kaartvedt 2014). Food chain theory proposes an alternating pattern of bottom-up and top-down
48 control from top consumers down to primary producers, where only trophic levels under bottom-
49 up control respond to increased nutrient availability (Fretwell 1985, Oksanen et al. 1981).
50 Adding or removing the top trophic level leads to a cascading effect down the food chain, due to
51 the shift in bottom-up and top-down control along the food chain (Oksanen et al. 1981). In
52 freshwater systems strong top-down control and corresponding trophic cascades have been
53 frequently observed (Carpenter et al. 1985, Shurin et al. 2002), however, results are not as
54 conclusive in the marine environment (Shurin et al. 2002). One argument in explaining the lack
55 of trophic cascades from top-consumers down to primary producers in marine systems is, that
56 biodiversity at each trophic level is much higher compared to most freshwater systems, leading
57 to attenuation of top down effects (Hessen and Kaartvedt 2014). Indeed, examples of clear
58 trophic cascades in marine systems come from areas with low species diversity, dominated by a
59 few strong interactors (Daskalov et al. 2007, Myers et al. 2007; Casini et al. 2008). However, it
60 has been also argued that trophic cascades, while present, may be masked at the total
61 phytoplankton level due to opposite responses of ‘small’ versus ‘large’ phytoplankton to bottom-
62 up and top-down forcing along parallel food chains (Stibor et al. 2004). It was shown that
63 differences in food size spectra between ciliates and copepods lead to alternative energy flow
64 pathways, one expanding from small pico- and nano-phytoplankton over ciliates to copepods, the
65 other from larger edible nano- and microphytoplankton directly to copepods (Stibor et al. 2004,
66 Sommer and Sommer 2006). Accordingly, high predation pressure by copepods leads to an
67 increase of small phytoplankton through top-down control on ciliates, but to a decrease of larger

68 phytoplankton through direct predation (Stibor et al. 2004). In the absence of any predation on
69 copepods, copepod biomass will increase with nutrient availability, leading to increasing
70 predation pressure on ciliates and large algae, while small algae are released from predation
71 pressure by ciliates as well as from resource competition with large algae. Correspondingly,
72 theoretical investigations on the dynamic features of this food web module predict dominance of
73 large phytoplankton at low nutrient availabilities and a shift to smaller sized phytoplankton with
74 increasing nutrient availability (Fig. 1a, Wollrab and Diehl 2015). This prediction is opposite to
75 the general assumption - based on nutrient uptake dynamics - that phytoplankton cell size should
76 increase with enrichment, shifting from small fast growing species to larger slow growing taxa,
77 mediated through increasing predation pressure on small fast growing species (Chisholm 1992,
78 Kiørboe 1993, Thingstad 1998). Furthermore theory predicts that in the presence of planktivore
79 predators such as fish/jellyfish, exerting strong top-down control on copepods, the response at
80 the phytoplankton level is reversed and, in line with general assumptions, larger sized
81 phytoplankton increases with enrichment (Fig. 1b, Wollrab and Diehl 2015). However, it is
82 difficult to achieve data from comparable systems with and without presence of predators along a
83 gradient of resource availability. Hence, until now no study exists confronting these general
84 predictions from food web theory (Fig. 1, Wollrab and Diehl 2015) with data from natural
85 communities.

86 The archipelago of Palau harbors numerous enclosed marine lakes and semi-enclosed coves
87 covering a wide range of nutrient levels. The marine lakes, located within an area of approx. 50
88 km² on various islands within the archipelago, have only underground connections to the
89 surrounding lagoon, resulting in strongly reduced immigration possibilities for animals such as
90 fish or jellyfish (Colin, 2009; Hamner and Hamner 1998). As a result, many lakes are lacking

91 large numbers of organisms at higher trophic levels (i.e. jellyfish or pelagic fish), while some of
92 the lakes are famous for their high density of jellyfish of the genus *Mastigias* (Dawson and
93 Hamner 2003). *Mastigias* is a zooxanthellate jellyfish, harbouring symbiotic dinoflagellates of
94 the genus *Symbodinium*, but still assert strong top down control on zooplankton, especially on
95 copepods (Graham et al. 2001, Dawson 2005). For these reasons, the archipelago of Palau offers
96 a unique opportunity to look for patterns of cascading top down control on phytoplankton size
97 distribution along an enrichment gradient in the presence vs. absence of large numbers of
98 planktivore predators (jellyfish). The marine lakes can be seen as natural marine “mesocosms”
99 which allow confronting/testing the above-described predictions of food web theory with
100 phytoplankton communities of natural complexity and shared evolutionary history. Additionally,
101 experimental mesocosms were set up in two of the marine lakes to characterize the cascading
102 effects of jellyfish on phytoplankton in the marine lakes in a controlled and causal manner.

103

104 **Methods**

105 **Sampling campaigns of marine lakes, coves and lagoons**

106 During the summer period of four consecutive years (2010 - 2013) 44 lakes, coves and lagoon
107 sites were sampled for phytoplankton community and nutrient analyses. All lakes, coves and
108 lagoon sites are situated in the archipelago of Palau (table 1). Integrated water samples were
109 collected with a 2 m long tube sampler from depths of 0 (surface) to 10 m, or from 0 to the
110 bottom in lakes less than 10 m in depth. Samples were stored dark in a cooling box until further
111 treatment in the laboratory. Total phosphorus measurements were performed after wet oxidation
112 of water samples according to standard water chemical methods (Raimbault et al. 1999).
113 Bioassay experiments performed in 2010 indicate phosphorus limitation for the majority of the

114 studied lakes (see supplemental material S1). Initial phytoplankton size and community
115 composition were analysed microscopically by using a standard Utermöhl technique with 50 -
116 100 ml sedimentation chambers (Utermöhl et al. 1958). 100 to 400 individuals per taxon were
117 counted, 10 - 20 individuals were additionally measured in several dimensions and biovolumes
118 were calculated based on geometric calculations. Cell counts were transformed to biovolume
119 according to these measurements.

120 The presence or absence of jellyfish was verified by data from a Lake monitoring program
121 (Dawson and Hamner 2005) and by visual surveys of sampling sites by snorkeling. Two of the
122 lagoon sites were sampled twice, during low and high-tide (Table 1: lagoon 3 and lagoon 4). In
123 the analysis they were treated as independent samples. However, adding or removing these data
124 points from analyses did not influence the qualitative results of the study.

125

126 **Mesocosm experiments:**

127 *Experimental set up:*

128 Both experiments were set up using free floating mesocosms in a gradient design. In 2010 ten
129 mesocosms (4.3 m depth, 3.1m³ volume, translucent PET foil) were filled randomly with
130 unfiltered subsurface lake water (Lake Ongeim'1 Tketau, OTM) by lifting up the empty
131 mesocosm bags from ca. 5m depth to the lake surface. Subsequently, mesocosms received a
132 population of the local *Mastigias* jellyfish ranging from 0 to 20 individuals/ mesocosm (all
133 individuals ~10cm bell diameter). The experiment was run for 3 weeks with regular sampling
134 (nutrients, copepods, phytoplankton) after one, two, and three weeks.

135 In 2011 mesocosm materials, procedures and dimensions were the same as in 2010 except for the
136 jellyfish gradient design: 14 mesocosms were set up in lake *Uet era Ngermeuangel* (NLK), 7

137 thereof were stocked with *Mastigias* from the lake (ranging from 0 to 16 individuals/ mesocosm,
138 bell diameter ~6cm). In both lakes, the jellyfish gradients were at the lower end of average
139 natural jellyfish densities. The experiment was run for 2 weeks with regular sampling (nutrients,
140 copepods, phytoplankton) after one and two weeks. In both years, the integrity of mesocosms
141 and the vitality of medusae were regularly controlled.

142

143 *Sampling procedures, counting, measurements, chemical analyses*

144 After one, two, (and three in 2010) weeks, depth-integrated water samples (10 litres) were taken
145 from each mesocosm to determine phytoplankton biomass and to measure nutrients. 100ml of
146 sampled water was immediately fixed with Lugol iodine for microscopic phytoplankton and
147 ciliate identification and counting. Phytoplankton and ciliates were identified and counted by
148 inverted microscopy using Utermöhl chambers aided by scanning electron microscopy (SEM).
149 Cell counts were converted into biovolumes [$\mu\text{m}^3 \text{L}^{-1}$] using measured or published specific cell
150 volumes. Samples for seston nutrient analyses were poured through a net (225 μm mesh size) to
151 retain zooplankton and large detrital particles. Algal biomass POC and PON, were determined
152 subsequent to filtration onto pre-combusted and acid-washed glass-fibre-filters (Whatman GF/C,
153 Whatman International Ltd.) by Elemental Analysis (Elemental Analyser, EA 1110 CHNS, CE
154 Instruments). Algal biomass particulate phosphorus (PP) was measured after sulphuric acid
155 digestion followed by a molybdate reaction. Copepod sampling was performed using a plankton
156 net (188 litres per net haul, 250 μm mesh size).

157

158 *Jellyfish fresh weight calculations*

159 At the end of each experiment, all jellyfish were removed from the mesocosms and bell

160 diameters were measured to assess the effective number and biomass of jellyfish per mesocosm
161 (some small medusae might have been trapped accidentally during filling of the bags, likewise
162 trapped polyps could have had strobilated during the experiment). Jellyfish biomass was
163 calculated using the following non-linear regression equations for fresh weight-to-bell diameter
164 relationships, obtained from medusae not used in the experiments:

165 *Mastigias* fresh weight [g] = $0.15 \cdot \text{bell diameter [cm]}^{2.92}$, $r^2=0.993$, $p<0.0001$, $n=34$.

166

167 **Data analysis of field data**

168 For each sampling site total phytoplankton biovolume was calculated and linear regression was
169 used to investigate the pattern of total phytoplankton biovolume with increasing phosphorous
170 levels. According to a meta-analysis on food size ranges of copepods and protozoa across
171 different marine habitats by Sommer and Sommer (2006), phytoplankton with an equivalent
172 spherical diameter (ESD) smaller than $10 \mu\text{m}$ ($\sim 523 \mu\text{m}^3$) belong to the preferred food size range
173 of ciliates, whereas phytoplankton with an ESD larger than $10 \mu\text{m}$ belong to the preferred food
174 size range of copepods. Accordingly we summed the biovolumes of ‘small’ ($<523 \mu\text{m}^3$) and
175 ‘large’ ($>523 \mu\text{m}^3$) phytoplankton for each sampling site (Sommer and Sommer 2006).
176 Phytoplankton larger than $74000 \mu\text{m}^3$ was considered inedible, restricting the summed large
177 phytoplankton to cell sizes between $523 \mu\text{m}^3$ and $74000 \mu\text{m}^3$. Total phytoplankton biovolume per
178 lake was calculated using the complete range of detected cell sizes. We investigated the
179 correlation of total phytoplankton biovolume and of small and large phytoplankton with TP level
180 for sites with and without jellyfish using the non-parametric Kendall correlation method, which
181 measures the correspondence between the ranking of x and y variables. Kendall correlation test
182 was done on the absolute biovolume data for small and large phytoplankton as well as on the

183 relative contribution of small and large algae to total phytoplankton per site.

184 Data analysis and plotting was performed with the Software R (Version 3.1.1) using the packages

185 *car*, *plyr*, *ggpubr*, *cowplot* and *gtools*.

186

187 **Data analysis of mesocosm experiment**

188 For both experiments (OTM in 2010 and NLK in 2011), the effect of the presence or absence of

189 jellyfish on the abundance or biovolume (N) of copepods, ciliates and phytoplankton was

190 assessed by calculating an effect value. For example, for copepods, the effect size (ES_{Cop}) has

191 been calculated as:

192

$$193 \quad ES_{Cop} = Ln(N_{encl-i}^{Cop}/N_{Control}^{Cop}) \quad (1)$$

194

195 Where N_{encl-i}^{Cop} is the copepod abundance (on the final sampling day) in the enclosure 'i' which

196 contained a manipulated number of jellyfishes; $N_{Control}^{Cop}$ is the copepod abundance in the

197 enclosure with no jellyfish on the last sampling day. Similarly, the effect size for ciliates (ES_{Cil} ,

198 based on abundance) and phytoplankton (ES_{Phyt} , based on cell biovolume) were calculated as

199 follow:

200

$$201 \quad ES_{Cil} = Ln(N_{encl-i}^{Cil}/N_{Control}^{Cil}) \quad (2)$$

202 and,

$$203 \quad ES_{Phyt} = Ln(N_{encl-i}^{Phyt}/N_{Control}^{Phyt}) \quad (3)$$

204

205 Two size-classes were distinguished for phytoplankton, i.e. phytoplankton with cell biovolume <

206 523 μm^3 , or cell biovolume $> 523 \mu\text{m}^3$, no cells larger than 74000 μm^3 were detected.

207

208 **Results**

209 *Patterns of total phytoplankton biovolume with enrichment for marine sights in presence vs.* 210 *absence of jellyfish*

211 Total phytoplankton biovolume is significantly positively correlated with nutrient enrichment for
212 both, sites with and without jellyfish (Fig. 2, lakes with jellies: $r = 0.45$, $N = 25$, $p < 0.01$, lakes
213 without jellies: $r = 0.32$, $N = 19$, $p < 0.1$). Thereby the increase of total phytoplankton with total
214 phosphorus is more pronounced in the presence of jellyfish compared to in the absence of
215 jellyfish.

216

217 *Patterns of small vs. large phytoplankton for marine sights along enrichment gradient in* 218 *presence vs. absence of jellyfish*

219 Overall, the summed biomasses of small and large phytoplankton are significantly positively
220 correlated with increasing TP-levels (Fig. 3a and c). In the presence of jellyfish (Fig. 3a), the
221 increasing trend is significant for large algae ($r = 0.41$, $N = 25$, $p < 0.01$) and small algae ($r =$
222 0.57 , $N = 24$, $p < 0.001$), with higher biomass of large algae throughout the enrichment gradient.
223 In the absence of jellyfish (Fig. 3c), the increasing trend is only significant for small algae ($r =$
224 0.38 , $N = 19$, $p < 0.05$), but not for large algae ($r = 0.1$, $N = 19$, $p > 0.1$).

225 Looking at the relative contributions of small vs. large phytoplankton to total phytoplankton
226 biovolume for each sampling site (Fig. 3b and d), in the absence of jellyfish (Fig. 3d), the
227 relative contribution of large algae is significantly negatively correlated with increasing TP-
228 levels ($r = -0.39$, $N = 19$, $p < 0.05$), whereas the relative contribution of small algae is

229 significantly positively correlated with increasing TP-levels ($r = 0.3$, $N = 19$, $p < 0.1$). In addition
230 we observe a shift from dominance of large algae to dominance of small algae for the highest
231 investigated TP-levels. In the presence of jellyfish (Fig. 3b), in line with the absolute values,
232 large algae dominate throughout the enrichment gradient for most sites. However, no significant
233 correlation between total phosphorus and relative biovolume of large vs. small phytoplankton
234 could be found (large phytoplankton, $r = -0.02$, $N = 25$, $p > 0.1$; small phytoplankton, $r = 0.0065$,
235 $N = 24$, $p > 0.1$).

236 The size fraction above $73000 \mu\text{m}^3$, considered to be inedible, dominated the phytoplankton
237 community only at one site (Lake New 1, see table 1). At sites where this size fraction was
238 detected ($N = 11$ for lakes with jellyfish and $N=3$ for lakes without jellyfish), in most cases it
239 contributed less than 20% to total phytoplankton (see supplemental material, Fig. S2).
240 Additionally, no significant correlation between the abundance of large inedible algae and
241 enrichment (inedible algae in presence of jellyfish: $r = -0.38$, $N=11$, $p = 0.1$, inedible algae in the
242 absence of jellyfish: $r = 1$, $N = 3$, $p > 0.1$).

243

244 ***Experimental evidence for trophic cascades mediated by Mastigias***

245 Increasing *Mastigias* biomass in the mesocosms established in the two different lakes resulted in
246 a significant reduction of copepod abundances (Fig. 4a). Decreasing copepod abundances
247 resulted in positive effect sizes of jellyfish on ciliates (Fig. 4b) and phytoplankton (Fig. 4c,d).

248 The positive slope of increasing jellyfish on ciliate abundances was however not significant on a
249 5% level (Fig. 4b). Both, small and large phytoplankton groups showed positive responses to
250 increasing jellyfish abundance. The effect size on large algae was considerably higher compared
251 to the effects on small algae, the slope of effect sizes vs. jellyfish fresh weight was about twice as

252 high for large phytoplankton (Fig. 4c,d).

253

254 **Discussion**

255 **Trophic cascades**

256 Our results support the importance of presence vs. absence of higher trophic levels in shaping
257 quantitative and qualitative responses of primary producers to resource enrichment. Within the
258 edible size range of phytoplankton for ciliates and copepods we observe clear differences
259 between the abundance patterns of small vs. large phytoplankton, dependent on the presence or
260 absence of jellyfish. In the presence of jellyfish, large edible phytoplankton dominates
261 throughout the enrichment gradient, whereas in the absence of jellyfish, a shift from dominance
262 of larger towards smaller size classes occurs. These observations are in line with theoretical
263 predictions on contrasting top-down control patterns along the large algae-copepod chain vs. the
264 small algae-ciliate-copepod chain (Wollrab and Diehl 2015) and highlight the relevance of
265 parallel food chains within food webs for bottom-up and top-down response patterns (Armstrong
266 1994; Shin et al. 2010; Wollrab et al. 2012). While the dominance of large algae in the presence
267 of jellyfish and their increase with total phosphorus levels is in line with theoretical predictions,
268 the increase of small algae in presence of jellyfish is not predicted by theory. However, one has
269 to take into account that the *in situ* natural food web complexity is higher than the model *in silico*
270 complexity and direct and indirect interactions between food web compartments which are not
271 part of the model structure, for example interactions between bacteria and algae, may lead to
272 deviations from model predictions.

273 Our conclusions are based on detailed knowledge on the presence and absence of the top
274 predator *Mastigias* sp. and quantitative analyses of the autotroph base of the food web

275 (phytoplankton abundance and cell size distribution). The data used for the analyses originate
276 from a sampling program investigating phytoplankton diversity in marine lakes, therefore we
277 lack quantitative zooplankton data. However, our data from the two mesocosm experiments
278 conducted in Palau lakes strongly support the idea that observed quantitative differences in
279 phytoplankton community composition with respect to cell size are linked to changes in top-
280 down control patterns dependent on the presence or absence of jellyfish. In the observed lakes,
281 jellyfish, if present, are top-predators in the system and usually reach very large population sizes.
282 For example in lake OTM the population of *Mastigias* can reach total densities of up to 24
283 million individuals (Dawson and Hamner 2005). While *Mastigias* are mixotrophic, they still
284 need zooplankton as part of their diet and exert high predation rates and therefore strong top-
285 down control on zooplankton (Fig. 4a; see also McCloskey et al. 1994). There is the possibility
286 that in lakes without jellyfish, zooplanktivorous chaetognaths might get the dominant predators
287 on zooplankton, however, their grazing impact is usually much lower (up to a few copepods per
288 day, Øresland 1987; Fulton 1984) in comparison to jellyfish grazing rates (McCloskey et al.
289 1994; Graham and Kroutil 2001; Bezio et al. 2018). Additionally, cannibalism is quite prevalent
290 among chaetognaths, thereby strongly controlling their own population densities (Øresland
291 1987). Jellyfish, also mixotrophic ones, are well known to induce trophic cascades (Stibor et al.
292 2004; West et al. 2009), while such evidence is lacking for chaetognaths.

293 The search for trophic cascades in real systems has often been focused on whole trophic level
294 responses (Carpenter et al. 1985; Shurin et al. 2002). Our study strengthens the necessity of
295 recognizing alternative energy pathways and highlights the relevance of parallel food chains in
296 mediating the response to bottom-up as well as top-down forcing at the phytoplankton level. The
297 expectation, that phytoplankton communities shift from dominance of small, fast growing, to

298 bigger, slow growing and less edible, cell sizes with increasing nutrient availability (Chisholm
299 1992; Kiørboe 1993; Arin et al. 2002; Irwin et al. 2006), is based on insight from food web
300 theory according to which coexistence between competing prey species is only possible in the
301 presence of a trade-off between resource use efficiency and edibility to a shared predator (Holt et
302 al. 1994; Leibold 1996). Theory predicts that along an enrichment gradient there is a shift from
303 the superior resource competitor to the inferior, but less edible, resource competitor,
304 corresponding to a shift from dominance of resource to apparent competition (Holt et al. 1994;
305 Leibold 1996). However, if alternative food chains are of different length, top-down control
306 patterns related to apparent competition can deviate from the above described pattern, leading to
307 counterintuitive predictions (Wollrab et al. 2012; Wollrab and Diehl 2015).

308 The clear and coherent patterns along the resource gradient that were found in our analyses of
309 natural phytoplankton communities are even more reassuring, since between lake variation in
310 terms of species composition is naturally high. The marine lakes and coves on Palau differ in
311 their connectivity to the surrounding ocean, ranging from direct surface connections for lagoon
312 sites and coves, to only underground connections for lakes (Hamner and Hamner 1998). Distance
313 and characteristics of the connection to the marine environment put potential restrictions on
314 species migration and invasion possibilities and thereby species distribution for marine lakes.
315 This might be one reason that leads to the observed high between site variability in species
316 composition and species richness, especially for sampling sites without jellyfish, which do not
317 have direct surface connections to the ocean. Therefore it is hardly surprising that the highest
318 variance in total phytoplankton biovolume was observed for mesotrophic lakes without jellyfish.
319 The still coherent responses of phytoplankton along the enrichment gradient in the presence vs.
320 absence of jellyfish, strongly point towards the generality of some of the predicted mechanisms

321 of how top-down control influence primary producer community composition responses to
322 resource availability by previous experimental (Stibor et al. 2004) and theoretical investigations
323 (Wollrab and Diehl 2015).

324 While the situation of low numbers or even the absence of planktivorous predators as such will
325 not be relevant for most marine systems, our results have several important implications for our
326 understanding of food web functioning. First, removing or reducing of higher trophic levels
327 within food webs (shifting the length of food chains) can result in opposite and unexpected
328 responses at lower trophic positions to simultaneous nutrient enrichment. Such scenarios are not
329 unrealistic at all following the large effects of anthropogenic stressors such as overfishing
330 (depletion of upper trophic levels) (Pauly et al. 1998) and eutrophication of coastal waters
331 (Rabalais et al. 2009). Second, effects of nutrient enrichment may not necessarily result in clear
332 increases of primary producer biomass with increasing nutrient availability, but responses may
333 differ between size classes of phytoplankton. It is therefore important to have knowledge about
334 food web structure before using phytoplankton biomass as an indicator for eutrophication or
335 over-fertilization (Garmendia et al. 2013).

336 In line with the approach of so called end-to-end models (Shin et al. 2010), our study shows that
337 focusing on major energy pathways in the analysis of community response patterns to
338 environmental forcing may be a useful way to derive valuable information on expected shifts.
339 However, this requires data that encompass all trophic levels and information on within trophic
340 level heterogeneity in terms of size distribution and food size ranges. Such data sets will enable
341 to develop appropriate food web approximations and to confront predicted patterns on
342 community structure with observed patterns in natural systems.

343

344 **Compliance with Ethical Standards**

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347 Conflict of Interest: All authors declare that he/she has no conflict of interest.

348 Ethical approval: All applicable international, national, and/or institutional guidelines for the care
349 and use of animals were followed. Experiments were approved by the Republic of Palau and the
350 State of Koror, research permit holders were Herwig Stibor & Philippe Pondaven. Jellyfish were
351 released into their natural habitat after the experiments.

352

353 **Data availability**

354 The datasets analysed during the current study are available from the corresponding author on
355 reasonable request.

356

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448

449 **Figure legends**

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451 Figure 1: Schematic figure of the plankton food web in the absence (a) versus presence (b) of
452 jellyfish. Arrows connecting circles indicate feeding interactions pointing from prey to predator,
453 circles represent R - shared nutrient P_S - small algae, P_L - large algae, Cil - ciliates, Cop -
454 copepods and J - jellyfish. Thick arrows next to circles indicate the expected longterm response
455 pattern with increasing total nutrient content following theoretical predictions from the analysis
456 of the equilibrium response of a corresponding differential equation system in Wollrab & Diehl
457 (2015).

458 Figure 2: Total phytoplankton biovolume [$\mu\text{m}^3 \text{L}^{-1}$] per sampling site along the total phosphorus
459 gradient [$\mu\text{g L}^{-1}$] for sites with (yellow triangles) and without (blue circles) jellyfish. All values
460 are \log_{10} -transformed.

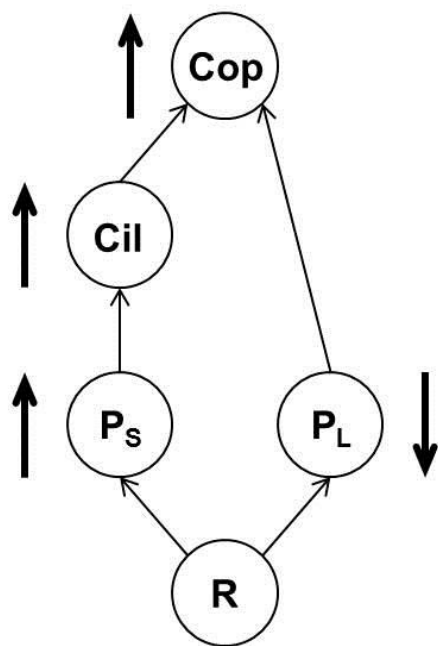
461 Figure 3: Absolute \log_{10} -transformed biovolumes (a. c) and relative (logit-transformed)
462 contribution (b. d) of small ($<523 \mu\text{m}^3$. blue circles) and large ($>523 \mu\text{m}^3$. yellow triangles)
463 phytoplankton per site [$\mu\text{m}^3 \text{L}^{-1}$] along the total phosphorous gradient [$\mu\text{g L}^{-1}$] for sites with jelly
464 fish (a. b) and for sites without jellyfish (c. d).

465 Figure 4: Effect size of jellyfish freshweight on (a) copepod. (b) ciliate. (c) small algae and (d)
466 large algae from mesocosm experiments in 2010 (black circles) and 2011 (open circles).

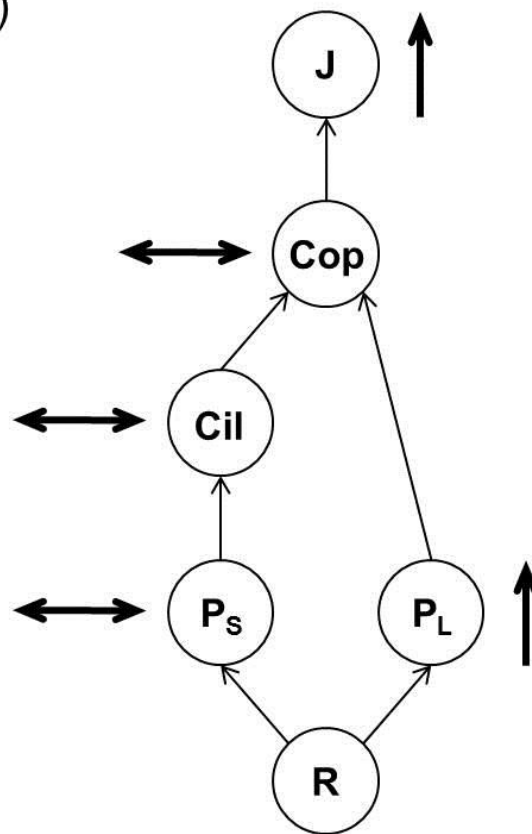
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468 Figure 1

(a)



(b)

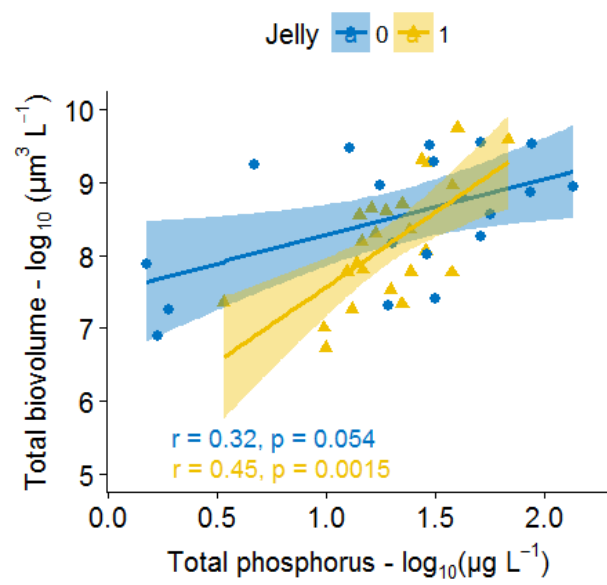


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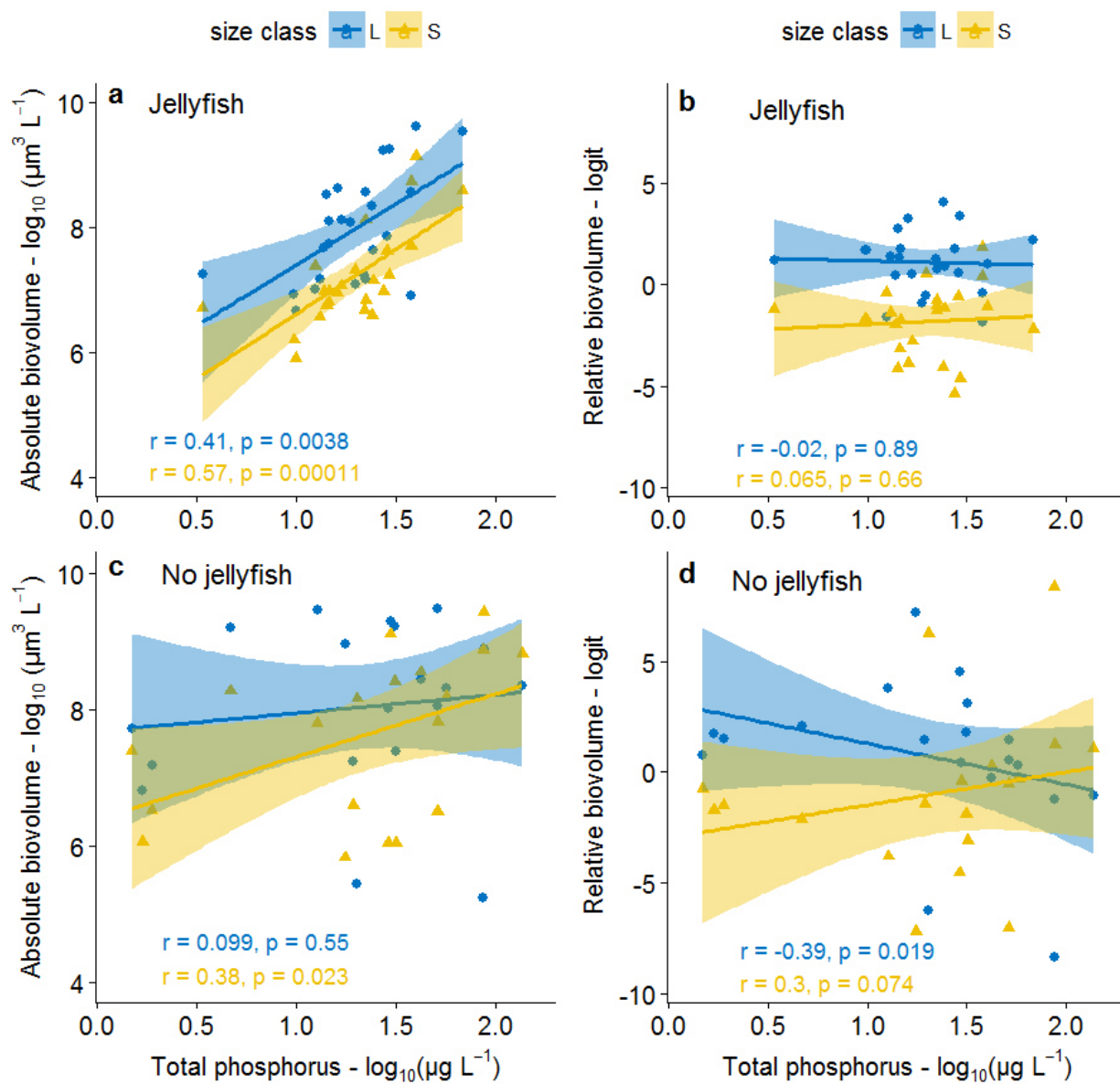
472 Figure 2



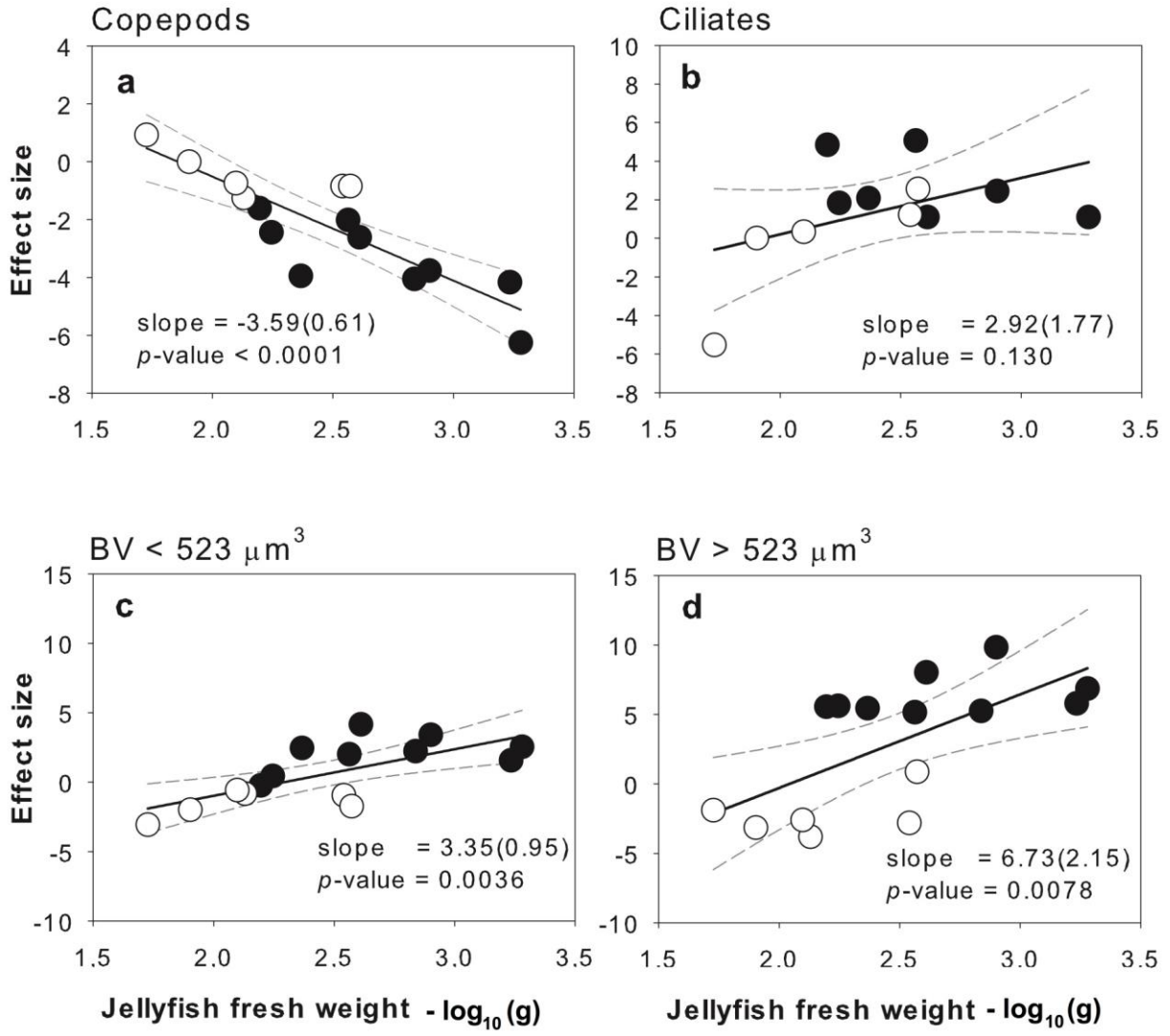
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475 Figure 3

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478 Figure 4



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481 Table 1. List of all sampling sites.

Year sampled	Name ^a	TP [$\mu\text{g/Liter}$]	Type	Jellyfish
2010	Mekeald	29.03	lake	No
2010	Ngchas	31.39	lake	No
2010	T Lake	51.23	lake	No
2010	Ngeruktabel	31.93	lake	No
2010	Spooky	136.83	lake	No
2010	Flatworm	29.83	lake	No
2010	Hot Water	20.32	lake	No
2010	Shrimp	87.73	lake	No
2010	Heliofungia	17.60	lake	No
2010	Ngel	19.45	lake	No
2011	Big crocodile	42.19	lake	No
2011	L-shape	51.38	lake	No
2011	Little crocodile	57.08	lake	No
2013	Lipstick	1.9	lake	No
2013	One Shark	4.7	lake	No
2013	Big Fish	12.8	lake	No
2013	Little Mangrove	1.5	lake	No
2013	IRO	1.7	lake	No
2013	Big Mangrove	87	lake	No
2010	Ulebsechel	24.09	Cove/lagoon	Yes
2010	Ongael	39.99	lake	Yes
2010	Ongeim'l Tketau (OTM)	29.32	lake	Yes
2010	Malakal Harbor	22.17	lagoon	Yes
2010	Short Drop-Off	9.76	lagoon	Yes
2010	Uet era Ngermeuangel (NLK).	28.66	lake	Yes

2010	Clear	37.74	lake	yes
2010	Goby	68.21	lake	yes
2010	Bablomekang	13.17	lagoon	yes
2010	German Channel	22.42	lagoon	yes
2010	Jurassic	9.98	Cove/lagoon	yes
2011	Ngelchael	22.34	lagoon	yes
2012	Long Lake/Bassin 1	27.49	lagoon	yes
2012	New 1	18.85	lake	yes
2012	New 2	37.85	lake	yes
2012	Secret	14.72	Cove/lagoon	yes
2012	Jurassic	12.49	Cove/lagoon	yes
2012	Lagoon 1	16.15	lagoon	yes
2012	Lagoon 2	13.87	lagoon	yes
2012	Lagoon 3	14.58	lagoon	yes
2012	Lagoon 3	24.43	lagoon	yes
2012	Lagoon 4	19.75	lagoon	yes
2012	Lagoon 4	16.85	lagoon	yes
2012	Lagoon 5	14.23	lagoon	yes
2013	Tarzan	3.4	lake	yes

Supplemental Material S1

Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

Marine Biology

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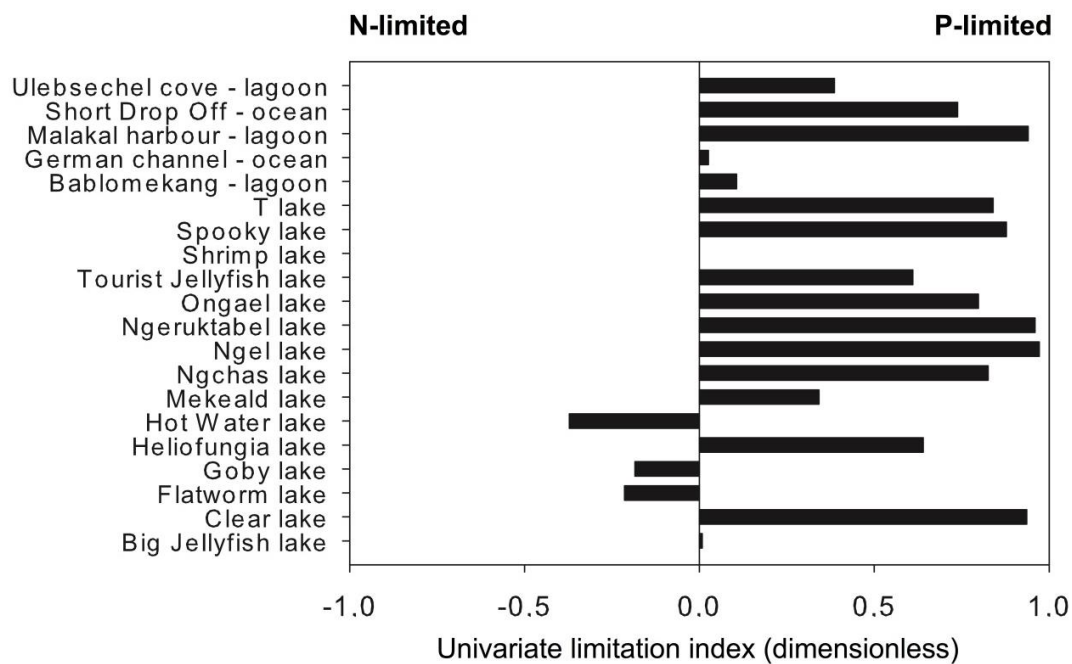


Fig. S1. Nutrient limitation for marine sites as indicated by bioassay experiments performed in Palau in 2010, following the modified procedure by Andersen et al. (2007) following Ptacnik et al. (2010). The x-axis represents the Univariate Limitation Index, ULI, which transforms the probabilities of N, P or the combined limitation of N and P into a one-dimensional scale (Ptacnik et al., 2010); a value of -1 (or +1) indicates that, during a bioassay, the phytoplankton community responded only to N (or P) addition. Conversely, when ULI= 0, this indicates that there is no nutrient limitation (i.e., there are no detectable differences between nutrient addition treatments and the control) or a combined N and P limitation (i.e., only the combined addition of N and P results in an increase in phytoplankton biomass).

Cited literature:

Andersen T. Saloranta TM. Tamminen T (2007) A statistical procedure for unsupervised classification of nutrient limitation bioassay experiments with natural phytoplankton communities. *Limnol Oceanogr-Meth* 5: 111-118.

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Supplemental material S2

Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

Marine Biology

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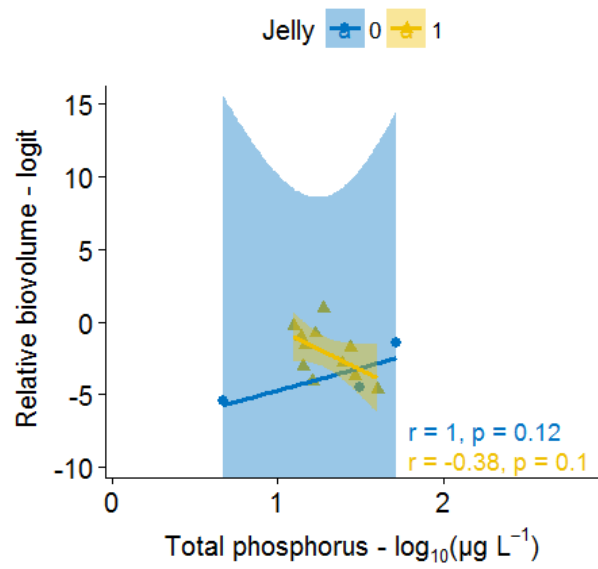


Fig. S2. Logit-transformed relative contribution of very large algae (> 73.000 m³), considered to be inedible, in presence vs. absence of jellyfish.

1 Supplemental Material S3

2 **Differences in size distribution of marine phytoplankton in presence versus absence of**
3 **jellyfish support theoretical predictions on top-down control patterns along alternative**
4 **energy pathways**

5

6 Marine Biology

7

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17 0003-2430-4845

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20 Table S3: Hydrological, physico-chemical, and biological characteristics of the experimental
 21 lakes measured during the experimental periods in 2010 (OTM) and 2011 (NLK). Surface
 22 temperature and salinity are averages of upper water layers (0-5 meter), the PAR attenuation
 23 coefficient is integrated from 0-10m water depth.

	Ongeim'i Tketau (OTM)	Uet era Ngermeuangel (NLK)
Estimated age (years)	10.000	12-15.000
Volume [10^6 m ³]	1.087	1.188
Surface area [10^3 m ²]	62.0	44.6
Mean / max. depth (m)	12.5 / 32.5	20.3 / 38.4
Surface temperature [°C]	31.8	32.5
Salinity [PSU]	28.4	22.2
Mixing regime ^a	Meromictic, chemocline at 15 m depth	Meromictic, chemocline at 17 m depth
Tidal lag time [min]	ca. 136	ca. 190
Total phosphorus [$\mu\text{g L}^{-1}$]	29.3	28.7 (2010)
PAR attenuation coefficient [m^{-1}]	0.30	0.10
Mastigias abundance [L^{-1}] ^b	0.0028-0.025	No data, abundant, but less than in OTM
<i>Aurelia</i> sp. abundance	No data; low	No data; high
Copepod abundance [L^{-1}] ^c	0.84	0.41
Chl a [$\mu\text{g L}^{-1}$]	1.71	1.26

24 ^a Data from Dawson and Hamner (2003)

25 ^b Data from CRRF (annual means 2000-2004) and M. N. Dawson (pers. comm.)

26 ^c Unpublished data from 2010 and 2011 (Stibor, pers. com.)