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Intertidal invertebrates locally enhance primary production

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1 ABSTRACT

2 The contribution of autochthonous versus allochthonous inputs to productivity is an important
3 determinant of ecosystem function across multiple habitats. In coastal marine systems, nutrients
4 are thought to come primarily from the upwelling of deep, nutrient rich water. Using
5 experimental manipulations of a dominant tidepool animal, the mussel *Mytilus californianus*, I
6 show that the presence of mussels greatly increases the supply of inorganic nitrogen and
7 phosphorus. Mussels further had a direct effect on productivity: benthic microalgal abundance
8 increased by a factor of 4 to 8, while the growth of a red alga was 4 times greater in the presence
9 of mussels. The increase in nitrite and nitrate associated with mussels further suggests nitrifying
10 activity by microbes. These findings have broad implications for coastal marine systems,
11 including that regenerated nutrients may contribute more to productivity than previously
12 recognized and that the presence of animal-generated nutrients sets the stage for numerous
13 positive interactions.

14 **KEYWORDS:** positive interactions, autochthonous productivity, tidepools, ammonium uptake,
15 regenerated nutrients, plant productivity, nutrient supply, nitrification

16 INTRODUCTION

17 A persistent question in a multitude of ecosystems is the extent to which local sources of
18 productivity (autochthonous) vs distant (allochthonous) drive ecosystem productivity (Dugdale
19 & Goering 1967, Polis & Hurd 1996, Polis et al. 1997, Helfield & Naiman 2001, Nakano &
20 Murakami 2001, Schindler et al. 2001). In marine coastal systems, most inorganic nitrogen is
21 thought to be provided via seasonal upwelling of deep and nitrate-rich colder waters. Upwelling
22 events occur over tens or hundreds of kms and, in some regions, large geographic areas have
23 been characterized by particular patterns of upwelling (Menge et al. 2004). At the same time,

1 many abundant marine species are often characterized by broad distributions and the potential
2 for large-scale dispersal via planktonic larvae (e.g. mussels, barnacles, fishes). The combination
3 of these two features of upwelling coastlines has resulted in a relative paucity of studies that have
4 investigated whether species are linked via local nutrient dynamics, with a few notable
5 exceptions (Bracken & Nielsen 2004, Bracken 2004). Considering the rich literature describing
6 and testing the trophic and competitive linkages among species in these systems, particularly in
7 rocky intertidal communities (Connell 1961, Dayton 1971, Paine 1966, 1974, 1992, Lubchenco
8 1978, Wootton 1994, Robles & Desharnais 2002), positive interactions among organisms that
9 may mediate nutrient availability are relatively little studied. This further contrasts with many
10 other ecosystems where we have evidence that animal excretion can provide necessary nutrients
11 and locally enhance ecosystem productivity (Eppley et al. 1973, Meyer et al. 1983, Huntly &
12 Inouye 1998, Vanni 2001, Croll et al. 2005).

13 One habitat where species could be linked via nutrient regeneration and where
14 autochthonous processes may be important is tidepools. Tidepools, especially those in the mid to
15 high intertidal, are emergent for many hours at a time and are thus disconnected from the oceanic
16 nutrient supply, setting up a scenario where nutrient limitation, especially of nitrogen, might
17 occur. Previous work has shown that tidepool animals can excrete ammonium (Jensen &
18 Muller-Parker 1994, Bracken 2004, Bracken & Nielsen 2004) and could thus be a continuous
19 source of available nitrogen. Recent work has shown that the growth of algae epiphytic on
20 mussels (*Odonthalia* spp) is enhanced in laboratory mesocosms (Bracken 2004) and that this
21 ammonium is correlated with higher algal species diversity in tidepools (Bracken & Nielsen
22 2004). In tidepools without animals, nitrate was depleted by algae during low tide periods
23 (Bracken & Nielsen 2004), further suggesting an important role for animal-excreted ammonium.

1 mussels that were removed from the tidepools were weighed and, on average, 3.98 kg of mussels
2 were removed per tidepool.

3 *Effects of mussels on water nutrients*

4 I quantified the effects of mussels on water nutrients on 7 dates (2002: 30 May, 1,16 Jun,
5 26 Aug; 2003: 18 Jun; 2005: Jun, Aug), including prior to the mussel manipulation (30 May
6 2002), by sampling water from the middle of the tidepool with a 60 ml syringe. The sample was
7 immediately filtered through a GF/C filter into acid-washed HDPE plastic bottles, placed on ice,
8 and then frozen within 4 hours of collection. Water nutrient concentrations (PO_4^{3-} , SiO_4 , NO_3^- ,
9 NO_2^- , NH_4^+) were analyzed by the Marine Chemistry Laboratory at the University of
10 Washington (methods from UNESCO, 1994). A corresponding sample (or two) was always
11 taken in open water at the end of the rocky bench at the same time the tidepools were sampled.
12 At each date samples were taken at low tide. Additional samples were also taken to compare
13 changes in nutrient levels after the tidepools had been emergent and isolated from the ocean for
14 several hours (26 Aug 2002, 18 Jun 2003, 14 Jun & 23 Aug 2005). The nutrient sampling
15 allowed me to test if mussel removal had an effect on nutrient levels both throughout the period
16 the removals were maintained, and during the interval of a low tide. I never sampled water
17 nutrients on rainy days to eliminate the potential effects of freshwater runoff.

18 *Effects of mussels on primary production*

19 I assessed the extent to which mussel presence affected productivity in tidepools by
20 estimating the production of benthic microalgae and the growth of a red alga common to
21 tidepools, *Prionitis lanceolata* (henceforth, *Prionitis*). The amount of chlorophyll extracted in
22 10 ml ethanol from two 2 x 2 cm glass cover slips was used as an estimate of grazer-free benthic
23 primary production. The cover slips were glued (with silicon cement) to a plastic film canister

1 lid that was affixed to the tidepool with Z-Spar™ Epoxy. The canister had been painted with a
2 copper-based antifouling paint to inhibit limpet and snail foraging (Johnson 1992). This copper
3 treatment seemed effective; I never noted radula marks on any of the cover slips with copper.
4 After a 2-week interval, both coverslips were removed from the film lid and placed in 10 ml
5 ethanol to extract chlorophyll *a* following Jespersen & Cristoffersen (1987) and Webb et al.
6 (1992). The samples were kept frozen until analysis 48 h later. Chlorophyll concentration was
7 estimated using pure chlorophyll *a* from spinach (Sigma Chemical) as a standard. Samples were
8 read on a Turner Model 450 Fluorometer. Chlorophyll was quantified from two 2-week periods
9 (26 Jul – 8 Aug & 8 Aug-23 Aug) during 2005.

10 I asked whether *Prionitis* growth was increased in the presence of mussels by transplanting
11 2 *Prionitis* individuals into each of the 10 tidepools. *Prionitis* were chiseled out from other pools
12 at the site, leaving a piece of rock to epoxy (Z-Spar™) to the surface of the target tidepool. Each
13 alga was photographed between 2 clear Plexiglass plates and digitized (Image-J software, NIH)
14 at the start of the experiment (12 Jun 2005) and again after 6 weeks (26 Jul) and 10 weeks (23
15 Aug). Because some *Prionitis* individuals died between the Jun and Jul censusing date, on 26
16 Jul, I added 1 new individual to each pool, except for 2 tidepools in the mussel removal
17 treatment where both *Prionitis* died and 2 additional algae were added. The transplanted algae
18 were dispersed throughout the tidepool and did not come in contact with or shade one another.

19 For statistical analyses of responses through time (for nutrients and *Prionitis* size), I used
20 Repeated Measures ANOVA. I report multivariate results because the sphericity assumptions
21 was generally violated. Data transformation was used to minimize homogeneity of variances.

22 RESULTS

23 *Effects of mussels on water nutrients*

1 Tidepools had a relatively constant composition of mussels throughout the experiment,
2 fluctuating between 26.0% and 29.0% cover. The other major components of the tidepools were
3 bare space, fleshy red crust, crustose coralline algae, and foliose red algae (mostly *Prionitis* spp,
4 *Endocladia*, *Odonthalia* spp), and limpets (*Lottia strigatella* , *Tectura scutum*). The anemones
5 *Anthopleura elegantissima* and *A. xanthagrammica*, the sea urchin *Strongylocentrotus*
6 *droebachiensis* and the seagrass *Phyllospadix serratulatus*, and the chitons *Mopalia* spp were
7 occasionally present.

8 The presence of mussels in tidepools was associated with a 2-fold increase in ammonium
9 over pools where mussels had been removed and a 10-fold increase in ammonium compared
10 with open water seawater (Fig. 1). Throughout the study there was high variation among dates
11 and tidepools in nutrient concentration, and data transformation was used. Following the
12 removal of mussels, there were significant reductions in ammonium and phosphorus (cube-root
13 transformed data, Repeated Measures ANOVA, $F_{1,8}=6.014$, $p=0.040$ & $F_{1,8}=5.168$, $p=0.053$,
14 respectively). Nitrite and nitrate did not decline significantly ($F_{1,8}=3.124$, $p=0.115$ & $F_{1,8}=1.393$,
15 $p=0.272$), although nitrite was consistently reduced by half when mussels were removed and was
16 almost always greater than the ocean sample (Fig. 1). There were no interactions between time
17 and mussel manipulation. The increase in ammonium and the depletion of nitrate in tidepools
18 relative to open ocean samples was a repeated pattern.

19 The presence of mussels was generally associated with an increase in nutrients through
20 time following tidepool isolation from the open ocean and was indicated by positive values in
21 Fig. 2. Significantly greater concentrations of ammonium, nitrite and nitrate occurred when
22 mussels were present (cube-root transformed data, Repeated Measures ANOVA, ammonium:
23 $F_{1,8}=6.871$, $p=0.034$, nitrite: $F_{1,8}=9.182$, $p=0.019$, nitrate: $F_{1,8}=6.194$, $p=0.042$). Phosphorus

1 changes were not significant ($F_{1,8}=3.714$, $p=0.118$) and nitrate was at times consumed, based on
2 the negative values for change. No nutrient showed a significant treatment by time (date)
3 interaction. A repeated pattern for the dynamics of inorganic nitrogen in tidepools with mussels
4 was an increase in ammonium and nitrite while pools were emergent (Fig. 3).

5 ***Effects of mussels on primary production***

6 The presence of mussels was associated with a 4 to 8-fold increase in benthic chlorophyll *a*
7 for both 2 week intervals it was sampled (9 Aug: with mussels, mean \pm SE=2857 \pm 1589, mussels
8 removed, 671 \pm 181 and 24 Aug: 8071 \pm 7130 and 1019 \pm 359, respectively, Wilcoxon, $p=0.037$ for
9 both dates). Chlorophyll *a* estimates were characterized by high variability, with the tidepool
10 with the highest mussel abundance consistently showing the highest benthic microalgal
11 abundance.

12 The red macroalga *Prionitis* also showed a marked response to the presence of mussels and
13 attained a size 4 times greater in the presence of mussels compared with removals. A Repeated
14 Measures ANOVA on mean alga size per tidepool resulted in a p-value of 0.034 ($F_{1,8} = 9.484$)
15 and a showed a significant time by treatment interaction ($p = 0.030$). Of the 15 *Prionitis*
16 transplanted to control tidepools and 17 transplanted to mussel removal tidepools, 8 died in the
17 absence of mussels while only 1 died where mussels were present (G test = 7.168, $p < .010$).

18 DISCUSSION

19 **Mussel excretion and positive species interactions**

20 The positive effect of mussels on benthic algal productivity demonstrated here as well as
21 reported by Bracken (2004) in mesocosms suggests that mussels may have persistently positive
22 effects on algae in tidepools via their effect on nutrient supply. Tidepools can be emergent for
23 hours at a time, cut-off from oceanic sources of nitrogen, especially nitrate, and the supply of

1 ammonium by mussels may prevent nitrogen limitation. Although not estimated here, the oxygen
2 production by algae in tidepools may in turn benefit mussels. The positive effect of mussels on
3 algal productivity has been shown to extend to algal diversity (Bracken & Nielsen 2004), where
4 high ammonium in tidepools is associated with an increased representation of algae that require
5 high nitrogen concentrations. Mussel excretion may positively affect algal species diversity via
6 complementarity; different tidepool species take up ammonium and nitrate at different rates
7 (Phillips & Hurd 2003, Bracken & Stachowicz 2006). Thus, excretion of ammonium by mussels
8 may provide an additional resource axis that facilitates increased algal diversity.

9 Although space can be strongly contested in tidepools (Dethier 1984), tidepool
10 environments are a stage for positive interactions among species via the supply of regenerated
11 nutrients. Several algal species are characteristic tidepool dwellers at this and adjacent
12 Washington coast locales, including the red algae *Neorhodomela larix* and *Odonthalia floccosa*
13 and members of the genera *Prionitis*, *Polysiphonia*, *Cladophora*, and the seagrasses *Phyllospadix*
14 *scouleri* and *P. serratulus* (personal observation, Dethier 1984). Some of these species are
15 common to other locales where nutrient inputs have been linked to algal diversity and
16 productivity (Nielsen 2001, Bracken & Nielsen 2004, Bracken & Stachowicz 2006). It is likely
17 that some of these species have adaptations not only to tolerate high levels of ammonium but
18 also to benefit from this added source of inorganic nitrogen.

19 Although mussels were usually the dominant invertebrate in these tidepools by biomass,
20 other invertebrates are also abundant and have been shown to excrete nitrogen, including
21 anemones (*Anthopleura elegantissima*, Jensen & Muller-Parker 1994) and barnacles (Williamson
22 & Rees 1994). Other potential sources of nitrogen are crabs, fishes, limpets, and invertebrates
23 other than mussels may contribute to the inorganic nitrogen levels that are elevated relative to

1 coastal seawater, even when mussels are absent (Fig. 1, 2). Seabirds and marine mammals are
2 not abundant at this site but are thought to contribute to nitrogen input at Tatoosh Island, ~12 km
3 to the west (Pfister et al. in revision).

4 The strong coupling between nitrate and upwelling events and the observation that most
5 inorganic nitrogen is in the form of nitrate means that ammonium values are rarely reported for
6 coastal upwelling systems (Menge et al. 1997, Corwith & Wheeler 2002, Chavez et al. 2002).
7 Thus, our understanding of the nitrogen dynamics in nearshore environments is still rudimentary.
8 The high density of animals along shores, especially rocky ones, suggests that through feeding
9 and excretion they may contribute significantly to regeneration of nutrients, a phenomenon
10 increasingly appreciated in a variety of ecosystems (e.g. Eppley et al. 1973, Val Klump &
11 Martens 1983, Polis et al. 1997, Helfield & Naiman 2001, Croll et al. 2005).

12 **Nitrogen dynamics and the indirect effects of microbes**

13 In addition to the expected increase in ammonium with the presence of mussels, nitrite and
14 nitrate could also have increased concentrations, an unexpected result because animals are not
15 thought to excrete nitrite and nitrate. Although nitrification, the microbial conversion of
16 ammonium to nitrite and nitrate, has been studied in a variety of marine habitats (Capone 2000,
17 Ward 2000), rocky shores are relatively little studied (but see Magalhaes et al. 2005). The recent
18 discovery of nitrifying Archaea in cold temperate waters (Konneke et al. 2005, Wuchter et al.
19 2006), the prevalence of ammonium-excreting animals, the possibility that invertebrates
20 themselves provide substrate for nitrifying bacteria (Welsh & Castadelli 2004), the abundance of
21 microsites, and the persistent supply of oxygen by seaweeds and seagrasses may make rocky
22 shores an unappreciated locus for regenerated nutrients. Furthermore, because tidepools are
23 emergent and thus disconnected from oceanic supplies of nitrogen for hours at a time, animal

1 excretion may be particularly important for providing critical nutrients in these habitats. The
2 demonstrated decline in tidepool nitrate relative to open water suggests rapid nitrate consumption
3 during low tide periods (Fig. 2); algae may thus rely on multiple forms of inorganic nitrogen.
4 Mussels and other invertebrates also exist outside of tidepools and data from nearby Tatoosh
5 Island show that ammonium and nitrite have consistently greater concentrations immediately
6 adjacent to the shore compared with water sampled 50 to 500m away from the island (Pfister et
7 al. in revision). In addition to the more traditionally discussed upwelling of nitrate-rich water,
8 ammonium excretion by nearshore animals may be a persistent source of nitrogen, and thus an
9 important means of buffering nearshore populations during periods of intermittent upwelling or
10 El Niño events. Thus, autochthonous sources of regenerated nitrogen may contribute to
11 nearshore productivity in an analogous way to other systems (Dugdale & Goering 1967, Strayer
12 et al. 1999, Vanni 2002, Helfield & Naiman 2001).

13 Although there has been increasing attention paid to positive interactions in ecology
14 (Bertness & Leonard 1997, Hacker & Gaines 1997) and their affect on ecosystem function
15 (Cardinale et al. 2002), temperate rocky shores have been characterized as nutrient rich with high
16 animal and plant biomass and strong structuring by predator-prey and competitive interactions
17 (Dethier 1984, Paine 1974, 1992, Wootton 1992, Pfister 2006). The tidepool research reported
18 here suggests that this rich suite of interactions may be underlain by positive species interactions
19 among animals, algae and microbes providing a foundation for a reliable supply of nutrients.

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FIGURE CAPTIONS

1
2 Figure 1. The mean concentration in (μM) of a. ammonium, b. nitrite, c. nitrate, and d. phosphate
3 near the middle of the low tide period in 5 tidepools with their natural complement of mussels, 5
4 tidepools where mussels were experimentally removed, and an open ocean sample (\pm SE). The
5 30 May 2002 census was immediately prior to mussel removal (note arrow). In the 6 censuses
6 following experimental manipulation, ammonium and phosphorus were significantly greater
7 where mussels were present (Repeated Measures, $F_{1,8}=6.014$, $p=0.040$ & $F_{1,8}=5.168$, $p=0.053$,
8 respectively based on cube-root transformed data), while nitrite and nitrate were not ($F_{1,8}=3.124$,
9 $p=0.115$ & $F_{1,8}=1.393$, $p=0.272$). Note that time intervals are not equivalent.

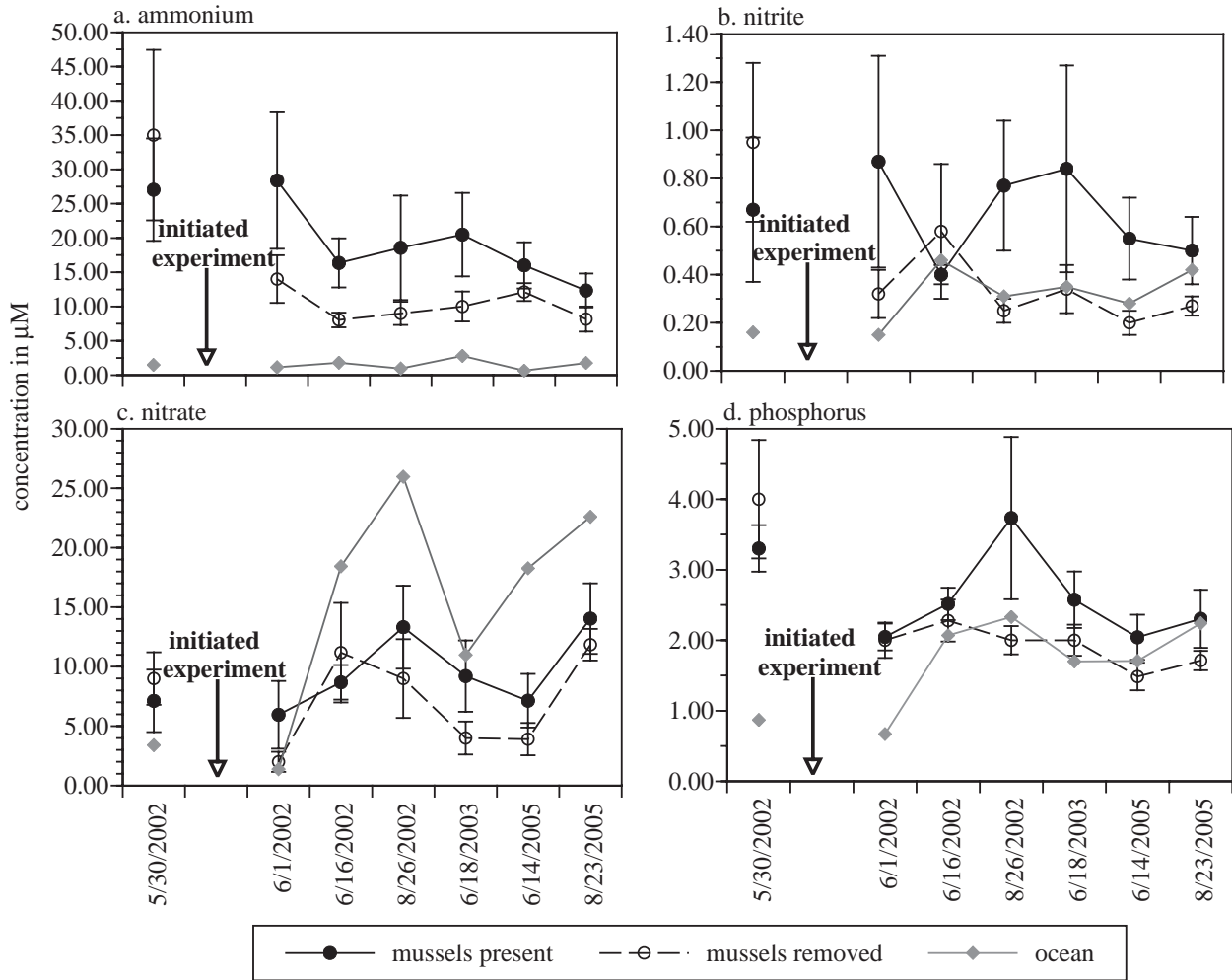
10 Fig. 2. The mean change in nutrient level (\pm SE) when experimental tidepools were isolated
11 from the open ocean for several hours during 4 dates from 2002 to 2005. Positive values indicate
12 a net increase (in μM), while a negative change indicates consumption or conversion. Cube-root
13 transformed data showed significantly greater increases for ammonium, nitrite and nitrate
14 (Repeated Measures ANOVA, ammonium: $F_{1,8}=6.871$, $p=0.034$, nitrite: $F_{1,8}=9.182$, $p=0.019$,
15 nitrate: $F_{1,8}=6.194$, $p=0.042$) in tidepools with mussels.

16 Fig. 3. The dynamics of inorganic nitrogen in a single tidepool (with mussels) through the low
17 tide period when the pool was emergent (23 Aug 2005). Concentrations in μM .

18 Fig. 4. The mean size (in area, \pm SE) of the red alga, *Prionitis lanceolata*, when transplanted
19 into tidepools with and without mussels. Those algae with mussels attained a significantly
20 greater size in Jul and Aug compared to algae in tidepools without mussels ($p=0.034$, $F_{1,8}$
21 $=6.526$, Repeated Measures ANOVA). There was also a time by treatment interaction
22 ($p=0.030$). Means are based on 1-3 individuals per tidepool.

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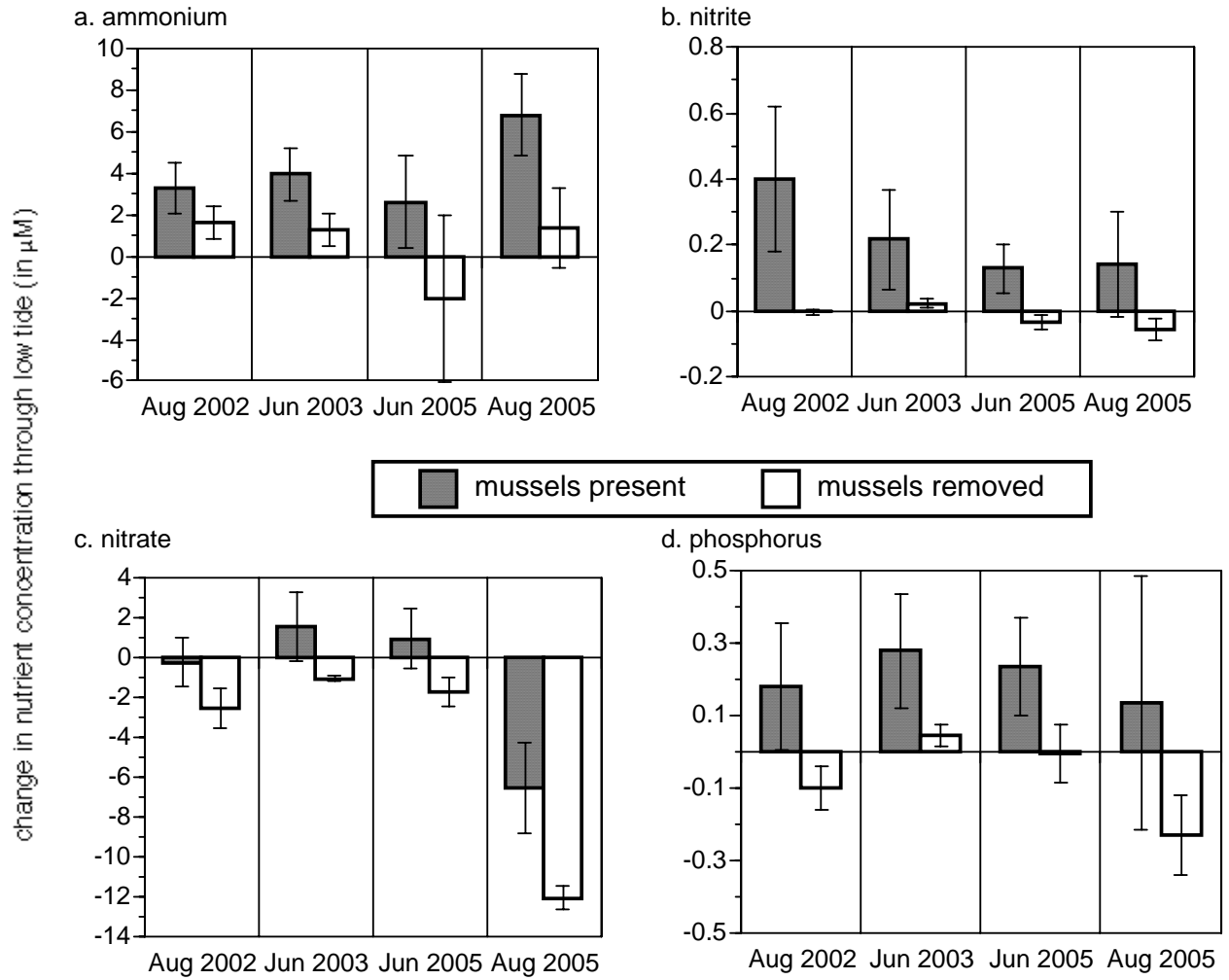
Figure 1



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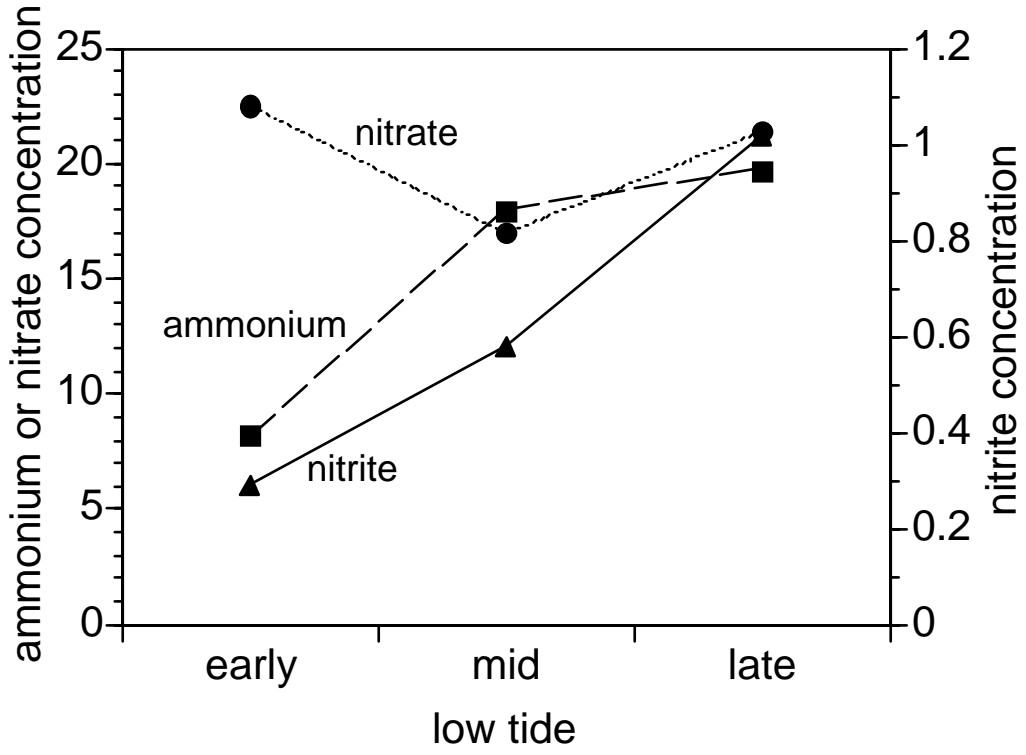
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Figure 2



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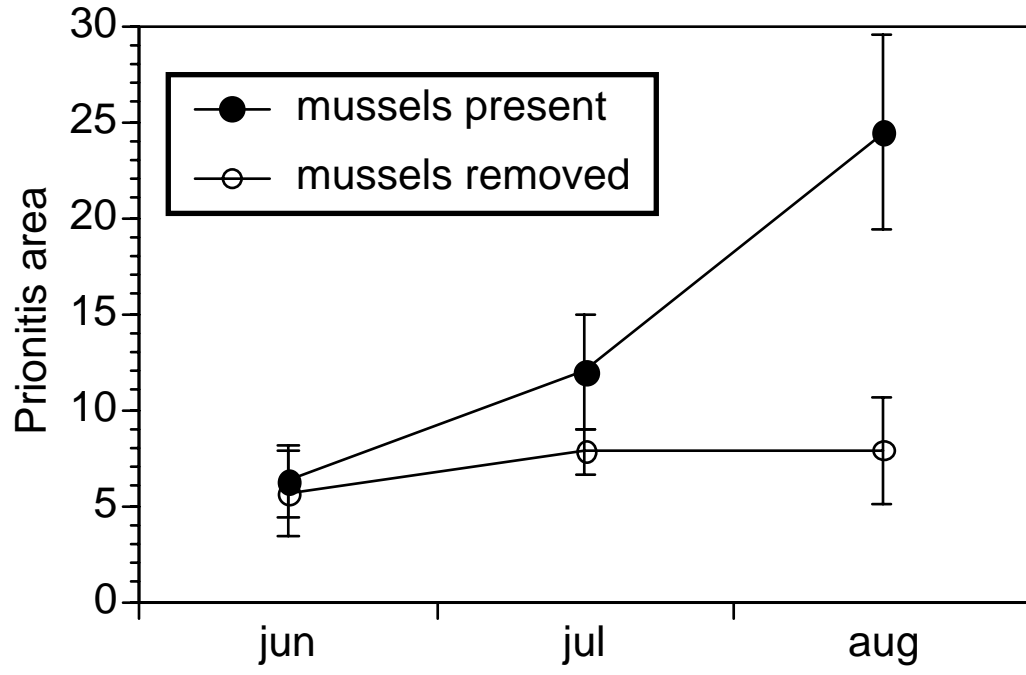
1 Figure 3
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Figure 4



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