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Growth of planktivorous bay anchovy *Anchoa mitchilli*, top-down control, and scale-dependence in estuarine mesocosms

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ABSTRACT: Growth of the zooplanktivorous bay anchovy *Anchoa mitchilli* and its potential to control plankton communities were investigated in estuarine mesocosms. The effects of mesocosm dimensions (size and shape) on anchovy growth and grazing impact were evaluated in 2 experiments, of 6 and 15 wk duration, respectively. Estuarine mesocosms of 1 and 10 m^3 volume and 2 shapes were used. The size–shape differences provided mesocosms with 3 volume-to-wall area ratios that determined how 'pelagic' the enclosures were. Anchovy growth rates scaled directly with mesocosm size and with mesocosm volume:wall area ratio. Growth was slowest in the least 'pelagic' enclosures, and fastest in the most 'pelagic' enclosures. The fish had a clear top-down impact on copepod populations. Mesocosms without fish supported copepods that were larger in size and of higher community biomass. Highest anchovy growth rates (and presumed consumption) occurred in mesocosms with lower mean copepod biomasses, further suggesting top-down control. Although not conclusive, trends in trophic relationships were consistent and supportive of the trophic cascade hypothesis. Mesocosms with high mean copepod biomasses tended to have low mean phytoplankton densities, and mesocosms with high anchovy growth rates tended to have high phytoplankton densities. There was no consistent evidence that top-down control by bay anchovy was related to mesocosm sizes or dimensions.

KEY WORDS: Mesocosms · Scale · Trophic cascades · Planktivorous fish

INTRODUCTION

The mechanisms and extent of top-down control and trophic cascades in structuring pelagic communities are poorly understood. The possibility that organisms at higher trophic levels, such as fish, exert influences that can register throughout the food chain via trophic interactions has been postulated frequently, but is not always well supported or documented (DeMelo et al. 1992, Micheli 1999). Many experimental investigations of such trophic interactions in aquatic ecosystems have been conducted in enclosures or mesocosms (Vanni 1987b, Horsted et al. 1988, McQueen & Post 1988, Riemann et al. 1988, Vanni & Findlay 1990, Isaksson et al. 1994, Drenner et al. 1996, Heiskanen et al. 1996, Perin et al. 1996, Proulx et al. 1996, Ramcharan et al. 1996, Brett & Goldman 1997, Petersen et al. 2003). In this context, the scale of experiments is undoubtedly important in the perception of ecosystem performance (Carpenter et al. 1987), and the size and dimensions of an enclosing mesocosm can alter ecosystem properties and processes (Petersen et al. 1999, Petersen & Hastings 2001). However, the scale-dependence of organism responses and trophic interactions in enclosure experiments are seldom evaluated. Enclosing higher trophic levels to identify

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'trophic cascades' or 'top-down' and 'bottom-up' controls can be difficult. Measuring and interpreting effects is challenging because experiments require enclosure of large, mobile predators such as zooplanktivorous fishes. Including such predators in relatively small mesocosm environments has the potential to alter behavior and foraging potential, possibly blurring predator–prey relationships and ecosystem responses (MacNally 1996, Heath & Houde 2001).

There are several ways in which enclosure dimensions might impact trophic cascades. The impacts may result from either artifacts of enclosure or from fundamental, natural ecosystem scaling properties (Petersen et al. 1999, 2003). Heath & Houde (2001) demonstrated in model simulations that enclosure size affects foraging efficiency of zooplanktivorous fishes, depending in part on fish behavior when encountering walls, a scaling artifact. Combining effects of the scaling artifact with the output of a bioenergetics model, they found that a 10% reduction in foraging rate due to scale-induced wall effects lead to declines of >50% in fish growth rates. Consequently, modeled fish growth scaled to mesocosm size and dimensions in which the relevant scaling factor was the amount of open water relative to wall area, which can be quantified by the volume:wall area ratio, or 'pelagicness' of the system. Systems that are more pelagic have more open water and, in theory, allow planktivorous fishes to forage with fewer constraints.

Fundamental or 'natural' scale-dependent responses also can be observed and measured in mesocosms. For example, predator–prey relationships may be altered at different spatial scales. Either natural ecosystems or mesocosms may be large enough to allow zooplankton patches to develop or to control other characteristic scales of variability in distributions. If zooplankton patchiness is scale-dependent, then vulnerability of zooplankton to predation may vary with spatial scale. Depending on ecosystem dimensions, some prey patches may escape predation through complexity in distribution (Huffaker 1958, MacNally 1996). Fundamental scale-dependent responses also can be generated via predator numbers and schooling behavior. For example, in experiments designed to achieve equal fish predation pressure in mesocosms of different sizes, fish density may be constant but the number of fish will vary. Differences in school size may fundamentally affect behavior and foraging efficiency of zooplanktivorous fishes, producing scale-dependent planktivory in enclosed ecosystems.

Our study was designed to investigate fish growth and trophic interactions in estuarine ecosystems and to evaluate how mesocosm size and dimensions affected trophic cascades. The bay anchovy *Anchoa mitchilli*, an abundant pelagic, zooplanktivorous fish in Chesapeake Bay and many estuaries, was selected as the predator. The study focused on 3 questions: (1) How do mesocosm dimensions affect growth (and presumed consumption) of bay anchovy? (2) Do anchovy exert a top-down controlling influence on plankton communities in estuarine mesocosms and does mesocosm size and shape modify this top-down effect? (3) Is the top-down control by anchovy altered by different nutrient regimes and can bottom-up influences play a controlling role?

MATERIALS AND METHODS

MEERC mesocosm system and operation. We conducted 2 experiments ('BP07' and 'BP09') in mesocosms of the Multiscale Experimental Ecosystem Research Center (MEERC). The MEERC facility housed 17 estuarine mesocosms of various shapes and sizes, constructed of a semi-transparent fiberglass material with an opaque, temperature-insulating blanket (see also Chen et al. 1997, Petersen et al. 1997, 1998). We used 3 types of experimental ecosystems, designated Mesocosms C, D, and E (Fig. 1). The C mesocosms were the smallest; they enclosed 1 m^3 of water, were 1 m deep, and had a diameter-to-depth ratio of 1.13. The D mesocosms enclosed 10 m^3 of water, were 2.15 m deep, 2.44 m in diameter, and had the same diameter to depth ratio (1.13) as the C mesocosms, and thus the same 'shape'. The E mesocosms also enclosed 10 m^3 of water, but had a depth of 1 m (the same as the

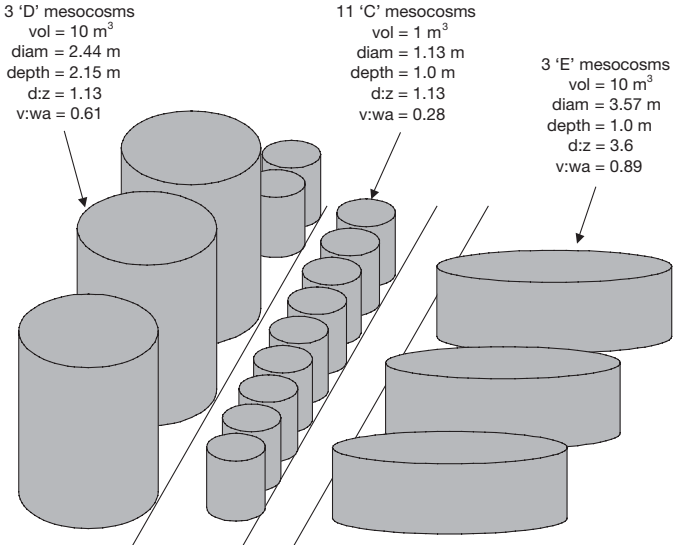

Fig. 1. Mesocosms D, C and E at Multiscale Experimental Ecosystem Research Center (MEERC) Facility used for Expts BP07 and BP09 showing layout, configuration and physical parameters. d:z: diameter:depth ratio; v:wa = volume-to-wall area ratio

C mesocosms), a diameter of 3.57 m, and a diameter-to-depth ratio of 3.57.

While each mesocosm type shared 1 quality (depth, volume or shape) with each of the other types, each mesocosm type was unique in an important way: their ratios of volume-to-wall area differed. The volume-to-wall area (v:wa) indexes the 'pelagicness' of the enclosed ecosystem, whereby the most-pelagic systems were expected to have the least relative wall effect. Since v:wa included only the walls and not the bottoms of the mesocosms, v:wa algebraically equals one-half the radius of the mesocosm. The C mesocosms were the least pelagic, with v:wa = 0.28 m. The D mesocosms were more pelagic, v:wa = 0.61 m, and the E mesocosms were most pelagic, v:wa = 0.89 m.

Turbulent mixing was provided by a system of impellers consisting of PVC paddles on a rotating shaft that extended into each tank. Paddle sizes, shapes, and rotation speed and period were scaled to accurately simulate the turbulent intensity and semi-diurnal tides in the Choptank River subestuary of Chesapeake Bay and to provide consistent mixing and diffusion rates among the mesocosm types (Sanford 1997). Banks of fluorescent lights on a 12:12 h light:dark cycle illuminated the mesocosm facility. Average surface light intensity was 190 µE m^{-2} s^{-1}. Room air-temperature was controlled and each mesocosm was fitted with a jacket of insulating material. On any given day, all mesocosm temperatures were within 1°C of each other and daily fluctuations were ±0.8°C.

Experimental design. The first experiment (BP07) was designed primarily to explore how mesocosm dimensions affected fish growth, and secondarily to evaluate how anchovy predation may have impacted mesocosm plankton communities. To ensure that anchovies were not subjected to a prolonged period of low prey levels, this experiment was limited to 45 d duration. The second experiment (BP09) was designed primarily to explore how anchovy predation affected plankton communities. To follow effects on trophic relationships, the BP09 experiment was of 97 d duration. In each experiment, all D and E mesocosms included bay anchovy predators. Only 3 D and 3 E mesocosms were available, too few to include both controls and replicated treatments. In the C mesocosms, each experiment included (1) treatments without fish ('no-fish'), (2) fish at the same density as in the D and E mesocosms ('low-fish'), and (3) a treatment with a higher fish density than the D and E mesocosms ('high-fish').

In Expt BP07, 3 C mesocosms were randomly assigned to each of the 3 treatments. The low-fish mesocosms contained 2 fish m^{-3} and the high-fish mesocosms 4 fish m^{-3} (Table 1). The mean biomass of stocked anchovy was 1.04 g m^{-3} in the 2 fish m^{-3} mesocosms and 2.08 g m^{-3} in the 4 fish m^{-3} mesocosms. Stocking densities were selected based on results of preliminary experiments designed to estimate foraging rates of planktivores in mesocosms (Malone 1996, Kennedy 1997).

Expt BP09 generally followed the same design as BP07, but with higher anchovy densities (Table 1). The low-fish treatment was 4 fish m^{-3} and the high-fish treatment was 6 fish m^{-3}. The 4 fish m^{-3} treatments con-

Table 1. Experimental design. Distribution of fish (*Anchoa mitchilli*) and, in Expt BP09, nutrient treatments among 3 mesocosm types (C, D, E) in Expts BP07 and BP09 (mesocosm sizes and dimensions in Fig. 1) showing no. of fish in each mesocosm (no. m^{-3} in parentheses). In Expt BP07, ~10 cm of Choptank River sediments were placed in each mesocosm; in Expt BP09, no sediments were added, but to make up for lost nutrient flux, 1.6 mol m^{-3} NH_4^+ and 0.1 mol m^{-3} PO_4 were added to each mesocosm daily. For mesocosms in 'high-nutrient' treatment, additional 32 mol m^{-3} NH_4^+ and 2 mol m^{-3} PO_4 were added twice weekly

Mesocosm (vol, shape)	Nutrient treatments (Expt BP09 only)	Fish treatments	Number of fish (fish density)	Number of mesocosms assigned
Expt BP07 (45 d)-no nutrient treatments				
C (1 m^3)		No fish	0	3
		Low fish	2 fish (4 m^{-3})	3
		High fish	4 fish (2 m^{-3})	3
D (10 m^3, deep)		Low fish	20 fish (2 m^{-3})	3
E (10 m^3, wide)		Low fish	20 fish (2 m^{-3})	3
Expt BP09 (97 d)-with nutrient treatments				
C (1 m^3)	High nutr.	No fish	0	2
	High nutr.	High fish	6 fish (6 m^{-3})	2
	Low nutr.	No fish	0	3
	Low nutr.	Low fish	4 fish (4 m^{-3})	2
	Low nutr.	High fish	6 fish (6 m^{-3})	2
D (10 m^3, deep)	Low nutr.	Low fish	40 fish (4 m^{-3})	3
E (10 m^3, wide)	Low nutr.	Low fish	40 fish (4 m^{-3})	3

tained a mean biomass of 2.84 g m^{-3}, and the 6 fish m^{-3} treatments contained a mean biomass of 4.26 g m^{-3}.

In addition to considering top-down effects, Expt BP09 was designed to explore possible bottom-up effects and interactions between top-down and bottom-up effects. To accomplish this, an additional 2 × 2 factorial design was employed, with a fish/no-fish factor and a high-nutrient/low-nutrient factor. Each treatment in the 2 × 2 factorial was duplicated in the C mesocosms, except for the low-nutrient, no-fish control, which had 3 replicates.

Mesocosms were filled with unfiltered Choptank River water. Salinities were 6.4 at the beginning of Expt BP07 and 10.0 at the beginning of Expt BP09. Individual mesocosms were filled sequentially in thirds to minimize founder effects in establishing plankton communities. In Expt BP07, 10 cm of Choptank River sediment was placed in each mesocosm (prior to the experiment sediments were held under anoxic condition to eliminate living macroorganisms). In Expt BP09, no sediments were placed in the mesocosms.

During experiments, 10% of the water and plankton it contained were discharged daily from each mesocosm and replaced with Choptank River water filtered to 0.6 µm. Nutrient and chlorophyll *a* (chl *a*) levels were measured twice each week from a 3 l sample of water from each mesocosm. Zooplankton were sampled by peristaltic pump from each mesocosm 3 times weekly in Expt BP07 and once weekly in Expt BP09; 20 l samples were filtered onto a 64 µm mesh and then preserved for later identification, enumeration and measurement.

In Expt BP07, in which the primary emphasis was on fish growth, an optical plankton counter (OPC) was used to enumerate zooplankton numbers. On each OPC sampling day, additional samples were pumped and filtered from 1 mesocosm of each treatment (randomly selected at the beginning of the experiment) from which individual zooplankters were both identified and measured to determine size structure of the population, and thus calibrate the OPC. Calibration results were then applied to the OPC numbers and sizes of zooplankters in each mesocosm to estimate biomass.

In Expt BP09, in which the primary emphasis was on trophic interactions and effects of the anchovy on the plankton community, zooplankton was collected and enumerated from pumped samples. All samples were examined under a stereomicroscope and organisms were counted, measured and assigned to major taxonomic groups (i.e. *Acartia* sp. copepods, *Eurytemora* sp. copepods, polychaetes, barnacle nauplii, copepod nauplii, etc.). Individual zooplankter lengths were converted to biomass using the weight–length equations of White & Roman (1992). Direct comparisons of equivalent spherical diameters (ESD) from the OPC in Expt BP07 and measured lengths in Expt BP09 are not possible (Herman 1992). We measured zooplankton in Expt BP09 to allow a nearly complete description of zooplankton taxa and sizes, and to allow comparison of zooplankton community structure between treatments. The direct identifications and measurements of zooplankton in Expt BP09 also allowed us to apply Schoener's similarity index (Schoener 1970) to compare treatment effects.

Abundances of microzooplankton and bacterioplankton were sampled twice a week in Expt BP07 and approximately biweekly in Expt BP09. Bacterial abundances were estimated using the acridine orange direct count (AODC) method (Hobbie et al. 1977).

Bay anchovies were collected by midwater-trawl and beach seine. They were acclimated and maintained in a 1 m^3 holding tank in the MEERC facility. Anchovies were stocked in the mesocosms on Day 15 of Expt BP07 and Day 25 of Expt BP09. In BP07, anchovy mean total length when stocked was 44 mm and mean wet weight was 0.52 g. In BP09, anchovy mean total length was 48 mm and mean wet weight was 0.73 g.

During the experiments, mesocosms were visually monitored for dead or dying anchovies. High turbidity often made it difficult or impossible to see fish well enough to count them. In Expt BP09, a few visible, dead anchovies were removed and replaced with anchovies from the holding tank. No dead anchovies were visible during Expt BP07.

Analysis. Correlations between growth, production and biomass of various trophic levels were analyzed for evidence of top-down or bottom-up effects. The signs and levels of the resulting correlations indicated if top-down or bottom-up control might be occurring (McQueen et al. 1986). For example, if low copepod abundances were correlated with high fish growth (indicating high fish consumption), then the fish were presumed to control the copepods. However, if copepod biomasses were positively correlated with high fish growth (and hence consumption), a bottom-up process presumably was responsible, i.e. copepods controlled fish production. Similar reasoning was applied to relationships between primary producer biomass and zooplankton levels.

To determine differences in zooplankton community composition in Expt BP09 (in which zooplankton were identified to taxa for all samples), the relative biomasses of zooplankton taxa were analyzed and compared among treatments using Schoener's index. The index ranges between 0 and 1, with 1 indicating complete similarity or overlap (Schoener 1970). Zooplankton communities in which overlap was <0.6 were considered to differ significantly. In this analysis, Expt BP09 was divided into 4 time periods: Days 1 to 23, 29

to 48, 57 to 76, and 83 to 97. The beginning and endpoints of each period represent days on which zooplankton samples were taken, and the gaps between periods result from sample timing (i.e. there were no samples taken between Days 23 and 29). The 4 time periods were selected to represent (1) a period before anchovies were added; (2) an early period with anchovies present, characterized by a polychaete bloom; and (3) and (4) 2 approximately equal periods of 'steady-state' following the polychaete bloom.

Organism abundances at all trophic levels were converted to carbon concentrations (µg l^{-1}) to compare the relative biomass (in a common carbon unit) among trophic levels in the various treatments. Bacteria were assumed to have a volume of 0.041 μm^3 $cell^{-1}$ and a carbon content of 0.35 pg C μm^{-3} (Kuuppo-Leinikki et al. 1994). Water column chl *a* was converted to phytoplankton carbon assuming that phytoplankton carbon concentration was 51 times chl *a* biomass (White & Roman 1992). Zooplankton biomasses were converted to carbon assuming C (µg C $individual^{-1}$) = 0.32 weight (µg dry wt $individual^{-1}$) (White & Roman 1992). Zooplankton taxa representing <1% of the carbon were not included in these analyses (e.g. barnacle nauplii).

All statistical tests were conducted using the SAS statistical language (SAS Institute 1990). Means were compared using analysis of variance. An experimentwise $\alpha = 0.05$ was selected to judge statistical significance. Fisher's protected LSD and Tukey's HSD test, which protect against inflated experimentwise Type I error, were applied in multiple comparisons of estimated means.

For the fish and nutrient treatments in the C mesocosms of Expt BP09, a traditional 2 × 2 factorial analysis was applied to the means of chl *a* and copepod biomass over the sampling dates from the initiation of treatments (i.e. when fish were placed in mesocosms) until termination of the experiment. The main effects of fish and nutrients, as well as any interactions, were tested for statistical significance using a factorial analysis of variance (Sokal & Rohlf 1995).

Many of the data from Expts BP07 and BP09 were based upon repetitive measurements of the same variable through time (e.g. copepod biomass within a mesocosm treatment). Such data often are analyzed with a repeated-measures approach, which models covariance and is predicated on the assumption that measurements made close in time will not be independent; rather, they will covary (Littell et al. 1996). We explored use of repeated-measures statistics, but they were of limited value in analyzing our time-series data because large peak-then-crash cycles of biomass and density, especially in Expt BP09, confounded the linear time response assumed in repeated-measures analysis.

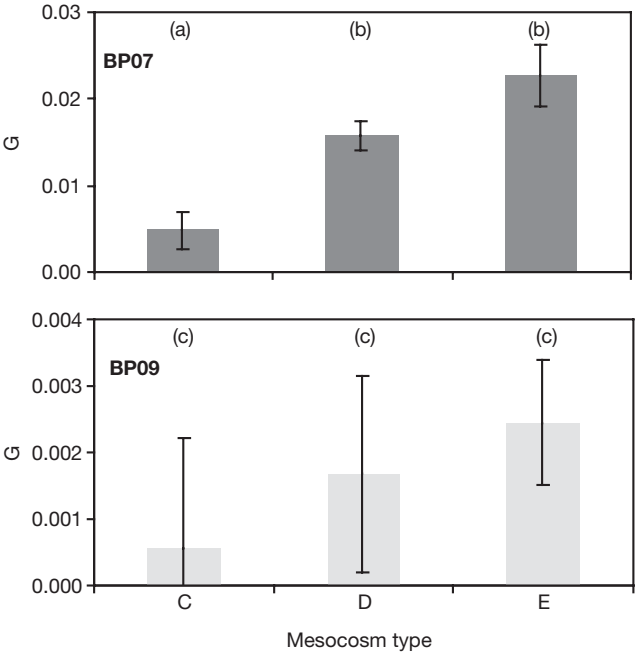

Fig. 2. *Anchoa mitchilli*. Mean (±1 SE) weight-specific growth rates (G) in mesocosms of 3 sizes and dimensions (see Fig. 1) in Expts BP07 and BP09. Means with same lower-case letter do not differ significantly ($p > 0.05$)

Since no modeled covariance structure improved the fit of the data, a multivariate linear model was used for analysis, with results on each day essentially tested independently

RESULTS

Fish growth

Growth patterns of bay anchovy with respect to mesocosm treatment were consistent in the 2 experiments. The fish grew slowest in the C (1 m^3, small) mesocosms, faster in the D (10 m^3, tall) mesocosms and fastest in the E (10 m^3, wide) mesocosms (Fig. 2). In Expt BP07, the probability of a mesocosm effect on growth was significant ($p = 0.002$). In this experiment, growth was significantly slower in the C mesocosms than in the D and E mesocosms (Fisher's protected LSD, $p < 0.002$ and $p < 0.0008$, respectively). The mean growth rates did not differ significantly between D and E mesocosms ($p > 0.13$). In Expt BP09, the same pattern of anchovy growth emerged, although the growth rates did not differ significantly among treatments (Fig. 2). The observed mean growth rates were slowest in the C (1 m^3, small) mesocosms, faster in the D (10 m^3, tall) mesocosms, and fastest in the E (10 m^3, wide) mesocosms.

Weight-specific growth rates were approximately 1 order of magnitude lower in the long, higher-fish-density BP09 experiment (97 d) than in the short, lower-fish-density BP07 experiment (45 d). Although the differences in growth rates within Expt BP09 were not significantly different among mesocosm types, the pattern of growth rates among mesocosm types was nearly identical in the BP07 and BP09 experiments. The ratios of weight-specific growth rates between mesocosm types (growth rates in C vs. D mesocosms, C vs. E mesocosms, D vs. E mesocosms) were very similar in the 2 experiments (Table 2).

Table 2. *Anchoa mitchilli*. Comparison of ratios of weight-specific growth rates (G, in parentheses) between Expts BP07 and BP09 for the 3 mesocosm types C, D and E

Mesocosm comparison	Expt BP07	Expt BP09
C vs. D	**0.31** (4.8×10^{-3}:1.6×10^{-2})	**0.34** (5.7×10^{-4}:1.7×10^{-3})
C vs. E	**0.21** (4.8×10^{-3}:2.3×10^{-2})	**0.23** (5.7×10^{-4}:2.5×10^{-3})
D vs. E	**0.69** (1.6×10^{-2}:2.3×10^{-2})	**0.69** (1.7×10^{-3}:2.5×10^{-3})

Within each experiment, body condition of anchovies did not differ among mesocosm types as measured by Fulton's condition index ($F = 10^{5} \times w \times l^{-3}$, where w = wet weight, g and l = length, mm) (mesocosm type p = 0.75, mesocosm type by experiment interaction p = 0.57). However, the mean condition of anchovies was significantly higher in the shorter BP07 experiment (p < 0.02, Tukey's HSD).

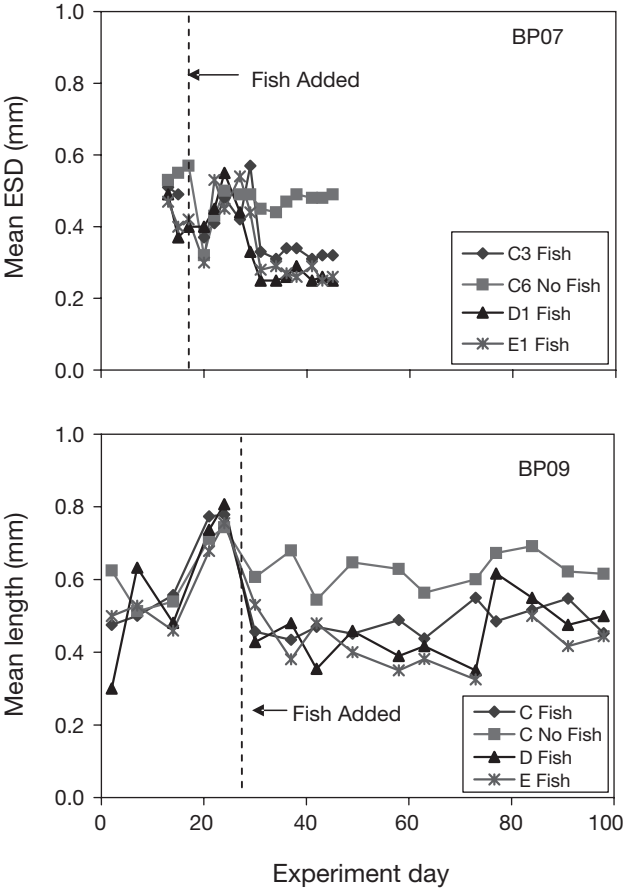

Fig. 3. Mean copepod and copepodite sizes in Mesocosms C, D and E in Expts BP07 and BP09. Expt BP07 sizes are from the 1 mesocosm per treatment measured, given as equivalent spherical diameters (ESD) determined with an optical plankton counter. Expt BP09 sizes are means of all mesocosms in a treatment, given as actual measurements of cephalothorax length

Zooplankton prey

Copepod populations were responsive to fish predation in both experiments, but there were relatively small differences among mesocosm types. The clearest impact of anchovy was on the mean sizes of the combined copepods and copepodites (primarily *Acartia tonsa* and *Eurytemora affinis*) (Fig. 3). By the end of Expt BP07, the mean equivalent spherical diameter (based on OPC measurements) of copepods and copepodites (combined) was approximately 1.5 times larger in mesocosms without anchovies than in mesocosms with anchovies. In Expt BP09, the mean copepod and copepodite lengths when anchovies were present (Days 25 to 97) were significantly larger in mesocosms without fish (0.63 mm) than in mesocosms with fish (means ranging between 0.49 and 0.52) (p < 0.0001; C no fish vs. C fish, p < 0.0006; C no fish vs. D p < 0.0007; C no fish vs. E p < 0.0001), indicating size-selective foraging by the anchovies.

The shift in sizes of copepods and copepodites for mesocosms with and without fish occurred much sooner after anchovy addition in Expt BP09 (after about 3 d) than in Expt BP07 (after about 14 d) (Fig. 3). This difference probably resulted from the higher anchovy densities in BP09 and greater predation pressure on the largest copepod instars. In both experiments, copepod nauplii sizes remained similar in mesocosms with and without fish, implying that the anchovy did not forage size-selectively on the naupliar stages.

Copepod biomasses also were strongly responsive to anchovy presence. In Expt BP07, after Day 30 (15 d after anchovies were added), copepod and copepodite mean biomasses were clearly higher in mesocosms without fish (Fig. 4). The decline in copepod biomasses in mesocosms with anchovies began at approximately the same time as the decline in sizes of individuals. In Expt BP09, the mesocosms without anchovies supported mean copepod biomasses 50 to 100 times higher than the mean bio-

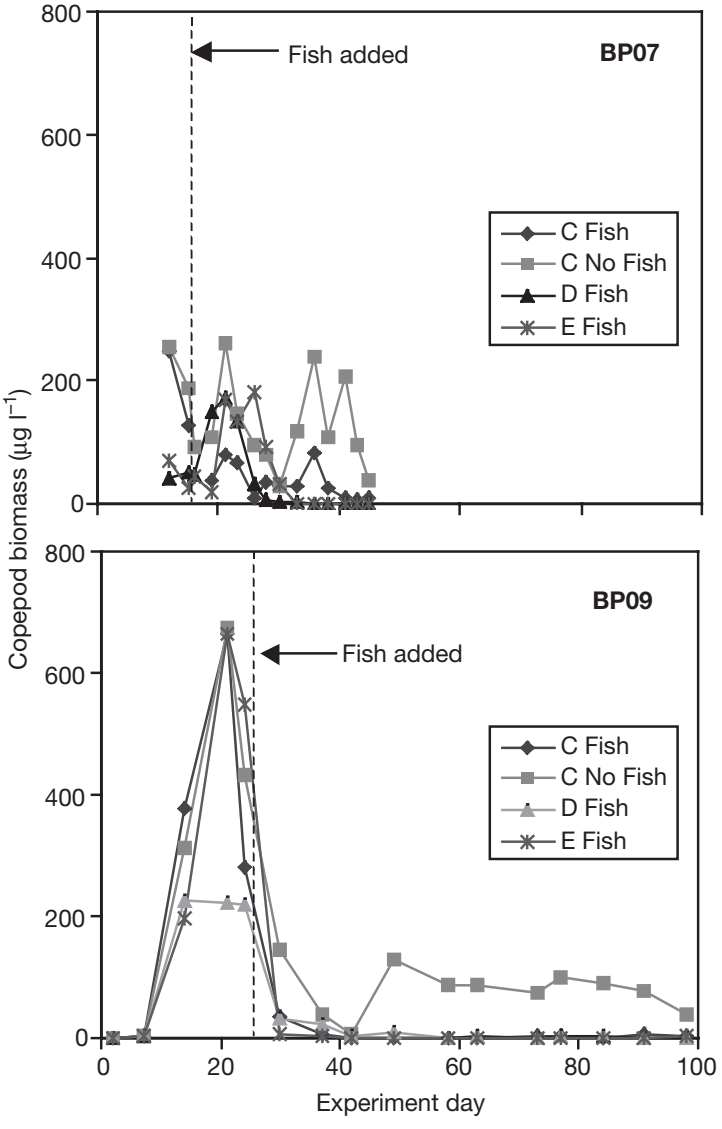

Fig. 4. Copepod and copepodite biomasses (µg l^{-1}) in Mesocosms C, D and E in Expts BP07 and BP09. Biomasses derived from sizes in Fig. 3 and size-to-weight relationships in White & Roman (1992). Plotted values are means for all mesocosms in a treatment

masses in mesocosms with anchovies. The evolution of copepod biomasses over the course of experiments was more consistent in Expt BP09 than in Expt BP07. In BP09, an early biomass peak occurred in all mesocosms around Day 20 (Fig. 4), followed by sharp declines.

In Expt BP07, the only significant differences in mean copepod biomasses between mesocosm types were detected on Days 12 to 15, before anchovies were stocked. In this period, the C mesocosms had copepod biomasses significantly higher than those in the D and E mesocosms (C fish vs. D, $p < 0.05$; C fish vs. E, $p < 0.05$; C no fish vs. D, $p = 0.03$; C no fish vs. E, $p = 0.03$) (Fig. 4). In the rest of Expt BP07, mesocosm type and treatment (after anchovies were added) had no demonstrable overall impact on copepod biomasses ($p > 0.8$).

In the longer BP09 experiment, differences were observed in copepod biomasses among mesocosm types/treatments ($p < 0.001$) and days ($p < 0.001$). There also was evidence of mesocosm type × days interactions ($0.001 < p < 0.27$). In testing for effects of anchovy presence (fish vs. no fish), the C mesocosms without anchovies had significantly higher copepod biomasses ($p < 0.05$) than the C mesocosms with anchovies on 7 of the 9 sampling dates. The C mesocosms without fish had significantly higher mean copepod biomasses than the D mesocosms on 5 of the 9 d tested, and higher biomasses than the E mesocosms on 6 of the 9 d tested ($p < 0.05$). In analyzing mesocosms that included anchovies (C fish vs. D vs. E), no significant differences in copepod biomasses were detected on any of the days tested during Expt BP09.

In the 2 × 2 factorial experiment within the C mesocosms of Expt BP09 (Table 1), copepod biomasses were influenced more by presence or absence of anchovies than by high or low nutrient levels. Mesocosms without anchovies supported, on average, 78.81 µg l^{-1} more copepod and copepodite biomass than mesocosms with anchovies (Table 3), a significant effect ($p < 0.006$). Nutrient additions, and the interaction between nutrient addition and fish presence/absence, had no significant effect on copepod biomasses.

Table 3. Mean copepod and copepodite biomass levels (µg l^{-1} for Days 21 to 97) in the C mesocosms of Expt BP09. Main effects of fish (*Anchoa mitchillii*), nutrients, and interaction between fish and nutrients were tested in standard 2 × 2 factorial ANOVA (Sokal & Rohlf 1995). Main effect: difference between means of a treatment (i.e. main effect of nutrients is difference between mean high nutrient and mean low nutrient; Interactions = ½ × (NF, LN – NF, HN – F, LN + F, HN) where NF, LN = mean biomass for 'no fish, low nutrients' and F, HN = mean for 'fish, high nutrients' treatments, etc. Fish and nutrient treatments began on Day 21 of the 97 d experiment

Treatment	Low nutrients	High nutrients	Fish treatment means	
No fish	75.43	132.57	104.00	Main effect of fish
Fish	35.12	15.26	25.19	78.81
Means of nutrient treatments	55.28	73.91		
	Main effect of nutrients	18.64	Interaction	–38.50

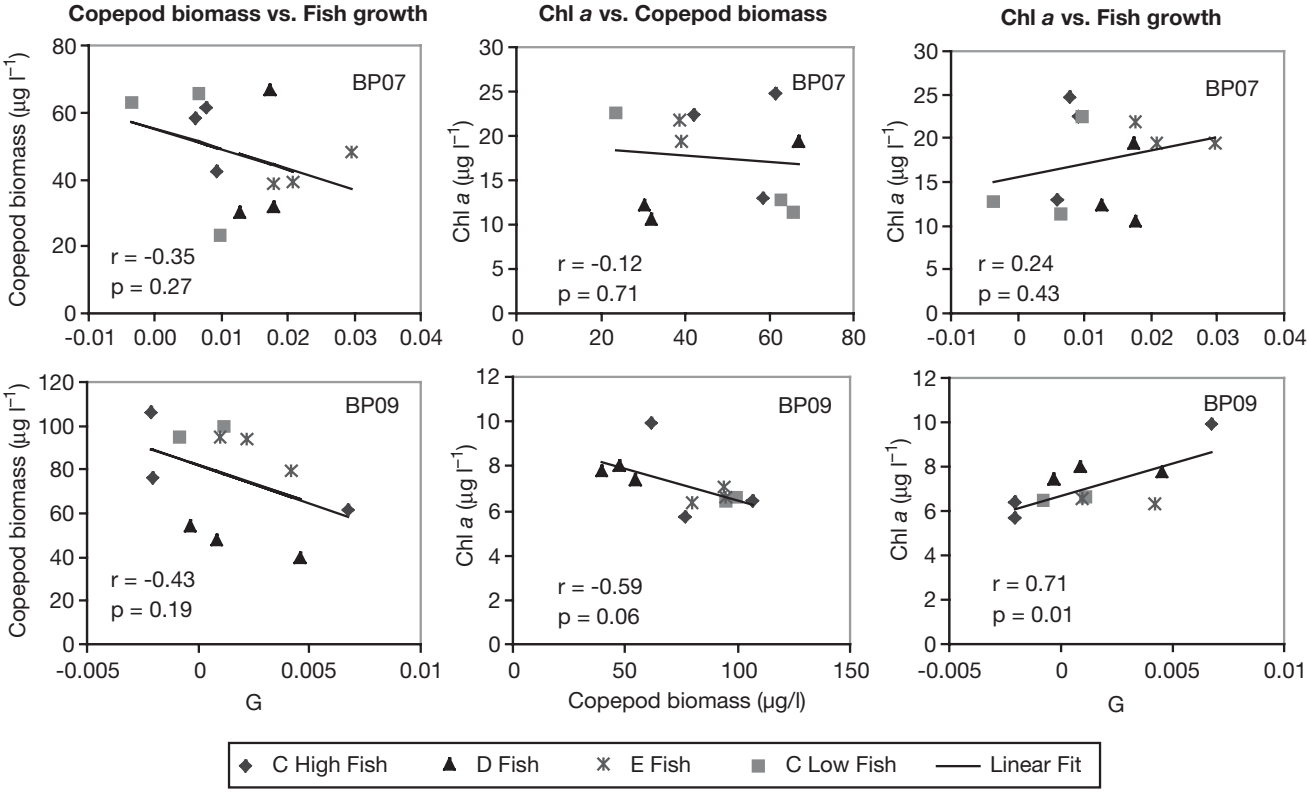

Fig. 5. Relationships between chlorophyll *a* concentrations (phytoplankton biomass), mean biomasses of copepod population and bay anchovy *Anchoa mitchilli* mean weight-specific growth rates (G) in Expts BP07 and BP09, showing simple correlations that provide evidence for top-down control and trophic cascades

Fish–zooplankton interactions

There is weak, but nevertheless consistent, evidence that anchovies exerted a top-down influence on copepod populations in both Expts BP07 and BP09. In addition to the shifts in mean copepod and copepodite size and biomass in the presence of fish, correlation coefficients between copepod biomass and weight-specific growth rates of anchovy were negative in each experiment (Fig. 5). Although the signs of correlation coefficients suggested top-down control, the relationships were not significant ($p = 0.27$ and 0.19 for Expts BP07 and BP09, respectively).

Zooplankton taxa other than copepods were important elements of the zooplankton community in the BP09 analysis. Blooms of polychaete trochophores (species unknown) appeared in all mesocosms around Days 30 to 40 (Fig. 6). In the C fish and E mesocosms, the biomasses of the polychaete blooms were approximately equal to the earlier copepod blooms, while in the D and C no fish treatments the polychaete blooms exceeded the biomasses of the copepod blooms. The polychaetes and copepods followed similar trajectories — initial increase to a high level, then rapid decline to lower and more stable levels. Polychaete blooms did not occur until copepods were in decline. In mesocosms with anchovies, polychaetes generally persisted at higher population biomasses than copepods.

Similarity indices

The composition of the plankton communities among mesocosm types/treatments changed during the course of Expt BP09, in part due to top-down control by anchovy predation. Early in the experiment, before addition of anchovies (Days 1 to 23), the mesocosms had similar plankton compositions, with zooplankton biomass dominated by the initial copepod blooms. By Days 57 to 76, when anchovies had been in the mesocosms for >34 d, the C no fish mesocosms held large copepod populations, and their zooplankton communities differed from mesocosms with anchovy predators that had suppressed copepod biomass (Fig. 7). All mesocosms with fish were similar during this period (C fish vs. D and E mesocosms). A bloom of barnacle nauplii peaked in all D mesocosms during this period and accounted for 44% of the total zooplankton biomass.

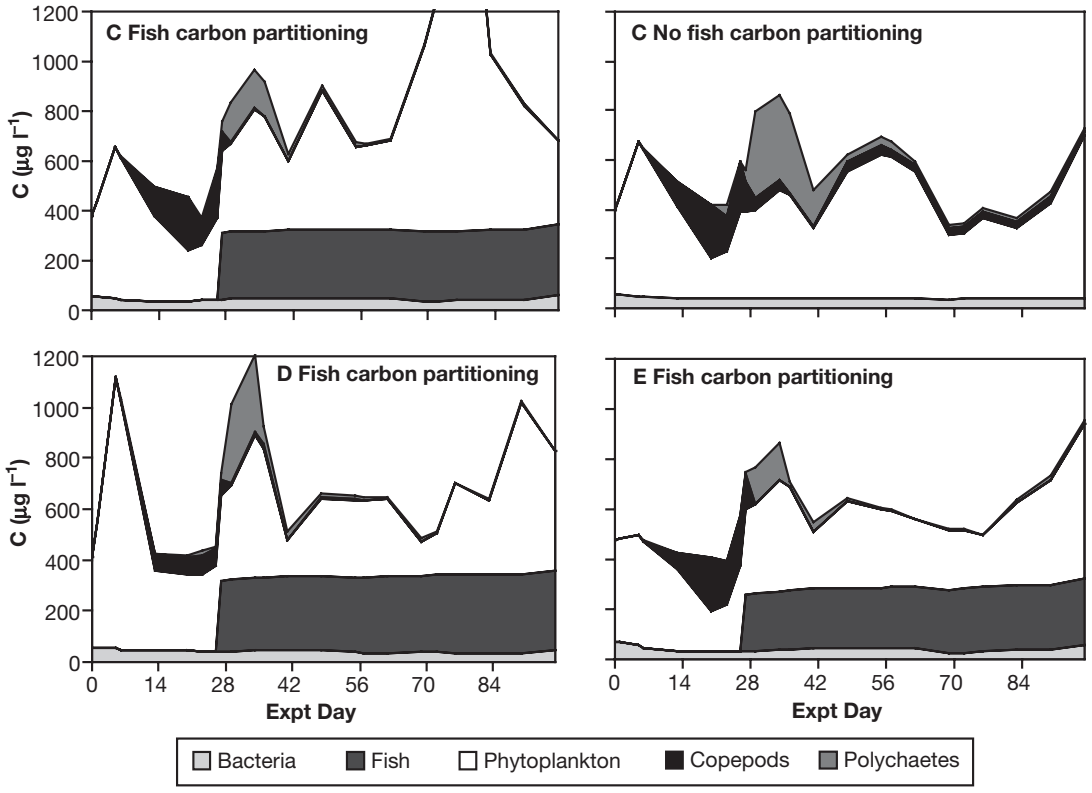

Fig. 6. Carbon partitioning among taxonomic groups during Expt BP09. Carbon concentrations are given for 5 taxonomic categories in each mesocosm type (Mesocosms C, D, E) treatment. Plotted concentrations are mean values for each mesocosm type/treatment

It was responsible for a large fraction of the dissimilarity between the D, and the E and C fish mesocosms. The barnacle nauplii bloom in the D mesocosms was small relative to the copepod and polychaete blooms and represented less than 1% of the carbon biomass in the mesocosms during this period.

Phytoplankton, bacteria, and nutrients

No clear, consistent differences in bacterial biomass or chl *a* levels were detected among mesocosm types and treatments in Expts BP07 or BP09. In BP09, 1 C fish mesocosm experienced a large phytoplankton bloom, but other mesocosms in that treatment did not. Consequently, the mean chl *a* levels (and carbon associated with chl *a*) in C fish mesocosms did not differ significantly from those in other mesocosm types (Fig. 6). Levels of nutrients were recorded throughout both experiments, but no differences or trends were detected between treatments. Results of the nutrient trends and analyses are detailed in Mowitt (1999).

In the BP09 2×2 factorial experiment in the C mesocosms, chl *a* levels were strongly affected by nutrient regime, but only weakly affected by the presence or absence of anchovy (Table 4). Mesocosms with high nutrients had, on average, levels of chl *a* 10.86 µg l^{-1} higher than mesocosms with low nutrient additions, a significant main effect ($p = 0.02$). The effects of anchovies on chl *a* and the interaction effect between the 2 factors were not significant ($p = 0.20$ and 0.23, respectively).

Zooplankton–phytoplankton interactions

Zooplankton may have played a weak, top-down role in the control of phytoplankton biomass in Expt BP09 (Fig. 5). In Expt BP07, high copepod biomasses were not obviously associated with low phytoplankton levels ($r = -0.12$, $p = 0.71$). However, the relationship was stronger in the longer BP09 experiment ($r = -0.59$, $p = 0.06$), although still failing significance at the $\alpha = 0.05$ level. The time-series of carbon biomasses (Fig. 6) provides additional evidence that zooplankton, particularly copepods, were exerting a top-down control on phytoplankton. In all mesocosm types/treatments, a decline of the initial phytoplankton peak occurred during the initial peak of copepod biomass. Peaks in polychaete biomass were not associated with declines in phytoplankton carbon levels.

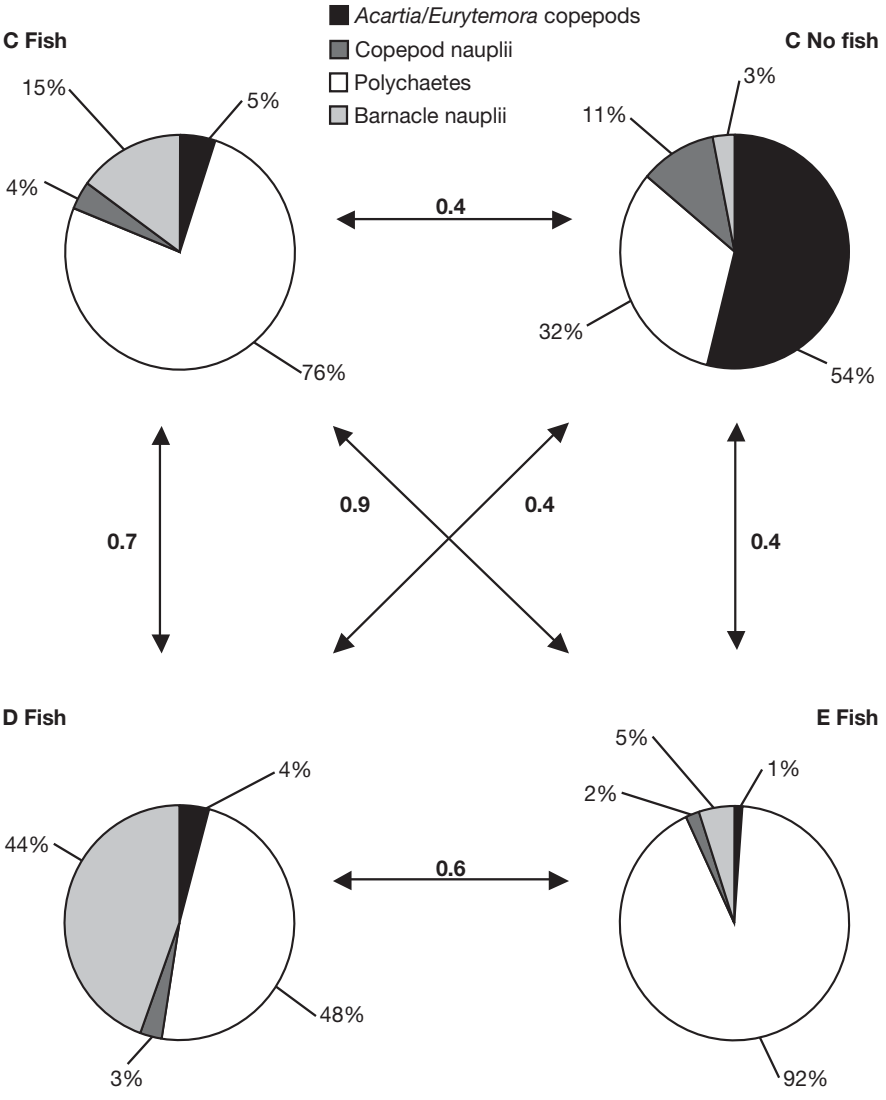

Fig. 7. Taxonomic distribution of zooplankton biomass (%) for each mesocosm type (Mesocosms C, D, E) treatment in Expt BP09, averaged for Days 57 to 76 (middle of period during which anchovy *Anchoa mitchilli* were present) during the 97 d experiment. Similarity index values (Schoener 1970) are given for each paired comparison. Index values ≥0.6 indicate similar zooplankton biomass distributions

DISCUSSION

Scaling of mesocosm dimensions and anchovy growth

The consistent relationship between anchovy growth rates and mesocosm dimensions in both the BP07 and BP09 experiments indicated that anchovies grew slower in the 1 m^3 C mesocosms than in the 10 m^3 D and E mesocosms. The relative differences in growth rates among mesocosm sizes were remarkably consistent in the 2 experiments (Table 2), suggesting that the scale-dependence may be predictable. In addition, the anchovy growth rates appear to have scaled to the shape of the enclosed ecosystem, with the most-pelagic ecosystems supporting higher growth rates. Mean growth rates were linearly correlated with the ratio of volume:wall area (pelagicness) in each experiment (Fig. 8). The linear relationship can, of course, only hold over a limited range that is constrained by the maximum rate of bay anchovy growth.

The high volume:wall area ratio of the wide, shallow, E mesocosms presumably reduced the frequency of wall encounters by the anchovies, thus improving foraging efficiency and growth potential. Restricted foraging efficiency at low prey levels ultimately would impact growth rates, leading to differences such as

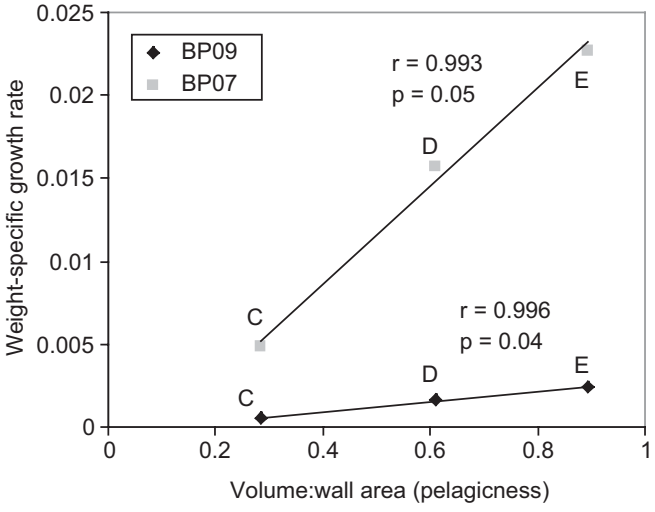

Fig. 8. *Anchoa mitchilli*. Relationships between weight-specific growth rates and mesocosm pelagicness for Expts BP07 and BP09

those observed in our experiments. A simulation model of planktivorous fishes foraging in enclosures of different sizes (Heath & Houde 2001) predicted similar decreases in growth rates in small enclosures, primarily as a response to reduced prey consumption, a consequence of wall-encounter behavior.

Bay anchovy in a natural ecosystem like Chesapeake Bay are essentially unconstrained by 'edges' or 'walls'. The spatial scale of hydrographic features that could act in a fashion similar to walls (e.g. pycnoclines, frontal regions, etc.) is considerably larger than constraining features in small enclosures. The Heath & Houde (2001) model suggested that 50 mm planktivorous fishes would require enclosures ≥2 m in diameter to allow foraging to be essentially unaffected by confinement (D mesocosm diameter = 2.44 m, E mesocosm diameter = 3.57 m). Our 10 m^3 mesocosms may therefore be above threshold dimensions for pelagicness that significantly restrict anchovy foraging-efficiency. This conclusion is reinforced by the observation that anchovy growth rates in the D and E mesocosms during the BP07 experiment (0.22 and 0.32 mm d^{-1}) were near the mean rates observed in Chesapeake Bay (between 0.20 and 0.33 mm d^{-1}) (Newberger & Houde 1995, Wang & Houde 1995).

Little is known about anchovy behavior in mesocosms and there may be explanations other than wall-encounter behavior that could account for the observed differences in growth of bay anchovy. For example, schooling or other interactive behavior may play a role in controlling growth rates. Growth rates of anchovies not only scaled to the size of mesocosms, but also scaled directly to numbers of fish in the mesocosms. Anchovies in the 1 m^3 C low-fish mesocosms (2 fish per mesocosm in Expt BP07, 4 in Expt BP09) consistently had lower growth rates than anchovies in the C high-fish mesocosms (4 fish per mesocosm in BP07, 6 in BP09). Anchovies in the 10 m^3 D and E mesocosms (with 20 fish per mesocosm in BP07, 40 in BP09) had the fastest growth rates. Determining whether relative effect of fish numbers or degree of pelagicness has the bigger effect on anchovy growth rates is a testable objective for future research.

Anchovy growth rates were much lower in the longer (97 d) BP09 experiment, and the condition index of anchovies from BP09 was significantly lower than in the shorter (45 d) BP07 experiment; 2 factors may explain the differences: (1) the higher stocking density, coupled with a prolonged period of low zooplankton densities, in Expt BP09 (Fig. 4) is the most likely explanation for this observed difference; (2) it is possible that growth rates of the anchovy were higher during the first half of the BP09 experiment then low during the long period of low zooplankton abundance. Since fish were not sampled until termination of the experiment, we can suggest, but not confirm, this possibility.

Trophic cascades

It was evident that anchovy predation controlled adult copepod populations in the mesocosms. Much weaker evidence suggested that anchovy predation might have induced a trophic cascade, indicated by higher chl *a* biomasses in mesocosms with anchovy. The effect, although statistically weak, was consistent between experiments (Fig. 5) and qualitatively consistent with the trophic cascade hypothesis (Carpenter et al. 1985). Correlations between trophic levels were consistently clearer in the longer BP09 experiment (Fig. 5), which may indicate that the shorter BP07 experiment was terminated before evidence of a trophic cascade could develop or be discerned.

In both Expts BP07 and BP09, anchovy not only reduced copepod and copepodite population abundances but also the mean sizes of copepods and copepodites by size-selective predation. The size-selective grazing we observed for bay anchovy produced effects similar to those reported previously for freshwater fishes feeding on zooplankton in enclosed ecosystems (Vanni 1987a, McQueen et al. 1989, Qin & Culver 1996). Copepod and copepodite sizes were smaller in Expt BP07 than in Expt BP09, which is at least partly a function of the difference between the OPC measurements of equivalent spherical diameter and total length measurements obtained under a microscope (Herman 1992).

Similarity indices of zooplankton taxa in Expt BP09 mesocosms provided more information on effects of anchovy predation on zooplankton community structure. After anchovies had been in the BP09 mesocosms for 20 to 30 d, zooplankton communities in mesocosms without anchovies diverged and differed significantly from communities in mesocosms with anchovies (Fig. 7). The major difference in the no-fish mesocosms was the continued presence of a high copepod population biomass, which represented 54% of zooplankton community biomass, compared to only 1 to 5% in mesocosms with anchovies.

There is little evidence that anchovy foraged heavily on taxa other than copepods in the mesocosms. Horsted et al. (1988) also found that the planktivorous 3-spined stickleback *Gasterosteus aculeatus* reduced abundances of copepods, but not of other zooplankton in estuarine mesocosms. For Chesapeake Bay, Vazquez (1989) and Klebasko (1991) reported that barnacle nauplii and larval polychaetes were generally unimportant in bay anchovy diets, although when abundant these prey could become significant. The biomass and mean size data for polychaete trochophores and barnacle nauplii in our mesocosms suggest that, even if anchovy were consuming these taxa, predation was not sufficient to induce detectable differences in sizes or biomass between mesocosms with and without anchovies (Mowitt 1999).

The impact of anchovies on copepods may have been propagated to the phytoplankton community in a trophic cascade. In the short (45 d) BP07 experiment there was no evidence of a relationship between copepod density and chl *a* concentrations, but in the longer (97 d) BP09 experiment, the relationship between the two was negative ($p = 0.06$) (Fig. 5). The time-series of carbon biomass in BP09 (Fig. 6) also indicated that as copepod abundance increased, phytoplankton biomass declined. The signs of correlation coefficients between anchovy growth rates and phytoplankton biomass were positive in both experiments, but significant ($p = 0.01$) only in the longer BP09 experiment (Fig. 5). This strongly positive correlation between the trophic levels farthest apart differs from some previous reports, which suggested an 'uncoupling' of the trophic cascade at the zooplankton–phytoplankton link (McQueen & Post 1988). Considered together, a trophic cascade is suggested in which high fish consumption reduced copepod biomasses, and low copepod biomasses allowed phytoplankton to escape zooplankton grazing.

The 2 × 2 factorial experiment evaluating effects of anchovy versus no anchovy, and high nutrients versus low nutrients in the C mesocosms of Expt BP09 indicated that fish presence exercised strong top-down control on copepod biomass, but not on chl *a* (Tables 3 & 4). On the other hand, mean chl *a* levels indicated that nutrients had a strong bottom-up effect on phytoplankton, but not on copepod biomasses. This outcome is supportive of the McQueen et al. (1986) hypothesis that top-down influences predominate at upper trophic levels, while bottom-up forces exercise control over lower trophic levels. It is also consistent with results from freshwater mesocosm experiments (Threlkeld 1987), other estuarine mesocosm experiments (Heiskanen et al. 1996), and meta-analyses of enclosure experiment results (DeMelo et al. 1992, Brett & Goldman 1997).

Scaling of the trophic cascade

There was no consistent evidence that the top-down control by anchovy in Expts BP07 and BP09 was scale-dependent over the spatial scales tested, i.e. top-down control did not scale to mesocosm dimensions. The lack of evidence could be a consequence of limitations of the experimental design. The major way that scale-dependent effects on the trophic cascade were detected was through responses of zooplankton to anchovy predation in the mesocosms of differing dimensions. The high variability in responses among individual mesocosms and the limited number of mesocosms available (and thus the few replicates) made it difficult to conclude that mesocosm dimensions affected the nature or level of top-down control by the anchovy.

Mesocosm experiments

The use of mesocosms to evaluate scale dependence of trophic interactions between planktivorous fish and other trophic levels in estuarine ecosystems proved to be difficult, despite the fact that anchovy growth

Table 4. Mean chl *a* levels (μg l^{-1} for Days 21 to 97) in the C mesocosms of Expt BP09. Further details as in Table 3 legend

Treatment	Low nutrients	High nutrients	Fish treatment means	
No fish	5.29	11.28	8.28	Main effect of fish
Fish	5.64	21.36	13.50	5.22
Means of nutrient treatments	5.46	16.32		
	Main effect of nutrients	10.86	Interaction	4.87

scaled directly with mesocosm volume. The variability in population dynamics of enclosed plankton was problematic, and is commonly reported for enclosure experiments (Kuuppo-Leinikki et al. 1994, Petersen et al. 1998, Dippner et al. 2002). At the initiation of each experiment there were small populations of phytoplankton and zooplankton introduced with the unfiltered water from the Choptank River. These populations grew rapidly, reaching peaks of abundance that probably exceeded the carrying capacities of the enclosed systems. Populations then declined to low levels and eventually rebounded to a more or less steady state, but at a relatively modest level—assumed to be near the carrying capacity of the enclosed ecosystems. This sequence represents classic behavior of a population in which the feedback mechanisms are dampened, for example by a time lag (May 1973). In Expt BP09, copepods and polychaete trochophores exhibited boom-and-bust behavior similar to that reported in other mesocosm research (Kuuppo-Leinikki et al. 1994, Petersen et al. 1998), although at different times during the experiment (Fig. 6).

Natural zooplankton populations do not exhibit such extreme cycles of boom-and-bust, at least on the short time scales observed here. It is probable that zooplankton populations in mesocosms are not subject to some of the natural feedback mechanisms that constrain populations from exceeding carrying capacity (May 1973). These feedback mechanisms in natural ecosystems could be density-independent and include diffusion, advection and predation, or could be density-dependent and include migration from overcrowded areas or cannibalism (Chesson 1996). Whatever the natural mechanisms, they probably operate at greater spatial scales than in the MEERC mesocosms. Of course, the presumption of zooplankton steady state in a natural ecosystem is only true for limited time and space scales. In fact, time-series plots of copepod biomass over annual cycles in Chesapeake Bay might look qualitatively similar to our BP07 or BP09 copepod biomass trajectories, but on a different time scale. In the bay, the boom-and-bust cycle is usually associated with hydrographically controlled events such as the spring bloom of phytoplankton biomass (Harding & Perry 1997).

The lack of 'natural' dynamics of zooplankton populations during the initial period of mesocosm experiments adds to the difficulty of accurately evaluating trophic relationships. Individual mesocosms tend initially to have similar characteristics, but then diverge over time due to founder effects or random events (Smith et al. 1982, Steele & Gamble 1982, Kemp et al. 2001). Thus, we are faced with a dilemma. To stabilize zooplankton populations, it is necessary to wait approximately 40 d for the boom-and-bust cycle to progress through the major zooplankton taxa. Yet, by 40 d, when predator additions seemingly would be ideal, individual mesocosms may be following quite different ecological trajectories, compromising the value of replication. Short mesocosm experiments have limitations, but longer ones also may be compromised by high variability and diverging properties. Our longer experiment indicated a significant, positive relationship between anchovy growth and phytoplankton biomass; thus, given sufficient time to develop, a trophic relationship 'signal' may overcome divergent 'noise.' It is important to carefully consider experimental objectives when determining experiment length. We found that stronger trophic relationships only appeared in the longer 15 wk BP09 experiment, while effects of enclosure on predator growth were expressed more clearly in the shorter 6 wk BP07 experiment.

Mesocosm design and experimental protocols also can be improved. For instance, if the mesocosms were not each run as completely isolated systems, zooplankton populations might behave more naturally. A parcel of water in a natural ecosystem is subject to advection and diffusion which may serve to stabilize zooplankton populations in such ecosystems (Chesson 1996). Our mesocosms were subjected to daily losses from the system (10% daily water changes), but were isolated from zooplankton inputs (analogous to advection and diffusion) into the system because replacement water was filtered.

Mesocosms, like laboratory experiments in even smaller containers, have real limitations for conducting research on population or community ecology in estuarine and marine ecosystems. Enclosed fish and zooplankton populations may not behave in a 'natural' manner. There are usually fewer mesocosms available than is desirable for good experimental design. Nonetheless, interpretable results may be obtained, and mesocosms are the only practical tool to isolate important ecosystem components and to investigate mechanisms that control production and community structure. Applying dimensional analysis and scaling considerations, as recommended by Petersen & Hastings (2001), can improve the design of mesocosm experiments and promote better interpretation of scale-dependent behavior.

The present research clearly demonstrated scale-dependence of bay anchovy growth in mesocosms of varying dimensions. Top–down control and trophic cascades were evident or suggested, but were not scale-dependent. Results of these experiments, combined with a dimensional analysis, could be used to design and conduct more rigorous mesocosm experiments, and to develop scaling rules that apply to predation effects in natural estuarine ecosystems.

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