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Multiple Trophic Levels in Soft-Bottom Communities

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Abstract
In order to assess the general applicability of recent field experiments with predatory infauna, we searched the literature and found 48 well-documented cases of infaunal consumption by such predators. In 63 % of the cases detailed enough to make a determination, the predators ate other predators. Multiple trophic levels within the infauna are probably a common feature of many soft-bottom communities.

Keywords
predatory infauna, trophic levels, soft-bottom communities

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NOTE

Multiple trophic levels in soft-bottom communities

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ABSTRACT: In order to assess the general applicability of recent field experiments with predatory infauna, we searched the literature and found 48 well-documented cases of infaunal consumption by such predators. In 63 % of the cases detailed enough to make a determination, the predators ate other predators. Multiple trophic levels within the infauna are probably a common feature of many soft-bottom communities.

The roles which predatory infauna play in controlling soft-bottom community structure are poorly understood (see Commito & Ambrose [in press] for review). Recent field experiments have demonstrated that predatory infauna (organisms which live within the sediment and ingest benthic animals) are important regulating agents and that multiple trophic levels exist within the infauna (Reise 1979, Commito 1982a, Commito & Shrader in press, Ambrose 1984a,b,c). In order to assess the general applicability of these field experiment results, we searched the literature for evidence of infaunal consumption by predatory infauna. Only results from gut and fecal analyses, feeding trials, laboratory and field observations, and immunological assays were included. Examples of predation inferred from field manipulations were excluded because predatory infauna may have effects other than direct predation mortality. Such effects include induced emigration of prey, sublethal effects on prey, nutrient enrichment from fecal material, sediment modification via creation of biogenic structures, and sediment disturbances (Kneib & Stiven 1982, Commito & Ambrose in press, Commito & Shrader in press).

We found 48 well-documented cases of predation by infaunal polychaetes, nemerteans, amphipods, tanaids, and gastropods on other benthic organisms (Table 1). Polynoid polychaetes and naticid and melongenid gastropods were considered predatory infauna even though they spend considerable time on the sediment surface. Our findings suggest that predatory infauna are important in many marine communities. Based primarily on information provided in the works cited, we also included in the table an estimate of the sediment disturbance caused by each predator. Too little information was available to evaluate the other types of non-predation effects.

In 21 of the 48 cases it was impossible to determine whether or not the predators ate other predators; either prey categories were too general (e.g. 'polychaetes') or researchers did not offer predatory infauna as prey to their test animals in feeding trials. In 17 (63 %) of the remaining 27 cases, the predators consumed other predators. We feel that many predatory infaunal species eat other predators and that the existence of multiple trophic levels within the infauna may be a common phenomenon in soft-bottom communities. If so, then analyses of energy flow (Ankar 1977, Mann 1982, Fasham 1984) and community organization (Peterson 1979, Woodin 1983) must continue to be re-evaluated for marine ecosystems.

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Table 1 Direct evidence of infaunal consumption by predatory infauna. Results from gut and fecal analyses, immunological assay, feeding trial, laboratory observation, and field observation studies

Predator	Life position in sediment	Location of prey capture	Sediment disturbance	Macrofaunal prey	Method of prey determination	Source	Comments
POLYCHAETA							
Polynoidae							
Harmothoe sarsi	Surface, shallow	Surface, shallow	Slight	Amphipods (esp. *Pontoporeia affinis*), *Macoma balthica*, *Harmothoe sarsi*, oligochaetes	Gut analysis	Sarvala 1971	Diet changes with age; large worms feed slmost exclusively on *Pontoporeia affinis*
Hesionidae							
Nereimyra punctata	Shallow	Surface, shallow	Slight	Polychaetes (esp. *Prionospio* spp.), amphipods	Gut and fecal analyses, feeding trials	Oug 1980	Lives in gallery; responds to tactile and chemical cues from prey
Ophiodromus flexuosus	Surface, shallow	Surface, shallow	Moderate	Polychaetes (esp. *Prionospio* spp.), crustaceans, gastropods, bivalves	Gut and fecal analyses, feeding trials	Oug 1980	Responds to moving prey, creeps along surface
Podarke pugettensis	Surface, shallow	Surface, shallow	Moderate	Polychaetes (11 families), tanaids, isopods	Gut and fecal analyses, feeding trials	Shaffer 1979	Responds to moving prey; usually rejects large prey
Nereidae							
Nereis diversicolor	Surface, shallow, deep	Shallow, deep	Slight	*Arenicola marina*	Laboratory observation	Witte & de Wilde 1979	Invades prey burrows; bites off tails or kills prey
Nereis diversicolor	Shallow	Surface	Moderate	*Corophium volutator*	Laboratory observation	Olafsson & Persson unpubl.	Disturbs prey burrows; attacks prey only on sediment surface
Nereis succinea	Surface, shallow, deep	Surface, shallow	Moderate	Amphipods (esp. *Corophium lacustre*, *Leptocheirus plumulosus*), nereid polychaetes	Gut analysis	Haddon & Hines unpubl.	Feeds primarily on surface organisms >1 mm long
Nereis virens	Surface, shallow, deep	Surface, shallow	Moderate	Polychaetes, oligochaetes, bivalves, amphipods	Fecal analysis	Ambrose 1984b	Moves anterior part of body out of burrow across sediment surface to attack prey
Nephtyidae							
Nephtys caeca	Shallow, deep	Shallow, deep	Slight	*Rhepoxynius abronius*	Feeding trials	Ambrose 1984d	Causes prey to leave sediment and enter water column
Nephtys cirrosa	Shallow, deep	Shallow, deep	Slight	Polychaetes (*Nephtys* spp., possibly maldanids and spionids)	Gut analysis	Clark 1962	Many guts empty or containing sediment
Nephtys hombergi	Shallow, deep	Shallow, deep	Slight	Polychaetes (esp. spionids)	Gut analysis	Clark 1962	Many guts empty or containing sediment
Glyceridae							
Glycera alba	Shallow, deep	Surface, shallow	Slight	Many polychaete species (esp. errant forms), amphipods	Fecal analysis, feeding trials	Ockelmann & Vahl 1970	Responds to moving prey; lives in gallery; injects toxin
Glycera convoluta	Shallow, deep	Surface, shallow	Slight	*Nephtys caeca*	Feeding trials	Ambrose 1984d	Lives in gallery; causes prey to leave sediment and enter water column
Glycera dibranchiata	Shallow, deep	Surface, shallow	Slight	*Nereis virens*, *Macoma balthica*, *Corophium volutator*	Fecal analysis, feeding trials	Ambrose 1984b	Lives in gallery; injects toxin
Spionidae							
Pseudopolydora kempi	Shallow	Surface	Moderate	*Abarenicola pacifica*	Gut analysis, feeding trials	Wilson 1981	Feeds on juvenile worms
Pygospio elegans	Shallow	Surface	Moderate	*Abarenicola pacifica*	Gut analysis, feeding trials	Wilson 1981	Feeds on juvenile worms
Terebellidae							
Eupolymmia heterobranchia	Shallow, deep	Surface	Moderate	Polychaetes, amphipods	Fecal analysis, feeding trials, laboratory observation	Wilson 1980	Feeds on small forms

Table 1. (Continued)

Predator	Life position in sediment	Location of prey capture	Sediment disturbance	Macrofaunal prey	Method of prey determination	Source	Comments
NEMERTEA							
Anopla							
Cephalothrix bioculata	Shallow	Surface, shallow	Slight	Oligochaetes	Gut analysis, feeding trials	Jennings & Gibson 1969	Responds to chemical cues from prey; no stylets, but proboscis secretions help immobilize prey
Cephalothrix linearis	Shallow	Surface, shallow	Slight	Oligochaetes	Gut analysis, feeding trials	Jennings & Gibson 1969	Responds to chemical cues from prey; no stylets, but proboscis secretions help immobilize prey
Cerebratulus lacteus	Shallow, deep	Deep	Slight	Large *Ensis directus*	Field observation	McDermott 1976	Engulfs anterior end of clam; no stylets
Lineus ruber	Shallow	Surface, shallow	Slight	Annelids (esp. *Clitellio arenarius*), crustaceans	Gut analysis, feeding trials	Jennings 1960	Possesses eyes; responds to chemical cues from prey; no stylets
Lineus ruber	Shallow	Surface, shallow	Slight	Oligochaetes, polychaetes, crustaceans	Gut analysis, feeding trials	Jennings & Gibson 1969	Possesses eyes; responds to chemical cues from prey; no stylets
Lineus sanguineus	Shallow	Surface, shallow	Slight	Phyllodocid and syllid polychaetes, oligochaetes, nemerteans	Gut analysis, feeding trials	Jennings & Gibson 1969	Possesses eyes; responds to chemical cues from prey; prefers moving prey; no stylets
Enopla							
Amphiporus lactifloreus	Shallow	Surface, shallow	Slight	*Gammarus locusta*	Feeding trials	Jennings & Gibson 1969	Refused all other prey; stylets and proboscis secretions immobilize prey
Nipponmemertes pulcher	Shallow	Surface, shallow	Slight	Amphipods (esp. *Haploops* spp.)	Feeding trials	McDermott 1984	Stylets and proboscis secretions immobilize prey
Paranemertes peregrina	Shallow	Surface	Slight	Polychaetes (esp. nereids)	Fecal analysis, feeding trials	Roe 1970, 1976	Feeds at low tide; stylets and proboscis secretions immobilize prey
Tetrastemma melanocephalum	Shallow	Surface, shallow	Slight	Oligochaetes	Gut analysis	Jennings & Gibson 1969	Refused all prey in laboratory
ARTHROPODA							
Amphipoda							
Phoxocephalidae							
Foxiphalus obtusidans	Surface, shallow	Surface, shallow	Slight	Annelids, crustaceans	Gut analysis	Oliver et al. 1982	Prefers small forms
Foxiphalus obtusidans	Surface, shallow	Surface, shallow	Slight	Spionid polychaetes	Gut analysis	Oakden 1984	Prefers small forms
Grandifoxus grandis	Surface, shallow	Surface, shallow	Slight	Annelids, crustaceans, other invertebrates	Gut analysis, feeding trials	Oliver et al. 1982	Prefers small forms
Grandifoxus grandis	Surface, shallow	Surface, shallow	Slight	Polychaetes, oligochaetes, archiannelids, bivalves, nemerteans	Gut analysis	Oakden 1984	Prefers small forms
Heterophoxus videns	Surface, shallow	Surface, shallow	Slight	Annelids, crustaceans	Gut analysis, feeding trials	Oliver et al. 1982	Prefers small forms
Mandibulophoxus gilesi	Surface, shallow	Surface, shallow	Slight	Annelids, other invertebrates	Gut analysis	Oliver et al. 1982	Prefers small forms
Mandibulophoxus gilesi	Surface, shallow	Surface, shallow	Slight	Polychaetes, archiannelids	Gut analysis	Oakden 1984	Prefers small forms
Paraphoxus spinosus	Surface, shallow	Surface, shallow	Slight	*Rhynchospio arenicola*	Fecal analysis	Wilson 1984	Removes prey tails by subsurface browsing
Paraphoxus sp.	Surface, shallow	Surface, shallow	Slight	Annelids, crustaceans, other invertebrates	Gut analysis	Oliver et al. 1982	Prefers small forms

Table 1. (Continued)

Predator	Life position in sediment	Location of prey capture	Sediment disturbance	Macrofaunal prey	Method of prey determination	Source	Comments
Rhepoxynius abronius	Surface, shallow	Surface, shallow	Slight	Polychaetes, gastropods	Gut analysis	Oakden 1984	Prefers small forms
Rhepoxynius dabouis	Surface, shallow	Surface, shallow	Slight	Annelids, crustaceans, other invertebrates	Gut analysis	Oliver et al. 1982	Prefers small forms
Rhepoxynius epistomus	Surface, shallow	Surface, shallow	Slight	Annelids, other invertebrates	Gut analysis, feeding trials	Oliver et al. 1982	Prefers small forms
Rhepoxynius fatigans	Surface, shallow	Surface, shallow	Slight	Polychaetes, crustaceans	Gut analysis	Oakden 1984	Prefers small forms
Corophiidae							
Corophium salmonis	Surface, shallow	Surface, shallow	Moderate	Polychaetes, bivalves, crustaceans, nemerteans	Immunoassay of gut contents	Feller et al. 1979	Accuracy of immunoassay technique not yet fully established
Gammaridae							
Pontoporeia affinis	Surface, shallow	Surface, shallow	Moderate	*Mytilus edulis*	Feeding trials	Segestråle 1962	Ingests bivalve larvae, probably *Macoma balthica* in field
Tanaidacea							
Leptochelia dubia	Surface, shallow	Surface	Moderate	*Dendraster excentricus*	Feeding trials	Highsmith 1982	Females capture larvae and juvenile forms
MOLLUSCA							
Gastropoda							
Naticidae							
Lunatia heros	Shallow, deep	Shallow, deep	Slight	*Mya arenaria, Macoma balthica*	Field observation	Commito 1982b	Usually forages deep below sediment surface; drills bivalve shells
Polinices duplicatus	Shallow, deep	Shallow, deep	Severe	*Mya arenaria*	Field observation	Edwards & Huebner 1977	Usually forages near sediment surface; leaves distinct trails; drills bivalve shells
Melongenidae							
Busycon spp.	Surface, shallow, deep	Shallow, deep	Severe	*Mercenaria mercenaria, Chione cancellata*	Field obvervation	Peterson 1982	3 ssp. *(canaliculatum, carica, contrarium)* analyzed as a group; plow through sediment; break bivalve shell margins

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