

FOOD RESOURCES RELATED TO HABITAT IN THE SCALLOP *PLACOPECTEN MAGELLANICUS* (GMELIN, 1791): A QUALITATIVE STUDY

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ABSTRACT The gut contents of the scallop, *Placopecten magellanicus*, were analysed seasonally. Two populations were compared, one shallow water (approximate depth 20 m) and one deep water (approximate depth 180 m). A total of 27 species of algae, ranging from 10-350 μm , were identified as well as a number of miscellaneous items including pollen grains, ciliates, zooplankton tests and considerable detrital material and bacteria. Benthic and pelagic food species were equally represented in shallow water scallops but benthic species outnumbered pelagic ones in the deep water population. Seasonal variations of food items occurred and coincided with bloom periods for the individual algal species. Gut contents generally reflected available organisms in the immediate habitat. It was concluded that *P. magellanicus* is an opportunistic filter feeder which takes advantage of both pelagic and benthic organisms as food.

INTRODUCTION

The sea scallop, *Placopecten magellanicus*, lives at the sediment-water interface in the Gulf of Maine at depths ranging from 2-180+ m and provides a valuable annual fishery along the Maine coast and on Georges Bank. In recent years, a substantial fishery has existed in the deeper waters of the Gulf of Maine. This fishery is supported by the survival at depth of a particularly strong year class in 1975 and of a few weaker year classes since then. These deep water scallops have been shown to differ from scallops found in shallower water in many of their allometric growth relationships (Schick *et al.* 1987a,b). Of particular interest to the fishery is the smaller meat size for equivalent shell diameter in the offshore scallops and their apparent inability to form completely ripened gonads (Barber *et al.* 1986).

The scallop is a semi-mobile filter feeder and utilizes available particulate matter for food. Several authors (Bayne and Widdow 1978; Newell and Bayne 1980; Newell *et al.* 1982; Berg and Newell 1986) have shown that the quality and quantity of food influence growth rate and fecundity in bivalve molluscs. Most recently, MacDonald and Thompson (1985 a,b 1986) demonstrated depth related differences in somatic growth and reproductive output in *Placopecten magellanicus* and attributed these differences to a combination of temperature and food availability. Undoubtedly, the quantity and quality of the food utilized by the scallops is responsible, to a large extent, for many of the observed differences in the growth rate, gonad development and indeed the survival of our study populations.

While there has been a multitude of laboratory studies on the feeding rates of bivalve molluscs (see Morton 1983; Bayne and Newell 1983 for reviews), little information is available on the specific food items utilized by these species in their natural habitats. It is generally assumed that these filter-feeding species rely on phytoplankton from the

water column as their main source of energy. Primary production at depths >30m is negligible and the deep-water animals must rely on sedimenting food sources or benthic material for their survival. Previous authors (Davis and Marshall 1961; Hall (pers. comm.) and Mikulich and Tsikhon-Lukaniana 1981) have indicated that benthic organisms plan an important role in the feeding ecology of other scallop species.

There has been considerable recent interest in the near bottom nepheloid layer and its associated "fluff" layer of unconsolidated sediment on the bottom and on the importance of sedimenting phytoplankton as a food source for benthic organisms (Christensen and Kannevorff 1985; Davies and Payne 1984; Graf *et al.* 1982, 1984). The ability of scallops to stir up the sediment surface places them in the unique position of being able to utilize both the suspended material in the near-bottom water and the recently deposited material to be found in the fluff layer.

In the current study we compare the potential food organisms of scallops from a "shallow water" population with those from a "deep-water" population on the basis of gut content analysis, in an effort to 1) characterize the nature of the food items consumed, 2) assess seasonal variation of food items and 3) provide preliminary information regarding the value of the sediment surface "fluff" layer and nepheloid layer to the nutrition of bottom dwelling invertebrates.

MATERIALS AND METHODS

Specimens of the sea scallop, *Placopecten magellanicus*, were collected throughout the year from two locations in the Gulf of Maine: Damariscotta River (43° 51.26', 69° 34.0'; depth approximately 20m) and 20 miles south of Boothbay (43° 26.5', 69° 33.3'; depth approximately 180m). Samples from the Damariscotta River were collected by divers and the offshore samples were collected by

trawlers. In all cases, animals were immediately returned to the laboratory and digestive gland/stomach complex removed. After careful removal of the dorsal shell valve, the animal was washed to be sure that no debris remained to be confused with food items/gut contents. In one group of scallops, the gut contents were removed with a hypodermic syringe for comparison with other samples. Gut contents recorded from these samples were identical to those collected by removing the digestive glands and the possibility of contamination was eliminated. Guts were not homogenized. Samples were drawn from the gut by pipette. Samples of 0.1–0.2 ml were drawn from each gut. In initial sampling trials, increasing the sample size to 1 ml did not yield additional species representation. In addition to the scallop samples, samples of the overlying water were collected from the Damariscotta River site and analysed for species content. Gut contents were identified using standard light and phase contrast microscopic techniques at the Provosolli-Guillard Center for the Culture of Marine Phytoplankton, Bigelow Laboratory for Ocean Sciences. A total of 78 fresh guts were analyzed from scallops ranging in size from 90–140 mm shell height.

TABLE 1.
Gut contents of inshore scallops.

Species	Habitat	Size (μm)
<i>Nitzschia</i> spp.	B	25–150
<i>Navicula</i> spp.	B	8–240
<i>Pleurosigma</i> sp.	B	200
<i>Thalassiothrix</i> sp.	B	50 (chain)
<i>Amphora</i> sp.	B	10–30
<i>Licmophora</i> spp.	B	25–180
<i>Acanthos</i> sp.	B	40–90
<i>Pinnularia</i> sp.	B	40–80
<i>Surirella</i> sp.	B	15–25
<i>Cylindrotheca closterium</i>	B	80–100
<i>Protogonyaulax</i> resting cyst	B	35–40
unidentified cyst	B	25–35
<i>Melosira</i> sp.	B	30–55 (chain)
<i>Striatella</i> sp.	B	40–50
<i>Coscinodiscus</i> spp.	B/P	40–180
<i>Ditylum brightwellii</i>	P	50–150
<i>Protoperdinium</i> sp.	P	60–70
<i>Eucampia zoodiacus</i>	P	40–75 (chain)
<i>Peridinium</i> sp.	P	20–30
<i>Prorocentrum micans</i>	P	45–55
<i>Skeletonema costatum</i>	P	30–50 (chain)
<i>Dinophysis acuminata</i>	P	50–60
<i>Dinophysis</i> spp.	P	32–60
<i>Thalassiosira rotula</i>	P	20 (chain)
<i>Thalassiosira nordenskioldii</i>	P	20 (chain)
<i>Thalassiosira</i> spp.	P	10–200 (chain)
Miscellaneous:		
Silicoflagellate strew; pollen grains (30–40 μm); green filamentous alga (1000 > μm); ciliates; zooplankton tests; bacteria; detritus; unidentified, unpigmented still active forms: (3 μm), multiflagellate (10 μm), ciliated mass (40–200 μm)		

RESULTS

The predominant food items identified from the guts of scallops from shallow water populations and deep water populations are summarized in Tables 1 and 2, respectively. A total of 27 species of algae ranging in size from approximately 10–350 μm were identified from the digestive glands along with several miscellaneous items including pollen grains, ciliates, zooplankton tests, considerable detrital material, and bacteria. Benthic and pelagic food species were equally represented in the shallow water scallops while, as might be expected, benthic species outnumbered pelagic species in the guts of deep water scallops in number of species but not necessarily in biomass. Resting cysts of the toxic dinoflagellate, *Protogonyaulax tamarensis*, were more prominent in the offshore population than in the shallow water animals. The theca of several *Dinophysis* spp. were a constant feature of both populations, though not seen consistently or in great numbers in water samples. While we did not do a taxonomic study, different morphological variations, attributed in the literature to different taxa, were observed.

Seasonal variations in occurrence of the food items from both populations are summarized in Tables 3 and 4. In the offshore scallops the pelagic species *Coscinodiscus* spp., *Prorocentrum micans*, *Dinophysis* spp., *Eucampia zoodiacus* and *Ditylum brightwellii* were prominent in the early fall (Oct/Nov), i.e. during the bloom period, and coincided

TABLE 2.
Gut contents of offshore scallops.

Species	Habitat	Size (μm)
<i>Melosira</i> sp.	B	50 (chain)
<i>Protogonyaulax</i> resting cyst	B	35–40
<i>Navicula</i> spp.	B	60–350
<i>Nitzschia</i> spp.	B	110
<i>Thalassiothrix</i> sp.	B	50 (chain)
<i>Acanthos</i> sp.	B	40–90
<i>Amphora</i> sp.	B	10–30
<i>Pleurosigma</i> sp.	B	280
<i>Licmophora</i> sp.	B	120–180
<i>Pinnularia</i> sp.	B	70–100
<i>Surirella</i> sp.	B	15–25
unidentified dinoflagellate		
cyst	B	25–35
<i>Coscinodiscus</i> spp.	P/B	50–160
<i>Prorocentrum micans</i>	P	45–55
<i>Dinophysis</i> spp.	P	32–60
<i>Thalassiosira</i> sp.	P	35–50
<i>Eucampia zoodiacus</i>	P	100 (chain)
<i>Ditylum brightwellii</i>	P	150
<i>Ditylum brightwellii</i>		
resting spore	P	40
Miscellaneous:		
Pollen grains (40–60 μm); zooplankton tests (100–250 μm); bacteria; detritus; unidentified, unpigmented, still active forms; uniflagellate (3 μm), multiflagellate (10 μm), ciliated mass (70–300 μm)		

with the period of greatest mixing of the water column. The most prominent pelagic food items of the inshore scallops were *Prorocentrum* (Oct/Nov; Jan), *Thalassiosira* sp. (March; Jan), and *Dinophysis* (Oct) again, coinciding with bloom periods and the subsequent settlement of the algae cells.

DISCUSSION

The quality and quantity of food available is a major limiting resource for suspension feeding organisms in general and for *Placopecten magellanicus* in particular (MacDonald and Thompson 1985a,b; 1986a,b). As pointed out by Levinton (1972), not only is the food supply constantly fluctuating, it is unpredictable and these suspension feeding organisms must maintain an adaptive feeding strategy which maximizes the generality of their food requirement. Although the majority of lamellibranch bivalves have been divided into two groups, the suspension feeders and the deposit feeders, there is no clear-cut distinction between these

two food sources (Morton, 1983). In a recent survey, Tsikhon-Lukanina (1982) showed that most bivalved molluscs are detritus feeders and that their main sources of food are detritus, unicellular algae and protozoa.

The surface deposits (fluff layer) can be stirred into suspension and thus made available to suspension feeding animals as seston (organic and inorganic suspended matter greater than 1 μm). The quantity of this particulate matter and its quality as a food resource varies both temporally and spatially in response to physical and biological factors (Brut, 1955; Berg and Newell, 1986). The results reported here clearly indicate that the scallop, *P. magellanicus* is an opportunistic filter feeder which takes advantage of these resuspended particles. The gut contents generally reflect the available organisms in the immediate habitat (Tables 1-4). One notable exception is *Chaetoceros* spp., usually available in the water column but not observed in gut content. This may be due to lack of resolution after spines have been altered or removed. It may also be an indication of

TABLE 3.

Seasonal variation in relative abundance of food items from inshore scallops.

Species	Oct/Nov 1985	Jan 1986	March 1986	July 1986	Oct/Nov 1986	Dec/Jan 1987
<i>Amphora</i> sp.	-	-	-	-	-	+
<i>Cylindrotheca closterium</i>	-	-	-	-	-	++
<i>Protogonyaulax tamarensis</i>						
resting cyst	+	+	-	+	+	-
unidentified cyst	+	-	-	+	+	-
<i>Nitzschia</i> spp.	+	+	++	+	+	++
<i>Navicula</i> spp.	++	++	+	++	++	++
<i>Pleurosigma</i> sp.	+	+	-	+	+	+
<i>Thalassiothrix</i> sp.	-	+	+	-	-	+
<i>Licmophora</i> spp.	+	+	++	+	+	+
<i>Acnantes</i> sp.	+	+	+	+	+	+
<i>Pinnularia</i> sp.	-	-	+	-	-	-
<i>Surirella</i> sp.	++	-	-	-	++	++
<i>Striatella</i> sp.	-	-	-	-	-	+
<i>Ditylum brightwellii</i>	+	-	-	-	+	+
<i>Protoperdinium</i> sp.	++	-	-	-	++	-
<i>Eucampia zoodiacus</i>	++	-	-	-	++	+
<i>Peridinium</i> sp.	+	-	-	-	+	+
<i>Prorocentrum micans</i>	+++	+++	-	++	+++	+
<i>Melosira</i> sp.	+	+	+	+	+	+
<i>Coscinodiscus</i> sp.	+	++	++	+	+	+
<i>Skeletonema costatum</i>	+	-	-	-	+	-
<i>Dinophysis acuminata</i>	-	-	-	-	-	+
<i>Dinophysis</i> spp.	+	+	++	++	+++	+
<i>Thalassiosira</i> spp.	+	++	+++	-	+	+++
<i>Thalassiosira rotula</i>	-	-	-	-	-	+
<i>Thalassiosira nordenskioldii</i>	-	-	-	-	-	+
Miscellaneous:						
Silicoflagellates (+), green filamentous alga, bacteria (+++), pollen grains (+), zooplankton tests and spines (+++), diatom strew (+++), detritus (+++)						

+++ common, very abundant

++ common, abundant

+ common, not abundant

TABLE 4.
Seasonal variation in relative abundance of food items of scallops
from 20 miles south of Boothbay.

Species	Sept 1985	Jan 1986	Nov 1986	Dec/Jan 1987
<i>Protogonyaulax tamarensis</i>				
resting cyst	++	++	++	+
<i>Navicula</i> spp.	++	++	++	++
<i>Nitzschia</i> spp.	+	+	+	++
<i>Thalassiothrix</i> sp.	-	+	-	-
<i>Amphora</i> sp.	-	-	-	+
<i>Acanthes</i> sp.	+	+	+	++
<i>Pleurosigma</i> sp.	+	+	+	
<i>Pinnularia</i> sp.	+	-	+	+
unidentified dinoflagellate				
cyst	+	-	+	-
<i>Surirella</i> sp.	-	-	-	+
<i>Coscinodiscus</i> spp.	++	++	+	+
<i>Licmophora</i> sp.	-	-	-	+
<i>Prorocentrum micans</i>	++	+	++	++
<i>Dinophysis</i> spp.	++	-	+	+
<i>Melosira</i> sp.	+	+	+	++
<i>Thalassiosira</i> sp.	-	++	-	++
<i>Eucampia zoodiacus</i>	++	-	++	+
<i>Ditylum brightwellii</i>	++	-	++	+
<i>Ditylum brightwellii</i>				
resting spore	+	-	+	-
Miscellaneous:				
Pollen grains (+), zooplankton tests (+), bacteria (++)				
detritus (++)				
motile forms: 10 μ m colorless multiflagellate, 3 μ m colorless arrowhead, uniflagellate 70–300 μ m ciliated mass				

+++ common, very abundant

++ common, abundant

+ common, not abundant

selective feeding. In a previous laboratory study (Shumway et al. 1985), it was shown that *P. magellanicus* exhibited both pre-ingestive selection on the labial palps and differential absorption in the gut.

The gut contents varied both with depth and with season and these differences were primarily reflected in the consumption of species abundant during bloom conditions. In addition, a greater number of predominantly benthic species were identified from deep water scallops than from shallow water animals. These findings mirror those of other workers (see Table 5) and are not intended to be a comprehensive or all inclusive listing of possible food items for this species. Some algal species, especially small forms (<10 μ m) may be quickly digested and not seen or resolved in stomach contents. Conversely, many of the observed species may be difficult to digest and of little consequence to the diet. In analyses performed over several days, from the same guts, large pennates (>150 μ m) remained intact and pigmented, while most other forms had degraded. During bloom concentrations of *P. micans*, many of these cells remained intact in untreated guts 5 days after the initial sampling. Further, much of the food is undoubtedly

comprised of the naked and minute nanoplankton which is probably too delicate to remain intact after ingestion.

In addition to the differences noted between the shallow and deep water habitats, several other points emerged that raise a number of questions. It was noted in the present study that the food organisms ranged from 10–350 μ m. Mikulich and Tsikhon-Lukanina (1981) also found a wide range of food particles (9–950 μ m). The majority of feeding studies on bivalve molluscs involve feeding pure cultures of rather small algae (4–20 μ m) to various species of molluscs. Several authors have demonstrated that scallops exhibit reduced efficiency of particle retention when fed particles less than 7 μ m (*Chlamys opercularis*, Vahl 1972; *Pecten opercularis* and *P. septemradiatus*, Møhlenberg and Riisgard 1978). Palmer and Williams (1980) demonstrated that *Argopecten irradians* was capable of adjusting the filtration efficiency in response to varying concentrations of particulate matter. The presence of zooplankton tests raises the question of whether or not these organisms are utilized as a food source. Crustacean larvae, tests and whole copepods have been identified from the guts of scallops and other bivalve molluscs; however, their role as a food resource is not clear. Wojtowicz (1972) studied a number of digestive enzymes in the digestive gland of *P. magellanicus* but found no chitinase. It seems most likely that these crustacean materials are taken incidentally with other organisms and are probably not a major food source. Future feeding studies on scallops should include species of algae in the larger size ranges and should investigate the possible role of zooplankton as a food source.

The presence of *Dinophysis* in such large quantities is of particular interest. Only unpigmented, digested thecae were observed in the guts. *Dinophysis* spp. have been implicated in outbreaks of diarrhetic shellfish poisoning (DSP) worldwide (Campos et al. 1982; Kat 1979; 1985; Guzman and Campodonico 1975; Freudenthal 1985; Dahl-Lyndastad 1985; Krough et al. 1985) although no known cases have been reported from the Gulf of Maine. Species known to accumulate the *Dinophysis* cells include mussels (*M. edulis* and *M. coruscum*), scallops (*Patinopecten yessoensis* and *Chlamys nipponensis akazara*) and clams (*Tapes (Venerupis) japonica* and *Gomphina melanaegis*). Preliminary investigations (Yasumoto et al. 1985) have indicated that the DSP toxin is concentrated in the digestive gland and that intoxication could be avoided, as in the case of PSP, by eliminating the digestive glands. This method is feasible with the scallops since usually only the adductor muscle is marketed. A market does exist, however, for whole scallop meats and current legislation is pending with regard to restricting the taking of whole scallops meats for human consumption due to PSP infestation. Further, it has been demonstrated that mussels and scallops may become toxic beyond the regulation level in the presence of *Dinophysis* spp. at cell densities of 200/L or less, Yasumoto et al.

TABLE 5.
A summary of the feeding habits of various species of scallops.

Species	Feeding Habits	Author
<i>Aequipecten irradians</i>	Microflora, detritus, bacteria and organic matter common in water immediately adjacent to the bottom; identified 26 species of diatoms (17 benthic/tychopelagic; 9 planktonic); proposed that some selective feeding might be in effect	Davis and Marshall (1961)
<i>Chlamys opercularis</i>	Dinoflagellates, diatoms, crustacean larvae, sand grains, detritus	Aravindakshan (1955)
<i>Chlamys operacularis</i>	Sedimenting phytoplankton; demonstrated that sedimentation of phytoplankton major factor regulating growth	Christensen and Kanneworff (1985)
<i>Chlamys tehuelchus</i>	Identified over 100 food items; dominant algal species benthic; planktonic species comprising the spring bloom; 90% of ingested particles less than 100 μm ; not all benthic algae of appropriate size range used: those attached to sand grains by gelatinous stalks very abundant but not found in guts presumably not easily resuspended	deHall (personal communication)
<i>Patinopecten yessoensis</i>	161 forms identified including algae and animals, spores, eggs, detritus and mineral particles (size range 9–950 μm); detritus main food source; animal and plant material most important during reproductive period;	Mikulich and Tsikhon-Lukanina (1981)
<i>Pecten septemradiatus</i>	Resuspended detritus	Blegvad (1915)
<i>P. opercularis</i>		
<i>P. varius</i>		
<i>Pecten varius</i>	“Unfailing occurrence of bottom, naviculoid diatoms and the frequency of sand-grains, spicules, and bottom living Foraminifera”; diatoms most important food organism; planktonic species important during their respective seasons of abundance	Hunt (1925)
<i>Placopecten grandis</i> (= <i>magellanicus</i>)	Detritus, ‘everything small that is to be found in the plankton’, their own and other veliger larvae, copepods, <i>Balanus nauplii</i> ; pine-tree pollen grains, <i>Pleurosigma</i> and <i>Navicula</i> not digested	Stevenson (1932, 1936)
<i>Placopecten grandis</i> (= <i>magellanicus</i>)	Identified 38 forms including algae, animals and eggs; diatoms comprised bulk of food, tintinnids and silicoflagellates	Borden (1928)
<i>Placopecten magellanicus</i>	Algae, pollen grains, silicoflagellate strew, ciliates, zooplankton tests, bacteria, detritus, 211 species of algae identified (10–350 μm); some seasonal variation attributed to algal blooms; both benthic and pelagic species prominent	Present study

(1983). The concentrations found in the present investigation could lead to cases of DSP if whole animals were ingested. Further studies are needed on the occurrence of these dinoflagellates and their role in the food habits of not only the scallops, but also of other commercially important species of shellfish.

Although the scallops are capable of some mobility, they remain essentially fixed in position and feed on particles in the sea water that passes by them. These currents of water may be environmentally induced or they may be created by the animals themselves. These factors take on special significance for scallops in that current orientation could be of real significance for maximizing the available food resources. Diver observations of scallops at various stages of the tide seem to indicate that scallops feed discontinuously and orientate with respect to current direction. Flume studies are currently underway to determine the significance of this orientation and/or feeding behavior.

Some scallop species are also known to exhibit “clapping activity” which resuspends some of the surface sediment (fluff layer) thus making the material available to the filter feeders. Davis and Marshall (1961) showed that the

bay scallop, *Aequipecten irradians*, obtained a considerable amount of its food through shell flapping i.e., resuspending the surface sediment materials. Divers have noted however, that this clapping activity is rarely seen in *P. magellanicus* in shallow water (Schick, unpublished). This shell clapping activity could be of considerable significance, however, to the deeper water animals where pelagic algal species are not always readily available as a food source.

Algal cells settling during spring and fall blooms are one of the main inputs of particulate organic matter from the pelagic to the benthic system. Downward mixing of plankton during certain times of the year undoubtedly plays a large part in making food organisms available to the deeper water scallops. The blooms (spring, summer) play an important role for shallow-water populations of *P. magellanicus* as has already been demonstrated by several authors with regard to the gametogenic cycle (Ehinger 1978; Thompson 1979; Robinson et al. 1981). The deep water scallops live well below the photic zone and it might well be assumed that they do not utilize living algae from planktonic blooms as a food resource. Our results (Tables 2 and

4) indicate, however, that a relatively large number of intact planktonic algal species reach the scallops, probably due to vertical mixing of the water column during the fall (October/November). These sudden bursts of energy/food input as a result of the phytoplankton blooms (rain or mixing) may provide just enough energy to sustain the population. Studies are currently underway to assess the extent of gonad production in the two populations. Preliminary indications are that the deep water scallops do not produce viable gonads (Barber *et al.* 1987).

Davies and Payne (1984) suggested that the substantial increase in fresh organic carbon and nitrogen associated with the spring phytoplankton bloom might have a stimulatory effect on the growth and reproduction of the benthic animals and might act as a triggering mechanism for their life cycle. It is possible in the offshore population of *P. magellanicus* studied here, that the influx of pelagic species after the fall bloom is the factor responsible for the survival of the population. This is the period of the year when the inshore animals have just spawned and their metabolic rate is at its lowest peak (Shumway *et al.*, in prep.). The exact extent of the energy input, however, is as yet not clear and still needs to be quantified.

Our results indicate that the scallops are ingesting both pelagic and benthic organisms. The relative importance of

these food organisms is not known, although it can be assumed that planktonic species such as *Thalassiosira*, *Dinophysis* and *Prorocentrum* must provide a significant portion of the energy intake of the scallops.

In 1972, Levinton stated that the role of resuspended sediment from the fluff layer in the nutrition of suspension feeding animals still needed investigation and the statement is as true now as it was then. A better understanding of the feeding habits of "interfacing" species such as *P. magellanicus* may provide a unique opportunity to determine not only their role in the transformation of energy between the benthic and pelagic ecosystems, but also to study the relationship between the fluff layer, the nepheloid layer and the benthic invertebrates.

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REFERENCES CITED

- Aravindakshan, I. 1955. *Studies on the biology of the queen scallop, Chlamys opercularis* (L.O. Ph.D Thesis, University of Liverpool, 79 p.
- Barber, B., Getchell, R., S. E. Shumway, & Schick, D. F. 1987. The effect of depth on the gametogenic cycle of the scallop, *Placopecten magellanicus*. Submitted.
- Bayne, B. L. & J. Widdows. 1978. The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia (Berl.)* 37:137-162.
- Berg, J. A. & R. I. E. Newell. 1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuar. Coast. and Shelf Science* 23:375-386.
- Blegvad, H. 1915. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. *Rept. Danis Biol. Sta. Vol.* 22:43-78.
- Burt, W. V. 1955. Distribution of suspended materials in Chesapeake Bay. *J. Mar. Res.* 14:47-62.
- Campos, M. J., Fraga, S., Marino, J. & F. J. Sanchez. 1982. *International Council for the Exploration of the Sea Report 1977-1981*, 8p.
- Christensen, H. & E. Kannevorf. 1985. Sedimenting phytoplankton as a major food source for suspension and deposit feeders in the Oresund. *Ophelia* 24:223-244.
- Dahl, E. & M. Yndestad. 1985. Diarrhetic shellfish poisoning (DSP) in Norway in the autumn 1984 related to the occurrence of *Dinophysis* spp. In: D. M. Anderson, A. W. White, & D. G. Baden, eds. *Toxic Dinoflagellates*. Elsevier. 495-500 p.
- Davies, J. M. & R. Payne. 1984. Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. *Mar. Biol.* 78:315-324.
- DAvis, R. L. & N. Marshall. 1961. The feeding of the bay scallop, *Aequipecten irradians*. *Proc. Natl. Shellfish. Assoc.* 52:25-29.
- Ehinger, R. E. 1978. *Seasonal energy balance of the sea scallop, Placopecten magellanicus, from Narragansett Bay*. M. S. Thesis, University of Rhode Island. p.
- Freudenthal, A. R. & J. Jijina. 1985. Shellfish poisoning epidodes involving or coincidental with dinoflagellates. In: D. M. Anderson, A. W. White, & D. G. Baden, eds. *Toxic Dinoflagellates*. Elsevier 461-466 p.
- Graf, G., W. Begntesson, A. Faubel, L. -A. Meyer-Reil, R. Schulz, H. Theede & H. Thiel. 1984. The importance of the spring phytoplankton bloom for the benthic system of Kiel Bight. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.*, 183:136-143.
- Graf, G., W. Bengtsson, U. Diesner, R. Schulz & H. Theede. 1982. Benthic response to sedimentation of a spring phytoplankton bloom: Process and budget. *Mar. Biol.* 67:201-208.
- Guzman, L. and Campodonico, I. 1975. *Publ. Inst. Patagonia Ser. Mon. No.* 9, 6 p.
- deHall, M. V. 1977. *Alimentacion de la vieyra tehuelche (Chlamys tehuelchus)*. Comision Nacional de Estudios Geo-Heliofisicos Centro Nacional Patagonico. Puerto Madryn-Chubut, Argentina.
- Hunt, O. D. 1925. The food of the bottom fauna of the Plymouth fishing grounds. *J. Mar. Biol. Assoc. U.K.* 13:560-599.
- Katz, M. 1979. The occurrence of *Prorocentrum* species and the coincidental gastrointestinal illness of mussel consumers. In: *Toxic Dinoflagellate Blooms*, eds. Taylor, D. L., & H. H. Seliger, Elsevier, North Holland: New York, 215-220 p.
- Katz, M. 1985. *Dinophysis acuminata* blooms, the distinct cause of Dutch mussel poisoning. In: *Toxic Dinoflagellates*, D. M. Anderson, A. W. White & D. G. Baden, eds. Elsevier, North Holland: New York, 73-78 p.
- Krogh, P., L. Edler, Graneli, & U. Nyman. 1985. Outbreak of diarrhetic shellfish poisoning on the west coast of Sweden. In: *Toxic Dinoflagellates*, D. M. Anderson, A. W. White & D. G. Baden, eds. Elsevier, North Holland: new York, 501-503 p.
- Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Am. Nat.* 106:472-486.
- MacDonald, B. A. & R. J. Thompson. 1985a. Influence of temperature

- and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. I. Growth rates of shell and somatic tissue. *Mar. Ecol. Prog. Ser.* 25, 279–294.
- MacDonald, B. A. & R. J. Thompson. 1985b. Influence of temperature and food availability on the ecological energetics of the giant scallop, *Placopecten magellanicus*. II. Reproductive output and total production. *Mar. Ecol. Prog. Ser.* 25, 295–303.
- MacDonald, B. A. & R. J. Thompson. 1986a. Influence of temperature and food availability on the ecological energetics of the giant scallop, *Placopecten magellanicus*. III. Physiological ecology the gametogenic cycle and scope for growth. *Mar. Biol.* 93:37–48.
- MacDonald, B. A. & R. J. Thompson. 1986b. Production, dynamics and energy partitioning in two populations of the giant scallop, *Placopecten magellanicus*. (Gmelin). *J. Exp. Mar. Biol. Ecol.* 101:285–299.
- Mikulich & A. Tsikhon-Lukanina. 1981. Food of the scallop. *Oceanology* 21:633–635.
- Møhlenberg, F. & H. U. Riisgard. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. *Ophelia* 17:239–246.
- Morton, B. A. 1983. Feeding and digestion in bivalvia. In: *The Mollusca*, A. S. M. Saleuddin, & K. M. Wilbur, eds. Academic Press 65–147 p.
- Newell, R. I. E. & B. L. Bayne. 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle, *Cardium (Cerastoderma) edule* (Bivalvia: Cardiidae). *Mar. Biol.* 56:11–19.
- Newell, R. I. E., T. J. Hilbish, R. K. Koehn & C. J. Newell. 1982. Temporal variation in the reproductive cycle of *Mytilus edulis* L. (Bivalvia, Mytilidae) from localities on the east coast of the United States. *Biol. Bull.* 162:299–310.
- Palmer, R. E. & L. G. Williams. 1980. Effect of particle concentration on filtration efficiency of the bay scallop, *Argopecten irradians*, and the oyster, *Crassostrea virginica*. *Ophelia* 19:163–174.
- Robinson, W. E., W. E. Wehling, M. P. Morse & G. C. McLeod. 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. *Fish. Bull.* 79:449–458.
- Schick, D. F., S. E. Shumway, & M. Hunter. 1987a. A comparison of growth rate between shallow water and deep water populations of scallops, *Placopecten magellanicus* (Gmelin, 1791) in the Gulf of Maine. In Press. Amer. Malac. Bull.
- Schick, D. F., S. E. Shumway, & M. Hunter. 1987b. Allometric relationship and growth in *Placopecten magellanicus*: The effects of season and depth. In press. *Malacological Review*.
- Shumway, S. E., T. L. Cucci, R. C. Newell & C. M. Yentsch 1985. Particle selection, ingestion and absorption in filter-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 91:77–92.
- Shumway, S. E., D. Campbell and J. Stahlnecker 1987. Seasonal changes in oxygen consumption of the giant scallop, *Placopecten magellanicus* (Gmelin) with a preliminary model of growth, respiration and spawning in coastal Maine waters. Submitted.
- Thompson, R. J. 1977. Blood chemistry, biochemical composition, and the annual reproduction cycle in the giant scallop, *Placopecten magellanicus* from southeast Newfoundland. *J. Fish. Res. Bd. Canada* 34:2104–2116.
- Tsikhon-Lukanina, Ye. A. 1982. Food spectra of bottom molluscs. *Oceanology* 22:751–754.
- Vahl, O. 1972. Particle retention and relation between water transport oxygen uptake in *Chlamys opercularis* (L.) (Bivalvia). *Ophelia* 10:67–74.
- Vahl, O. 1973. Efficiency of particle retention in *Chlamys islandica* (O. F. Muller). *Astarte* 6:21–25.
- Wojowicz, M. B. 1972. Carbohydrases of the digestive gland and the crystalline style of the Atlantic deep-sea scallop (*Placopecten magellanicus*, Gmelin). *Comp. Biochem. Physiol.* 43A:131–142.
- Yasumoto, T., Murata, M., Oshima, Y., Matsumoto, G. K. & J. Clardy. 1984. Diarrhetic shellfish poisoning. In: *Seafood Toxins*, Ragelis, ed. American Chemical Society Symposium Series 262. 207–214 p.
- Yasumoto, T., Yasukatsu, O. and M. Yamaguchi. 1978. Occurrence of a new type of shellfish poisoning in the Tohoku District. *Bull. Jap. Soc. Scient. Fish.* 44:1249–1255.

FOOD RESOURCES RELATED TO HABITAT IN THE SCALLOP *PLACOPECTEN MAGELLANICUS* (GMELIN, 1791): A QUALITATIVE STUDY

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ABSTRACT The gut contents of the scallop, *Placopecten magellanicus*, were analysed seasonally. Two populations were compared, one shallow water (approximate depth 20 m) and one deep water (approximate depth 180 m). A total of 27 species of algae, ranging from 10-350 μm , were identified as well as a number of miscellaneous items including pollen grains, ciliates, zooplankton tests and considerable detrital material and bacteria. Benthic and pelagic food species were equally represented in shallow water scallops but benthic species outnumbered pelagic ones in the deep water population. Seasonal variations of food items occurred and coincided with bloom periods for the individual algal species. Gut contents generally reflected available organisms in the immediate habitat. It was concluded that *P. magellanicus* is an opportunistic filter feeder which takes advantage of both pelagic and benthic organisms as food.

INTRODUCTION

The sea scallop, *Placopecten magellanicus*, lives at the sediment-water interface in the Gulf of Maine at depths ranging from 2-180+ m and provides a valuable annual fishery along the Maine coast and on Georges Bank. In recent years, a substantial fishery has existed in the deeper waters of the Gulf of Maine. This fishery is supported by the survival at depth of a particularly strong year class in 1975 and of a few weaker year classes since then. These deep water scallops have been shown to differ from scallops found in shallower water in many of their allometric growth relationships (Schick *et al.* 1987a,b). Of particular interest to the fishery is the smaller meat size for equivalent shell diameter in the offshore scallops and their apparent inability to form completely ripened gonads (Barber *et al.* 1986).

The scallop is a semi-mobile filter feeder and utilizes available particulate matter for food. Several authors (Bayne and Widdow 1978; Newell and Bayne 1980; Newell *et al.* 1982; Berg and Newell 1986) have shown that the quality and quantity of food influence growth rate and fecundity in bivalve molluscs. Most recently, MacDonald and Thompson (1985 a,b 1986) demonstrated depth related differences in somatic growth and reproductive output in *Placopecten magellanicus* and attributed these differences to a combination of temperature and food availability. Undoubtedly, the quantity and quality of the food utilized by the scallops is responsible, to a large extent, for many of the observed differences in the growth rate, gonad development and indeed the survival of our study populations.

While there has been a multitude of laboratory studies on the feeding rates of bivalve molluscs (see Morton 1983; Bayne and Newell 1983 for reviews), little information is available on the specific food items utilized by these species in their natural habitats. It is generally assumed that these filter-feeding species rely on phytoplankton from the

water column as their main source of energy. Primary production at depths >30m is negligible and the deep-water animals must rely on sedimenting food sources or benthic material for their survival. Previous authors (Davis and Marshall 1961; Hall (pers. comm.) and Mikulich and Tsikhon-Lukaniana 1981) have indicated that benthic organisms play an important role in the feeding ecology of other scallop species.

There has been considerable recent interest in the near bottom nepheloid layer and its associated "fluff" layer of unconsolidated sediment on the bottom and on the importance of sedimenting phytoplankton as a food source for benthic organisms (Christensen and Kannevorff 1985; Davies and Payne 1984; Graf *et al.* 1982, 1984). The ability of scallops to stir up the sediment surface places them in the unique position of being able to utilize both the suspended material in the near-bottom water and the recently deposited material to be found in the fluff layer.

In the current study we compare the potential food organisms of scallops from a "shallow water" population with those from a "deep-water" population on the basis of gut content analysis, in an effort to 1) characterize the nature of the food items consumed, 2) assess seasonal variation of food items and 3) provide preliminary information regarding the value of the sediment surface "fluff" layer and nepheloid layer to the nutrition of bottom dwelling invertebrates.

MATERIALS AND METHODS

Specimens of the sea scallop, *Placopecten magellanicus*, were collected throughout the year from two locations in the Gulf of Maine: Damariscotta River (43° 51.26', 69° 34.0'; depth approximately 20m) and 20 miles south of Boothbay (43° 26.5', 69° 33.3'; depth approximately 180m). Samples from the Damariscotta River were collected by divers and the offshore samples were collected by

trawlers. In all cases, animals were immediately returned to the laboratory and digestive gland/stomach complex removed. After careful removal of the dorsal shell valve, the animal was washed to be sure that no debris remained to be confused with food items/gut contents. In one group of scallops, the gut contents were removed with a hypodermic syringe for comparison with other samples. Gut contents recorded from these samples were identical to those collected by removing the digestive glands and the possibility of contamination was eliminated. Guts were not homogenized. Samples were drawn from the gut by pipette. Samples of 0.1–0.2 ml were drawn from each gut. In initial sampling trials, increasing the sample size to 1 ml did not yield additional species representation. In addition to the scallop samples, samples of the overlying water were collected from the Damariscotta River site and analysed for species content. Gut contents were identified using standard light and phase contrast microscopic techniques at the Provosolli-Guillard Center for the Culture of Marine Phytoplankton, Bigelow Laboratory for Ocean Sciences. A total of 78 fresh guts were analyzed from scallops ranging in size from 90–140 mm shell height.

TABLE 1.
Gut contents of inshore scallops.

Species	Habitat	Size (μm)
<i>Nitzschia</i> spp.	B	25–150
<i>Navicula</i> spp.	B	8–240
<i>Pleurosigma</i> sp.	B	200
<i>Thalassiothrix</i> sp.	B	50 (chain)
<i>Amphora</i> sp.	B	10–30
<i>Licmophora</i> spp.	B	25–180
<i>Acanthos</i> sp.	B	40–90
<i>Pinnularia</i> sp.	B	40–80
<i>Surirella</i> sp.	B	15–25
<i>Cylindrotheca closterium</i>	B	80–100
<i>Protogonyaulax</i> resting cyst	B	35–40
unidentified cyst	B	25–35
<i>Melosira</i> sp.	B	30–55 (chain)
<i>Striatella</i> sp.	B	40–50
<i>Coscinodiscus</i> spp.	B/P	40–180
<i>Ditylum brightwellii</i>	P	50–150
<i>Protoperdinium</i> sp.	P	60–70
<i>Eucampia zoodiacus</i>	P	40–75 (chain)
<i>Peridinium</i> sp.	P	20–30
<i>Prorocentrum micans</i>	P	45–55
<i>Skeletonema costatum</i>	P	30–50 (chain)
<i>Dinophysis acuminata</i>	P	50–60
<i>Dinophysis</i> spp.	P	32–60
<i>Thalassiosira rotula</i>	P	20 (chain)
<i>Thalassiosira nordenskioldii</i>	P	20 (chain)
<i>Thalassiosira</i> spp.	P	10–200 (chain)
Miscellaneous:		
Silicoflagellate strew; pollen grains (30–40 μm); green filamentous alga (1000 > μm); ciliates; zooplankton tests; bacteria; detritus; unidentified, unpigmented still active forms: (3 μm), multiflagellate (10 μm), ciliated mass (40–200 μm)		

RESULTS

The predominant food items identified from the guts of scallops from shallow water populations and deep water populations are summarized in Tables 1 and 2, respectively. A total of 27 species of algae ranging in size from approximately 10–350 μm were identified from the digestive glands along with several miscellaneous items including pollen grains, ciliates, zooplankton tests, considerable detrital material, and bacteria. Benthic and pelagic food species were equally represented in the shallow water scallops while, as might be expected, benthic species outnumbered pelagic species in the guts of deep water scallops in number of species but not necessarily in biomass. Resting cysts of the toxic dinoflagellate, *Protogonyaulax tamarensis*, were more prominent in the offshore population than in the shallow water animals. The theca of several *Dinophysis* spp. were a constant feature of both populations, though not seen consistently or in great numbers in water samples. While we did not do a taxonomic study, different morphological variations, attributed in the literature to different taxa, were observed.

Seasonal variations in occurrence of the food items from both populations are summarized in Tables 3 and 4. In the offshore scallops the pelagic species *Coscinodiscus* spp., *Prorocentrum micans*, *Dinophysis* spp., *Eucampia zoodiacus* and *Ditylum brightwellii* were prominent in the early fall (Oct/Nov), i.e. during the bloom period, and coincided

TABLE 2.
Gut contents of offshore scallops.

Species	Habitat	Size (μm)
<i>Melosira</i> sp.	B	50 (chain)
<i>Protogonyaulax</i> resting cyst	B	35–40
<i>Navicula</i> spp.	B	60–350
<i>Nitzschia</i> spp.	B	110
<i>Thalassiothrix</i> sp.	B	50 (chain)
<i>Acanthos</i> sp.	B	40–90
<i>Amphora</i> sp.	B	10–30
<i>Pleurosigma</i> sp.	B	280
<i>Licmophora</i> sp.	B	120–180
<i>Pinnularia</i> sp.	B	70–100
<i>Surirella</i> sp.	B	15–25
unidentified dinoflagellate cyst	B	25–35
<i>Coscinodiscus</i> spp.	P/B	50–160
<i>Prorocentrum micans</i>	P	45–55
<i>Dinophysis</i> spp.	P	32–60
<i>Thalassiosira</i> sp.	P	35–50
<i>Eucampia zoodiacus</i>	P	100 (chain)
<i>Ditylum brightwellii</i>	P	150
<i>Ditylum brightwellii</i> resting spore	P	40
Miscellaneous:		
Pollen grains (40–60 μm); zooplankton tests (100–250 μm); bacteria; detritus; unidentified, unpigmented, still active forms; unflagellate (3 μm), multiflagellate (10 μm), ciliated mass (70–300 μm)		

with the period of greatest mixing of the water column. The most prominent pelagic food items of the inshore scallops were *Prorocentrum* (Oct/Nov; Jan), *Thalassiosira* sp. (March; Jan), and *Dinophysis* (Oct) again, coinciding with bloom periods and the subsequent settlement of the algae cells.

DISCUSSION

The quality and quantity of food available is a major limiting resource for suspension feeding organisms in general and for *Placopecten magellanicus* in particular (MacDonald and Thompson 1985a,b; 1986a,b). As pointed out by Levinton (1972), not only is the food supply constantly fluctuating, it is unpredictable and these suspension feeding organisms must maintain an adaptive feeding strategy which maximizes the generality of their food requirement. Although the majority of lamellibranch bivalves have been divided into two groups, the suspension feeders and the deposit feeders, there is no clear-cut distinction between these

two food sources (Morton, 1983). In a recent survey, Tsikhon-Lukanina (1982) showed that most bivalved molluscs are detritus feeders and that their main sources of food are detritus, unicellular algae and protozoa.

The surface deposits (fluff layer) can be stirred into suspension and thus made available to suspension feeding animals as seston (organic and inorganic suspended matter greater than 1 μm). The quantity of this particulate matter and its quality as a food resource varies both temporally and spatially in response to physical and biological factors (Brut, 1955; Berg and Newell, 1986). The results reported here clearly indicate that the scallop, *P. magellanicus* is an opportunistic filter feeder which takes advantage of these resuspended particles. The gut contents generally reflect the available organisms in the immediate habitat (Tables 1-4). One notable exception is *Chaetoceros* spp., usually available in the water column but not observed in gut content. This may be due to lack of resolution after spines have been altered or removed. It may also be an indication of

TABLE 3.
Seasonal variation in relative abundance of food items from inshore scallops.

Species	Oct/Nov 1985	Jan 1986	March 1986	July 1986	Oct/Nov 1986	Dec/Jan 1987
<i>Amphora</i> sp.	-	-	-	-	-	+
<i>Cylindrotheca closterium</i>	-	-	-	-	-	++
<i>Protogonyaulax tamarensis</i>						
resting cyst	+	+	-	+	+	-
unidentified cyst	+	-	-	+	+	-
<i>Nitzschia</i> spp.	+	+	++	+	+	++
<i>Navicula</i> spp.	++	++	+	++	++	++
<i>Pleurosigma</i> sp.	+	+	-	+	+	+
<i>Thalassiothrix</i> sp.	-	+	+	-	-	+
<i>Licmophora</i> spp.	+	+	++	+	+	+
<i>Acnanthes</i> sp.	+	+	+	+	+	+
<i>Pinnularia</i> sp.	-	-	+	-	-	-
<i>Surirella</i> sp.	++	-	-	-	++	++
<i>Striatella</i> sp.	-	-	-	-	-	+
<i>Ditylum brightwellii</i>	+	-	-	-	+	+
<i>Protoperdinium</i> sp.	++	-	-	-	++	-
<i>Eucampia zodiacus</i>	++	-	-	-	++	+
<i>Peridinium</i> sp.	+	-	-	-	+	+
<i>Prorocentrum micans</i>	+++	+++	-	++	+++	+
<i>Melosira</i> sp.	+	+	+	+	+	+
<i>Coscinodiscus</i> sp.	+	++	++	+	+	+
<i>Skeletonema costatum</i>	+	-	-	-	+	-
<i>Dinophysis acuminata</i>	-	-	-	-	-	+
<i>Dinophysis</i> spp.	+	+	++	++	+++	+
<i>Thalassiosira</i> spp.	+	++	+++	-	+	+++
<i>Thalassiosira rotula</i>	-	-	-	-	-	+
<i>Thalassiosira nordenskioldii</i>	-	-	-	-	-	+
Miscellaneous:						
Silicoflagellates (+), green filamentous alga, bacteria (+++), pollen grains (+), zooplankton tests and spines (+++), diatom strew (++), detritus (+++)						

+++ common, very abundant

++ common, abundant

+ common, not abundant

TABLE 4.
Seasonal variation in relative abundance of food items of scallops
from 20 miles south of Boothbay.

Species	Sept 1985	Jan 1986	Nov 1986	Dec/Jan 1987
<i>Protogonyaulax tamarensis</i>				
resting cyst	++	++	++	+
<i>Navicula</i> spp.	++	++	++	++
<i>Nitzschia</i> spp.	+	+	+	++
<i>Thalassiothrix</i> sp.	-	+	-	-
<i>Amphora</i> sp.	-	-	-	+
<i>Acanthes</i> sp.	+	+	+	++
<i>Pleurosigma</i> sp.	+	+	+	
<i>Pinnularia</i> sp.	+	-	+	+
unidentified dinoflagellate				
cyst	+	-	+	-
<i>Surirella</i> sp.	-	-	-	+
<i>Coscinodiscus</i> spp.	++	++	+	+
<i>Licmophora</i> sp.	-	-	-	+
<i>Prorocentrum micans</i>	++	+	++	++
<i>Dinophysis</i> spp.	++	-	+	+
<i>Melosira</i> sp.	+	+	+	++
<i>Thalassiosira</i> sp.	-	++	-	++
<i>Eucampia zoodiacus</i>	++	-	++	+
<i>Ditylum brightwellii</i>	++	-	++	+
<i>Ditylum brightwellii</i>				
resting spore	+	-	+	-
Miscellaneous:				
Pollen grains (+), zooplankton tests (+), bacteria (++), detritus (++)				
(++), motile forms: 10 μ m colorless multiflagellate, 3 μ m colorless arrowhead, uniflagellate 70-300 μ m ciliated mass				

+++ common, very abundant

++ common, abundant

+ common, not abundant

selective feeding. In a previous laboratory study (Shumway et al. 1985), it was shown that *P. magellanicus* exhibited both pre-ingestive selection on the labial palps and differential absorption in the gut.

The gut contents varied both with depth and with season and these differences were primarily reflected in the consumption of species abundant during bloom conditions. In addition, a greater number of predominantly benthic species were identified from deep water scallops than from shallow water animals. These findings mirror those of other workers (see Table 5) and are not intended to be a comprehensive or all inclusive listing of possible food items for this species. Some algal species, especially small forms (<10 μ m) may be quickly digested and not seen or resolved in stomach contents. Conversely, many of the observed species may be difficult to digest and of little consequence to the diet. In analyses performed over several days, from the same guts, large pennates (>150 μ m) remained intact and pigmented, while most other forms had degraded. During bloom concentrations of *P. micans*, many of these cells remained intact in untreated guts 5 days after the initial sampling. Further, much of the food is undoubtedly

comprised of the naked and minute nanoplankton which is probably too delicate to remain intact after ingestion.

In addition to the differences noted between the shallow and deep water habitats, several other points emerged that raise a number of questions. It was noted in the present study that the food organisms ranged from 10-350 μ m. Mikulich and Tsikhon-Lukanina (1981) also found a wide range of food particles (9-950 μ m). The majority of feeding studies on bivalve molluscs involve feeding pure cultures of rather small algae (4-20 μ m) to various species of molluscs. Several authors have demonstrated that scallops exhibit reduced efficiency of particle retention when fed particles less than 7 μ m (*Chlamys opercularis*, Vahl 1972; *Pecten opercularis* and *P. septemradiatus*, Møhlenberg and Riisgard 1978). Palmer and Williams (1980) demonstrated that *Argopecten irradians* was capable of adjusting the filtration efficiency in response to varying concentrations of particulate matter. The presence of zooplankton tests raises the question of whether or not these organisms are utilized as a food source. Crustacean larvae, tests and whole copepods have been identified from the guts of scallops and other bivalve molluscs; however, their role as a food resource is not clear. Wojtowicz (1972) studied a number of digestive enzymes in the digestive gland of *P. magellanicus* but found no chitinase. It seems most likely that these crustacean materials are taken incidentally with other organisms and are probably not a major food source. Future feeding studies on scallops should include species of algae in the larger size ranges and should investigate the possible role of zooplankton as a food source.

The presence of *Dinophysis* in such large quantities is of particular interest. Only unpigmented, digested thecae were observed in the guts. *Dinophysis* spp. have been implicated in outbreaks of diarrhetic shellfish poisoning (DSP) worldwide (Campos et al. 1982; Kat 1979; 1985; Guzman and Campodonico 1975; Freudenthal 1985; Dahl-Lyndastad 1985; Krough et al. 1985) although no known cases have been reported from the Gulf of Maine. Species known to accumulate the *Dinophysis* cells include mussels (*M. edulis* and *M. coruscum*), scallops (*Patinopecten yessoensis* and *Chlamys nipponensis akazara*) and clams (*Tapes (Venerupis) japonica* and *Gomphina melanaegis*). Preliminary investigations (Yasumoto et al. 1985) have indicated that the DSP toxin is concentrated in the digestive gland and that intoxication could be avoided, as in the case of PSP, by eliminating the digestive glands. This method is feasible with the scallops since usually only the adductor muscle is marketed. A market does exist, however, for whole scallop meats and current legislation is pending with regard to restricting the taking of whole scallops meats for human consumption due to PSP infestation. Further, it has been demonstrated that mussels and scallops may become toxic beyond the regulation level in the presence of *Dinophysis* spp. at cell densities of 200/L or less, Yasumoto et al.

TABLE 5.
A summary of the feeding habits of various species of scallops.

Species	Feeding Habits	Author
<i>Aequipecten irradians</i>	Microflora, detritus, bacteria and organic matter common in water immediately adjacent to the bottom; identified 26 species of diatoms (17 benthic/tychopelagic; 9 planktonic); proposed that some selective feeding might be in effect	Davis and Marshall (1961)
<i>Chlamys opercularis</i>	Dinoflagellates, diatoms, crustacean larvae, sand grains, detritus	Aravindakshan (1955)
<i>Chlamys opercularis</i>	Sedimenting phytoplankton; demonstrated that sedimentation of phytoplankton major factor regulating growth	Christensen and Kannevorff (1985)
<i>Chlamys tehuacensis</i>	Identified over 100 food items; dominant algal species benthic; planktonic species comprising the spring bloom; 90% of ingested particles less than 100 μm ; not all benthic algae of appropriate size range used: those attached to sand grains by gelatinous stalks very abundant but not found in guts presumably not easily resuspended	deHall (personal communication)
<i>Patinopecten yessoensis</i>	161 forms identified including algae and animals, spores, eggs, detritus and mineral particles (size range 9–950 μm); detritus main food source; animal and plant material most important during reproductive period;	Mikulich and Tsikhon-Lukanina (1981)
<i>Pecten septemradiatus</i>	Resuspended detritus	Blegvad (1915)
<i>P. opercularis</i>		
<i>P. varius</i>		
<i>Pecten varius</i>	“Unfailing occurrence of bottom, naviculoid diatoms and the frequency of sand-grains, spicules, and bottom living Foraminifera”; diatoms most important food organism; planktonic species important during their respective seasons of abundance	Hunt (1925)
<i>Placopecten grandis</i> (= <i>magellanicus</i>)	Detritus, ‘everything small that is to be found in the plankton’, their own and other veliger larvae, copepods, <i>Balanus nauplii</i> ; pine-tree pollen grains, <i>Pleurosigma</i> and <i>Navicula</i> not digested	Stevenson (1932, 1936)
<i>Placopecten grandis</i> (= <i>magellanicus</i>)	Identified 38 forms including algae, animals and eggs; diatoms comprised bulk of food, tintinnids and silicoflagellates	Borden (1928)
<i>Placopecten magellanicus</i>	Algae, pollen grains, silicoflagellate strew, ciliates, zooplankton tests, bacteria, detritus, 21 species of algae identified (10–350 μm); some seasonal variation attributed to algal blooms; both benthic and pelagic species prominent	Present study

(1983). The concentrations found in the present investigation could lead to cases of DSP if whole animals were ingested. Further studies are needed on the occurrence of these dinoflagellates and their role in the food habits of not only the scallops, but also of other commercially important species of shellfish.

Although the scallops are capable of some mobility, they remain essentially fixed in position and feed on particles in the sea water that passes by them. These currents of water may be environmentally induced or they may be created by the animals themselves. These factors take on special significance for scallops in that current orientation could be of real significance for maximizing the available food resources. Diver observations of scallops at various stages of the tide seem to indicate that scallops feed discontinuously and orientate with respect to current direction. Flume studies are currently underway to determine the significance of this orientation and/or feeding behavior.

Some scallop species are also known to exhibit “clapping activity” which resuspends some of the surface sediment (fluff layer) thus making the material available to the filter feeders. Davis and Marshall (1961) showed that the

bay scallop, *Aequipecten irradians*, obtained a considerable amount of its food through shell flapping i.e., resuspending the surface sediment materials. Divers have noted however, that this clapping activity is rarely seen in *P. magellanicus* in shallow water (Schick, unpublished). This shell clapping activity could be of considerable significance, however, to the deeper water animals where pelagic algal species are not always readily available as a food source.

Algal cells settling during spring and fall blooms are one of the main inputs of particulate organic matter from the pelagic to the benthic system. Downward mixing of plankton during certain times of the year undoubtedly plays a large part in making food organisms available to the deeper water scallops. The blooms (spring, summer) play an important role for shallow-water populations of *P. magellanicus* as has already been demonstrated by several authors with regard to the gametogenic cycle (Ehinger 1978; Thompson 1979; Robinson et al. 1981). The deep water scallops live well below the photic zone and it might well be assumed that they do not utilize living algae from planktonic blooms as a food resource. Our results (Tables 2 and

4) indicate, however, that a relatively large number of intact planktonic algal species reach the scallops, probably due to vertical mixing of the water column during the fall (October/November). These sudden bursts of energy/food input as a result of the phytoplankton blooms (rain or mixing) may provide just enough energy to sustain the population. Studies are currently underway to assess the extent of gonad production in the two populations. Preliminary indications are that the deep water scallops do not produce viable gonads (Barber *et al.* 1987).

Davies and Payne (1984) suggested that the substantial increase in fresh organic carbon and nitrogen associated with the spring phytoplankton bloom might have a stimulatory effect on the growth and reproduction of the benthic animals and might act as a triggering mechanism for their life cycle. It is possible in the offshore population of *P. magellanicus* studied here, that the influx of pelagic species after the fall bloom is the factor responsible for the survival of the population. This is the period of the year when the inshore animals have just spawned and their metabolic rate is at its lowest peak (Shumway *et al.*, in prep.). The exact extent of the energy input, however, is as yet not clear and still needs to be quantified.

Our results indicate that the scallops are ingesting both pelagic and benthic organisms. The relative importance of

these food organisms is not known, although it can be assumed that planktonic species such as *Thalassiosira*, *Dinophysis* and *Prorocentrum* must provide a significant portion of the energy intake of the scallops.

In 1972, Levinton stated that the role of resuspended sediment from the fluff layer in the nutrition of suspension feeding animals still needed investigation and the statement is as true now as it was then. A better understanding of the feeding habits of "interfacing" species such as *P. magellanicus* may provide a unique opportunity to determine not only their role in the transformation of energy between the benthic and pelagic ecosystems, but also to study the relationship between the fluff layer, the nepheloid layer and the benthic invertebrates.

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REFERENCES CITED

- Aravindakshan, I. 1955. *Studies on the biology of the queen scallop, Chlamys opercularis* (L.O. Ph.D Thesis, University of Liverpool, 79 p.
- Barber, B., Gatchell, R., S. E. Shumway, & Schick, D. F. 1987. The effect of depth on the gametogenic cycle of the scallop, *Placopecten magellanicus*. Submitted.
- Bayne, B. L. & J. Widdows. 1978. The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia (Berl.)* 37:137-162.
- Berg, J. A. & R. I. E. Newell. 1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuar. Coast. and Shelf Science* 23:375-386.
- Blegvad, H. 1915. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. *Rept. Danis Biol. Sta. Vol.* 22:43-78.
- Burt, W. V. 1955. Distribution of suspended materials in Chesapeake Bay. *J. Mar. Res.* 14:47-62.
- Campos, M. J., Fraga, S., Marino, J. & F. J. Sanchez. 1982. *International Council for the Exploration of the Sea Report* 1977-1981, 8p.
- Christensen, H. & E. Kammerhoff. 1985. Sedimenting phytoplankton as a major food source for suspension and deposit feeders in the Oresund. *Ophelia* 24:223-244.
- Dahl, E. & M. Yndestad. 1985. Diarrhetic shellfish poisoning (DSP) in Norway in the autumn 1984 related to the occurrence of *Dinophysis* spp. In: D. M. Anderson, A. W. White, & D. G. Baden, eds. *Toxic Dinoflagellates*. Elsevier, 495-500 p.
- Davies, J. M. & R. Payne. 1984. Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. *Mar. Biol.* 78:315-324.
- Davis, R. L. & N. Marshall. 1961. The feeding of the bay scallop, *Aequipecten irradians*. *Proc. Natl. Shellfish. Assoc.* 52:25-29.
- Ehinger, R. E. 1978. *Seasonal energy balance of the sea scallop, Placopecten magellanicus, from Narragansett Bay*. M. S. Thesis, University of Rhode Island. p.
- Freudenthal, A. R. & J. Jijina. 1985. Shellfish poisoning episodes involving or coincidental with dinoflagellates. In: D. M. Anderson, A. W. White, & D. G. Baden, eds. *Toxic Dinoflagellates*. Elsevier 461-466 p.
- Graf, G., W. Bengtsson, A. Faubel, L. -A. Meyer-Reil, R. Schulz, H. Theede & H. Thiel. 1984. The importance of the spring phytoplankton bloom for the benthic system of Kiel Bight. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.*, 183:136-143.
- Graf, G., W. Bengtsson, U. Diesner, R. Schulz & H. Theede. 1982. Benthic response to sedimentation of a spring phytoplankton bloom: Process and budget. *Mar. Biol.* 67:201-208.
- Guzman, L. and Campodonico, I. 1975. *Publ. Inst. Patagonia Ser. Mon. No.* 9, 6 p.
- deHall, M. V. 1977. *Alimentacion de la vieyra tehuelche (Chlamys tehuelchus)*. Comision Nacional de Estudios Geo-Heliofisicos Centro Nacional Patagonico. Puerto Madryn-Chubut, Argentina.
- Hunt, O. D. 1925. The food of the bottom fauna of the Plymouth fishing grounds. *J. Mar. Biol. Assoc. U.K.* 13:560-595.
- Katz, M. 1979. The occurrence of *Prorocentrum* species and the coincidental gastrointestinal illness of mussel consumers. In: *Toxic Dinoflagellate Blooms*, eds. Taylor, D. L., & H. H. Seliger, Elsevier, North Holland: New York, 215-220 p.
- Katz, M. 1985. *Dinophysis acuminata* blooms, the distinct cause of Dutch mussel poisoning. In: *Toxic Dinoflagellates*, D. M. Anderson, A. W. White & D. G. Baden, eds. Elsevier, North Holland: New York, 73-78 p.
- Krogh, P., L. Edler, Graneli, & U. Nyman. 1985. Outbreak of diarrhetic shellfish poisoning on the west coast of Sweden. In: *Toxic Dinoflagellates*, D. M. Anderson, A. W. White & D. G. Baden, eds. Elsevier, North Holland: New York, 501-503 p.
- Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Am. Nat.* 106:472-486.
- MacDonald, B. A. & R. J. Thompson. 1985a. Influence of temperature

- and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. I. Growth rates of shell and somatic tissue. *Mar. Ecol. Prog. Ser.* 25, 279–294.
- MacDonald, B. A. & R. J. Thompson. 1985b. Influence of temperature and food availability on the ecological energetics of the giant scallop, *Placopecten magellanicus*. II. Reproductive output and total production. *Mar. Ecol. Prog. Ser.* 25, 295–303.
- MacDonald, B. A. & R. J. Thompson. 1986a. Influence of temperature and food availability on the ecological energetics of the giant scallop, *Placopecten magellanicus*. III. Physiological ecology the gametogenic cycle and scope for growth. *Mar. Biol.* 93:37–48.
- MacDonald, B. A. & R. J. Thompson. 1986b. Production, dynamics and energy partitioning in two populations of the giant scallop, *Placopecten magellanicus*. (Gmelin). *J. Exp. Mar. Biol. Ecol.* 101:285–299.
- Mikulich & A. Tsikhon-Lukanina. 1981. Food of the scallop. *Oceanology* 21:633–635.
- Møhlenberg, F. & H. U. Riisgard. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. *Ophelia* 17:239–246.
- Morton, B. A. 1983. Feeding and digestion in bivalvia. In: *The Mollusca*, A. S. M. Saleuddin, & K. M. Wilbur, eds. Academic Press 65–147 p.
- Newell, R. I. E. & B. L. Bayne. 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle, *Cardium (Cerastoderma) edule* (Bivalvia: Cardiidae). *Mar. Biol.* 56:11–19.
- Newell, R. I. E., T. J. Hilbish, R. K. Koehn & C. J. Newell. 1982. Temporal variation in the reproductive cycle of *Mytilus edulis* L. (Bivalvia, Mytilidae) from localities on the east coast of the United States. *Biol. Bull.* 162:299–310.
- Palmer, R. E. & L. G. Williams. 1980. Effect of particle concentration on filtration efficiency of the bay scallop, *Argopecten irradians*, and the oyster, *Crassostrea virginica*. *Ophelia* 19:163–174.
- Robinson, W. E., W. E. Wehling, M. P. Morse & G. C. McLeod. 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. *Fish. Bull.* 79:449–458.
- Schick, D. F., S. E. Shumway, & M. Hunter. 1987a. A comparison of growth rate between shallow water and deep water populations of scallops, *Placopecten magellanicus* (Gmelin, 1791) in the Gulf of Maine. In Press. *Amer. Malac. Bull.*
- Schick, D. F., S. E. Shumway, & M. Hunter. 1987b. Allometric relationship and growth in *Placopecten magellanicus*: The effects of season and depth. In press. *Malacological Review*.
- Shumway, S. E., T. L. Cucci, R. C. Newell & C. M. Yentsch 1985. Particle selection, ingestion and absorption in filter-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 91:77–92.
- Shumway, S. E., D. Campbell and J. Stahlnecker 1987. Seasonal changes in oxygen consumption of the giant scallop, *Placopecten magellanicus* (Gmelin) with a preliminary model of growth, respiration and spawning in coastal Maine waters. Submitted.
- Thompson, R. J. 1977. Blood chemistry, biochemical composition, and the annual reproduction cycle in the giant scallop, *Placopecten magellanicus* from southeast Newfoundland. *J. Fish. Res. Bd. Canada* 34:2104–2116.
- Tsikhon-Lukanina, Ye. A. 1982. Food spectra of bottom molluscs. *Oceanology* 22:751–754.
- Vahl, O. 1972. Particle retention and relation between water transport oxygen uptake in *Chlamys opercularis* (L.) (Bivalvia). *Ophelia* 10:67–74.
- Vahl, O. 1973. Efficiency of particle retention in *Chlamys islandica* (O. F. Muller). *Astarte* 6:21–25.
- Wojowicz, M. B. 1972. Carbohydrases of the digestive gland and the crystalline style of the Atlantic deep-sea scallop (*Placopecten magellanicus*, Gmelin). *Comp. Biochem. Physiol.* 43A:131–142.
- Yasumoto, T., Murata, M., Oshima, Y., Matsumoto, G. K. & J. Clardy. 1984. Diarrhetic shellfish poisoning. In: *Seafood Toxins*, Ragelis, ed. American Chemical Society Symposium Series 262. 207–214 p.
- Yasumoto, T., Yasukatsu, O. and M. Yamaguchi. 1978. Occurrence of a new type of shellfish poisoning in the Tohoku District. *Bull. Jap. Soc. Scient. Fish.* 44:1249–1255.

