Substratum associations of natural populations of Iceland Scallops, *Chlamys islandica* Müller 1776, on the northeastern Grand Bank of Newfoundland

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Abstract.   Live, Iceland scallops, *Chlamys islandica*, were enumerated and their occurrences assigned to substratum coarseness grades along five photographic transects (8-10 km in length) covering areas of the northeastern Grand Bank of Newfoundland. Scallops were disproportionately (53-94%) associated with the coarsest grade of substratum comprising dense gravel-cobble (80-100% by area). Overall, scallops were uncommon to rare on predominantly sand substrata. Average densities of scallops per photograph (5.4 m²) ranged from 0.5 to 13.8 in cobble fields and from 0.02 to 1.7 on open sand.

   It is hypothesized that Iceland scallops on the northeastern Grand Bank are aggregated on coarse substrata because of a strong propensity towards byssal attachment at all post-larval life history stages. A survey of substratum associations of extant species of *Chlamys* reveals that, with few exceptions, association with coarse substrata is common within the genus.

The Iceland scallop *Chlamys islandica* Müller, 1776, is a subarctic-boreal species, extending from Hudson Strait, N.W.T., south to the Massachusetts region (Lubinsky, 1980). Its bathymetric range extends to about 180 m and over the expansive Newfoundland continental shelf, it can occur at commercial densities (Naidu and Cahill, 1989). Apart from mostly anecdotal accounts, very little is known about substratum associations of natural populations of this species and the family Pectinidae in general. To date, research on substrata associations has focused on the settlement and growth of pectinid spat on artificial collectors within an overall aquaculture context. While it is generally known that pectinid spat will settle on substrata such as algae, hydrozoans, bryozoans and various artificial surfaces (Fraser, 1983), the natural settlement substrata for *C. islandica* are unknown (Wallace, 1982). Subsequent to spat settlement, it is believed that juvenile scallops display an overall movement from primary settlement substrata to substrata where they will reside during juvenile and adult stages. In the case of *C. islandica*, this could take place about one year after settlement when they have attained a shell height of >5 mm (Wallace, 1982).

Based on the contents of scallop dredges, Naidu (1988) found that Newfoundland populations of Iceland scallops are found normally at depths greater than 55 m, usually on hard bottom of variable substratum composition including mixtures of sand, gravel, shell fragments, rocks and boulders. Dense, commercial concentrations of Iceland scallops are known to occur on St. Pierre Bank (Newfoundland Grand Banks) (Naidu and Cahill, 1989) in areas with sediments characterized as Sable Is. gravel, which is a mixture of gravel and < 10% sand (Fader *et al.*, 1982). Most of the specimens of North American continental shelf *Chlamys islandica* in the collection of the National Marine Fisheries Service (Woods Hole) were collected from coarse substrata comprising gravel, sand-gravel, till and sand (Theroux and Wigley, 1983). Wiborg (1962, cited in Vahl and Clausen 1980) stated that *C. islandica* lives on coarse sediments or on hard bottom. In a shallow water study in the Gulf of St. Lawrence, Jalbert *et al.* (1989) determined that *C. islandica* occurred most frequently on coarse substrata, primarily cobble and gravel.

The objective of this investigation was to identify natural substratum associations in offshore populations of Iceland scallops from the Newfoundland Grand Bank. Based on a series of photographic transects across areas of the northeastern Grand Bank, spatial distribution patterns of the megafauna and major substratum types (coarseness grades) were described (Schneider *et al.*, 1987). The scope of this paper is threefold. First, Iceland scallop-substrata associations are documented for the northeastern Grand Bank. This is followed by an assessment of physical and behavioural mechanisms which could potentially influence these associations. Finally, observed patterns of substrata association in *Chlamys islandica* are compared with existing information on substrata and habitats occupied by extant *Chlamys* spp.

STUDY AREA

The Grand Banks of Newfoundland represents the most extensive shallow (< 200 m) feature on the continental

shelf of eastern Canada and is comprised of a series of major banks: St. Pierre, Green, Whale and Grand. The study area is situated on the northeastern edge of the Grand Bank of Newfoundland in the vicinity of the Hibernia oilfield (Fig. 1). Water depths range from 70 to 100 m. The most complete description of this area in terms of the surficial sediments and seabed processes is found in Barrie *et al.* (1984). Sedimentary cover typically consists of reworked sand and gravel deposits, generally < 2 m thick. Bedforms include sand ripples (≤ 1 m wide), sand megaripples (5-10 m wide), sand ribbons (100 m to 1 km wide) and sand ridges (generally > 3 km in width). Coarse sediment is incorporated into the sand, in places. Coarse sediment consists of gravel and cobble-sized clasts (Grand Bank Gravel) which are believed to represent Pleistocene glacial deposits which have been reworked subsequently into coastal environments by an early Holocene marine transgression as a result of a eustatic rise in sea level. Overall, sedimentary bedforms on the Grand Banks are believed to be dynamic and are being reworked by unidirectional storm-driven currents, ocean currents and extreme waves.
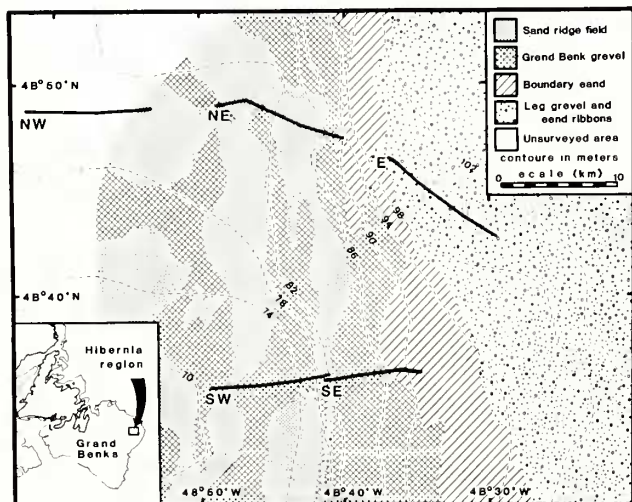

Fig. 1. Location of photographic transects on the northeastern Grand Bank.

METHODS

Five photographic transects, ranging in length from 8 to 10 km, were conducted across the northeastern edge of the Grand Bank (Fig. 1). Colour 35 mm slide photographs were taken at 10 s intervals with the BRUTIV system (Vilks, 1984) which consists of a sled-mounted camera (aligned vertically) towed 3 m above the seabed. Technical details are provided in Schneider *et al.* (1987). The area defined by each photograph was 5.4 m².

Each frame (slide) was examined under low magnification (X16) and classified into one of six substratum categories

based on a gross classification scheme of sediment texture and estimated areal coverage:
1- pure sand;
2- sand with scattered cobble;
3- scattered gravel on sand;
4- sand with cobble and shell;
5- 50 to 80% cobble and gravel;
6- > 80% cobble and gravel.
Sand and gravel were distinguished on the basis of textural differences. While gravel is defined as particles with diameter > 5 mm (ASTM, 1988), much of the sediment in categories 5 and 6 were dominated by large-sized rocks (> 20 mm diameter) and are referred to as cobble.
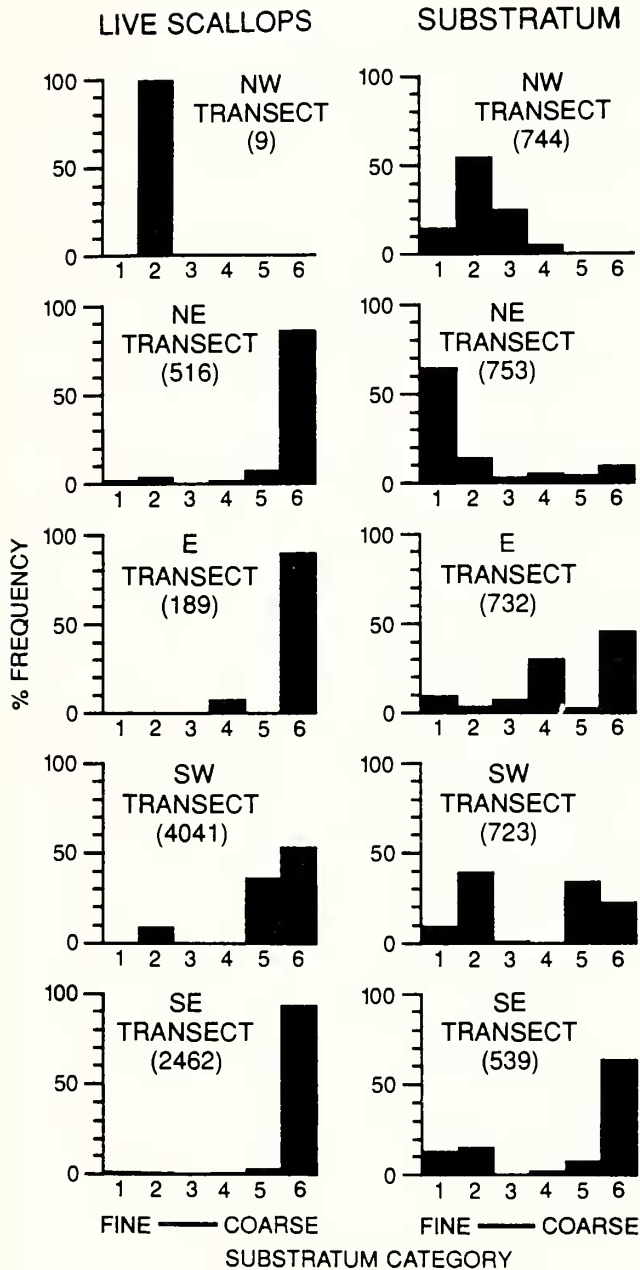
All identifiable Iceland scallops were enumerated by superimposing a 5 X 5 grid over each slide and recording the number of organisms in each cell. Analyses were carried out on the sum of counts in each slide. Megafauna less than about 2 cm in shell height were visible, but generally could not be identified to the species level. Scallops were classified as live if they were in normal life position (epifaunal) with normal colouration (i.e. not bleached). While there could be a tendency to overestimate the abundance of live scallops by inclusion of articulated, collapsed cluckers (*sensu* Naidu, 1988), there were probably instances where live, ''bleached-looking'' scallops were classified as dead. All identifiable scallops displayed a sculpture of coarse ribs and had unequal hinge ''ears,'' features which distinguish the Iceland scallop from the sea scallop *Placopecten magellanicus* (Gmelin, 1791). The only scallop reported from the northeastern Grand Bank has been the Iceland scallop (Mobil, 1985).

For each transect, the frequency distributions of live scallops, by substratum type, were tested statistically for significant departures from random distributions based on the proportion of available substratum types (G-test for goodness of fit, Sokal and Rohlf, 1981). It was assumed that scallops would be distributed randomly at similar densities for all substratum types.

RESULTS

The bedforms which the photographic transects crossed are shown in figure 1. Transect Northwest (NW), which over most of its length traversed previously unsurveyed territory, crossed a sand ridge field with areas of scattered cobble and gravel. Transect Northeast (NE) intersected two sand ridge fields with minor amounts of cobble, gravel and shell. Transect East (E) crossed sand ribbons developed on top of a lag gravel. Transect Southwest (SW) crossed a gravel and cobble field (Grand Bank gravel) with a regular alternation of sand and cobble and Transect Southeast (SE) crossed a gravel and cobble field (Grand Bank gravel) which intersected a sand field (boundary sand) at its eastern end.

Substratum composition varied between transects (Fig.

Fig. 2. Frequencies of occurrence of (i) live Iceland scallops by substratum category and (ii) substratum categories along photographic transects. Numbers in parentheses refer to total number of enumerated live scallops (left column) and photographs examined (right column) along each transect.

substrata (i.e. gravel and cobble) (Fig. 2). Along Transects NE, E and SE, greater than 80% of the total number of live scallops occurred on the coarsest substratum (category #6). This was in spite of the fact that predominantly fine substrata occurred at frequencies ranging from 15 to 80% along these transects. In particular, along Transect NE where the pure sand substratum category (#1) had a frequency of occurrence of 65%, approximately 85% of the scallops occurred on cobble substrata which had a frequency of occurence of only 10%. Along Transect SW, approximately 10% of the scallops were counted from substrata comprised predominantly of sand and scattered cobble (Fig. 2). It is noted that this occurred along the transect with the highest densities of live scallops (Fig. 3). Frequencies of scallops along these transects showed a highly significant deviation from a random distribution across all substratum types (G-test statistic range: 176-2869, $p < < 0.01$). Transect NW crossed a sand ridge field with areas of scattered gravel. Along this entire 10 km transect, represented by 744 photographs, only 9 live scallops were counted.

There was considerable variation in the substratum-specific densities of live scallops between transects (Fig. 3). Average densities on the coarsest substratum (> 80% cobble and gravel) ranged from 0.5 to 13.8 scallops per photograph (0.09 to 2.5 scallops/m²) while average densities on the next coarsest substratum (50% to 80% cobble and gravel) ranged from 0.1 to 5.7 scallops per photograph (0.02 to 1 scallop/m²). The highest densities on fine substrata occurred on Transect SW with an average density of 1.7 scallops per photograph (0.3 scallops/m²) on a substratum consisting primarily of open sand with scattered cobble. It was noted previously that this transect displayed the highest densities of scallops on most substratum categories. On the remaining transects, densities ranged from 0.02 to 0.4 scallops per photograph (0.003 to 0.07 scallops/m²) on the two finest substratum categories.

DISCUSSION

It is obvious that there is a strong association between Iceland scallops and coarse substrata (gravel, cobble) on the northeastern Grand Bank. At the outset, there are several explanations which could account for the observed aggregated distribution of scallops on coarse substrata. These include (1) substratum-specific predation pressure and (2) behavioural and physical mechanisms maintaining scallop-substratum associations.

PREDATORS

The underlying premise of substratum-specific predation pressure is that scallops suffer heavy mortality from predators after movement of juveniles or adults onto fine

2). Transects E and SE had a high percentage (50-60%) occurrence of predominantly coarse substrata, comprised of gravel and cobble (some shell), whereas Transects NE and NW had high occurrences of primarily sand substrata (> 60% in both cases). Along Transect SW there was more or less equal representation of fine and coarse substrata.

Along those transects which included the two coarsest substratum categories, scallops were aggregated on coarse
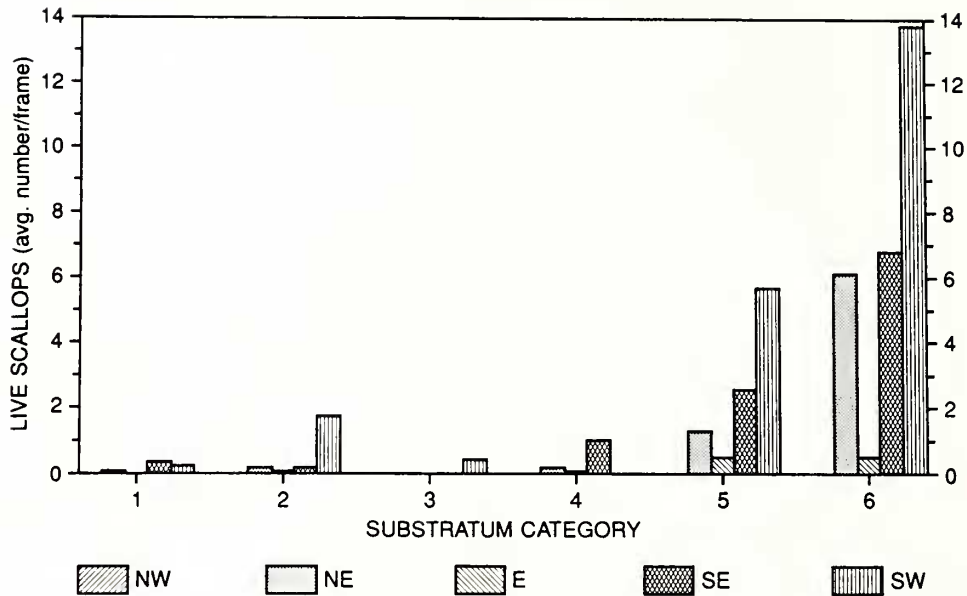
Fig. 3. Average densities of live Iceland scallops by substratum type along photographic transects.

substrata. As mentioned previously, evidence to date on pectinid spat substratum preference rules out primary settlement on fine substrata (i.e. sand). While disproportionate predation pressure due to predator-substrata associations cannot be ruled out as a contributing factor, we believe that predators on the northeastern Grand Bank are not responsible for the skewed distribution of scallops on coarse vs. fine substrata.

Potential predators of Iceland scallops on the Grand Banks are listed in Table 1. Of these, only the pleuronectids, American plaice (*Hippoglossoides platessoides* Fabricius, 1780) and yellowtail flounder (*Limanda ferruginea* Storer, 1839), are known predators of Iceland scallops on the Grand Banks (Pitt, 1976; Naidu and Meron, 1986) and other continental shelf regions (Langton and Bowman, 1981). Naidu and Meron (1986) determined that Iceland scallops occurred in plaice stomachs with a frequency of 22% on St. Pierre Bank. They found that Iceland scallops were susceptible to predation until the age of five years, at which point they achieved a size refuge which was a function of predator mouth gape. While probably not accounting for the rarity of scallops on fine substrata on the northeastern Grand Bank, American plaice would enhance the contrast in distribution of scallops between coarse and fine substrata through predation on these relatively rare occurring individuals on fine substrata.

Other large predatory fish such as Atlantic cod (*Gadus morhua* Linnaeus, 1758) are not known to be associated with any particular substratum type and are typical opportunistic feeders. Examination of cod stomach contents from the Grand Banks reveals a very low incidence of Iceland scallops (G. Lilly, pers. comm.).

Little is known about invertebrate predators of Iceland scallops. The Buccinidae and the Naticidae are probably the

Table 1. Potential predators of the Iceland scallop, *Chlamys islandica*, on the northeastern Grand Bank of Newfoundland.

Predator[1]	Substratum	
	Fine	Coarse
MOLLUSCA		
Buccinidae	P	P
Naticidae	P*	
CRUSTACEA		
Majidae- includes *Hyas* spp.,	P	P
and *Chionocetes opilio*		
ECHINODERMATA		
Asteroidea		
Asterias vulgaris		P*
Leptasterias sp.		P*
CHORDATA		
Rajidae	P*	
Gadidae	P	P
Zoarcidae	P	P
Cottidae	P	P
Pleuronectidae	K*	
Pseudopleuronectes americanus		
Limanda ferruginea		

[1] -Identified along photographic transects (Schneider *et al.*, 1987)
* -Typical substratum association
P-potential predator
K-known predators (Langton and Bowman, 1981; Naidu and Meron, 1986)

two major predatory gastropod groups on the Grand Banks. Species lists are incomplete for the study area and ecological relationships are poorly documented. However, from studies conducted in coastal areas, it is known that adult *Buccinum undatum* (Linnaeus, 1758) can be attracted over considerable distances (> 50 m/day) in search of bivalves which are their primary prey, on substrata including sand, mud and rock

(Himmelman, 1988; Jalbert *et al.*, 1989). Buccinid snails were common over all photographic transects and substratum types, although never abundant. The maximum average density for a transect was 0.4 snails/photograph (0.07 snails/m²) (Schneider *et al.*, 1987). Although uncommon in photographs, naticid gastropods were observed along the study transects on sand substrata. Most species of Naticidae are relatively stenotypic and prefer sand or muddy substrata (Golikov and Sirenko, 1988). If these gastropods were exerting a heavy mortality on scallops, one would expect to find a surface accumulation of empty scallop shells; this was not observed. Alternatively, naticids could be preying upon small scallops in the size range below the limits of resolution in photographs (i.e. < 2 cm).

Crabs are known predators of various scallop species (Elner and Jamieson, 1979; Lake *et al.*, 1987). While potentially important predators of scallops such as majid crabs (*Hyas* spp. and *Chionocetes opilio* O. Fabricius, 1780) were common over most transects, they were not restricted to a particular substratum (Schneider *et al.*, 1987). The extent of predation by various echinoderms (e.g. Asteroidea) on scallops is unknown, however, it is noted that asteroids were primarily associated with the coarsest substrata on the transects (Schneider *et al.*, 1987) and, therefore, would not be expected to cause excessive mortalities on sand substrata. In conclusion, it is considered unlikely that Iceland scallops are concentrated on coarse substrata due to differential survivorship from intense predation pressure on fine substrata.

BEHAVIOURAL AND PHYSICAL MECHANISMS MAINTAINING SCALLOP-SUBSTRATUM ASSOCIATIONS

The most plausible explanation for the association of Iceland scallops with coarse substrata is the propensity, at all life history stages, towards byssal attachment to a stable substratum. It is known that a high percentage of individuals in a population of Iceland scallops are attached to the substratum by the byssus at any given time. Frequencies of 76% (laboratory) and 97% (field) byssally attached adult scallops have been reported by Naidu and Meron (1986) and Vahl and Clausen (1980), respectively. From diving observations in West Greenland, Pedersen (1989) reported that Iceland scallops were attached to the substratum by the byssus, large scallops were attached directly to the substratum while small scallops were attached to larger scallops or empty shells. Vahl and Clausen (1980) postulate that because *Chlamys islandica* cannot recess on coarse sediments, it remains in danger of being swept away by currents and because *C. islandica* tends to occur in habitats with strong currents (Wiborg, 1962 *fide* Vahl and Clausen, 1980) byssal attachment remains necessary at all sizes.

An important aspect in assessing the importance of water movements in shaping the distribution of scallops is the current speed required to dislodge byssally attached scallops. Gruffydd (1976) determined "wash-away" velocities for Iceland scallops which ranged from 21 cm/s for 10-20 mm individuals to 26 cm/s for 65-70 mm individuals. For the northeastern Grand Bank of Newfoundland, Barrie *et al.* (1984) hypothesized that periodic, high unidirectional flow velocities (> 50 cm/s) occur, possibly every year to every few years at depths less than 110 m. Under these extreme flow conditions, the coarsest sediments become mobile and move as bedforms. At other times, maximum tidal current velocities (15 cm/s, Mobil, 1985) in the study area are less than those required to "wash-away" scallops. Therefore, within the study area, scallops are probably washed away infrequently although major storms would have the capability of dislodging large numbers of scallops. At present, the extent of the impact of such extreme events is unknown.

Swimming activity would make *Chlamys islandica* susceptible to being "washed-away" from preferred substrata. Gruffydd (1976) determined that all sizes of Iceland scallops, and particularly medium-sized (30-40 mm shell height) individuals, displayed a tendency to swim. However, Vahl and Clausen (1980) considered swimming activity to be a relatively rare phenomenon, with individual scallops making, on average, a swimming excursion every 31 days. This is in spite of the fact that byssus production is a minor item in the energy budget of *C. islandica* (Vahl and Clausen, 1980). There are limited data regarding conditions which initiate the swimming response. While Gruffydd's (1976) experiments showed that the swimming response was strongest at the fastest current speed (15 cm/s), Vahl and Clausen (1980) determined the flight reaction to be less evident during periods when current speeds were strong (about 50 cm/s) and speculated that this was probably due to the high risk to scallops associated with being carried to unsuitable habitats in strong currents. Byssal attachment rate of adult *C. tehuelcha* (d'Orbigny, 1835) increased dramatically over relatively small changes in current velocity, from 65% attachment at 6.6 cm/s to 90% at 8.3 cm/s (Ciocco *et al.*, 1983 *fide* Orensanz *et al.*, in press). Patterns of swimming behaviour in *C. islandica* may be determined by a combination of factors including habitat type and critical current velocity (in terms of initiating the swimming response) specific to these habitat types.

SUBSTRATA AND HABITATS OCCUPIED BY EXTANT *CHLAMYS* SPP.

In the evolution of the Bivalvia, neotenous retention of the byssus was an adaptive break-through in terms of physical stabilization, giving rise to an invasion of new habitats by epifaunal species (Stanley, 1972). The oldest (Triassic) pectinids are of the adult-byssate *Chlamys* type (Triassic) while the emergence of post-Triassic free-living pectinids evolved from byssate forms (Stanley, 1972).

Table 2. Approximate maximum sizes (shell height) and substrata and depths occupied by extant *Chlamys* spp.[1]

	Shell Height (mm)	Habitat Substratum	Depth[2]	Source
NORTHWEST ATLANTIC				
Chlamys islandica (Müller, 1776)	100	gravelly sand, shell rock	offshore (to 220 m)	this study; Theroux and Wigley, 1983; Naidu and Cahill, 1989
SOUTHWEST ATLANTIC				
C. benedicti (Verrill and Bush, 1897)	13	?	?	Abbott, 1974
C. mildredae (Bayer, 1943)	38	undersides of rocks	inshore (upper subtidal)	Abbott, 1974
C. sentis (Reeve, 1853)	38	undersides of rocks	inshore (< 15 m)	Abbott, 1974; Rehder, 1981
C. ornata (Lamarck, 1819)	40	undersides of rocks	inshore (to 4 m)	Abbott and Dance, 1986
C. imbricata (Gmelin, 1791)	44	undersides of rocks	inshore (< 6 m)	Abbott, 1974
C. multisquamata (Dunker, 1864)	59	rock crevices	inshore/offshore (6-56 m)	Abbott, 1974
C. patagonica (King and Broderip, 1832)	79	consolidated sand, shell	offshore (to 300 m)	Orensanz *et al.*, in press; O. Iribarne, pers. comm.
C. tehuelcha (d'Orbigny, 1835)	100	consolidated sand; shell-gravel, rocky bottoms	inshore/offshore (< 60 m)	Orensanz *et al.*, in press; O. Iribarne, pers. comm.
EASTERN ATLANTIC				
C. furtiva (Loven)	19	muddy, gravelly sand	inshore/offshore (< 200 m)	Tebble, 1966
C. striata (Müller, 1776)	19	muddy sand, gravel, shell	inshore/offshore	Tebble, 1966
C. tigerina (Müller, 1776)	25	sandy mud, gravel, rock	inshore/offshore (to 550 m)	Madson, 1949; Tebble, 1966
C. multistriata (Poli, 1795)	30	?	inshore/offshore (to 2000 m)	Abbott and Dance, 1986
C. tincta (Reeve, 1853)	30	?	?	Abbott and Dance, 1986
C. sulcata (Müller, 1776)	40	?	offshore (to 850 m)	Abbott and Dance, 1986
C. distorta (da Costa)	50	?	inshore/offshore (to > 90 m)	Tebble, 1966
C. flabellum (Gmelin, 1791)	50	?	inshore	Abbott and Dance, 1986
C. septemradiata (Müller, 1776)	51	mud	inshore/offshore (11-183 m)	Allen, 1953; Tebble, 1966
C. nivea (MacGillivray, 1825)	60	?	offshore	Abbott and Dance, 1986
C. varia (Linnaeus, 1758)	64	rocks, muddy gravel, shell	inshore/offshore (to 1000 m)	Allen, 1953; Tebble, 1966
ICELAND				
C. islandica (Müller, 1776)	110	clay, sand, shell	inshore/offshore (to 300 m)	Madson, 1949
BERING SEA				
C. behringiana (Middendorff, 1849)	?	?	offshore (40-150 m)	Bernard, 1983
C. pseudislandica (MacNeil, 1967)[3]	75	?	inshore/offshore	MacGinitie, 1959; Bernard, 1979
EASTERN PACIFIC				
C. jordani (Arnold, 1903)	?	?	inshore/offshore (2-60 m)	Bernard, 1983
C. lowei (Hertlein, 1935)	?	?	inshore/offshore (2-175 m)	Bernard, 1983; Keen, 1971
C. amandi (Hertlein, 1935)	40	?	offshore	Abbott and Dance, 1986
C. incantata (Hertlein, 1972)	60	?offshore (200 m)		Abbott and Dance, 1986
C. rubida (Hinds, 1845)	60	rocks, gravel, shell	inshore/offshore (to 183 m)	Rehder, 1981; Kozloff, 1983
C. hastata hastata (Sowerby, 1842)	64	rocks, gravel	inshore/offshore (5-150 m)	Rehder, 1981; Bourne, 1987
C. hastata hericius (Gould, 1850)	83	rocks, sand, mud	inshore/offshore (to 152 m)	Rehder, 1981
SOUTHWEST PACIFIC				
C. dichroa (Suter, 1909)	42	?	offshore (to 100 m)	Abbott and Dance, 1986; Powell, 1979
C. zelandiae (Gray, 1843)	30	undersides of rocks	inshore (to 30 m)	Abbott and Dance, 1986
C. gemmulata (Reeve, 1853)	30	?	inshore (to 30 m)	Abbott and Dance, 1986
C. kiwaensis (Powell, 1933)	33	?	inshore?/offshore	Powell, 1979
C. zeelandona (Hertlein, 1931)	35?	?	inshore	Powell, 1979
C. atkinos (Petterd, 1886)	38	?	inshore/offshore?	MacPherson and Gabriel, 1962
C. luculenta (Reeve, 1853)	40	?	offshore	Abbott and Dance, 1986
C. lentiginosa (Reeve, 1853)	40	coral reefs	inshore	Abbott and Dance, 1986
C. taiaroa (Powell, 1952)	43	?	inshore?/offshore	Powell, 1979
C. funebris (Reeve, 1853)	50	?	inshore?	Abbott and Dance, 1986
C. australis (Sowerby, 1847)	60	?	offshore	Abbott and Dance, 1986

Table 2. (continued)

	Shell Height (mm)	Habitat Substratum	Depth[2]	Source
C. scabricostata (Sowerby, 1915)	60	?	offshore	Abbott and Dance, 1986
C. squamosa (Gmelin, 1791)	60	?	inshore	Abbott and Dance, 1986
C. dieffenbachi (Reeve, 1853)	64	?	inshore/offshore (to 35 m)	Abbott and Dance, 1986; Powell, 1979
C. delicutula (Hutton, 1873)	70	gravel and shell	offshore (to 200 m)	Bull, in press
C. asperrimus (Lamarck, 1819)	100	muddy sand to sand[4]	inshore/offshore (to 100 m)	Young and Martin, 1989; R. McLoughlin, pers. comm.
C. bifrons (Lamarck, 1819)	150	sandy and coarse bottoms	inshore/offshore (to 100 m)	Young and Martin, 1989; R. McLoughlin, pers. comm.
C. consociata (E. A. Smith, 1915)	?	?	inshore/offshore (to 182 m)	Powell, 1979
NORTHWEST PACIFIC				
C. albida (Arnold, 1906)	?	?	offshore (to 200 m)	Bernard, 1983
C. princessae (Kuroda and Habe)	23?	sand, shell	offhsore (to 200 m)	Kuroda et al., 1971
C. asperulata (Adams and Reeve, 1850)	25	?	inshore (to 20 m)	Abbott and Dance, 1986
C. albolineata (Sowerby, 1887)	25	?	inshore	Abbott and Dance, 1986
C. empressae (Kuroda and Habe)	30?	sand, shell	offshore (to 200 m)	Kuroda et al., 1971
C. irregularis (Sowerby, 1842)	40	rocks, gravel	inshore/offshore (to 600 m)	Abbott and Dance, 1986; Kuroda et al., 1971
C. jousseaumei (Bavay, 1904)	40	fine sand	inshore/offshore	Abbott and Dance, 1986; Kuroda et al., 1971
C. larvata (Reeve, 1853)	40	?	offshore	Abbott and Dance, 1986
C. farreri nipponensis (Kuroda)	?	rock, gravel	inshore/offshore (to 60 m)	Kuroda et al., 1971
C. lemniscata (Reeve, 1853)	50	sand, shell	inshore/offshore (to 300 m)	Abbott and Dance, 1986; Kuroda et al., 1971
C. squamata (Gmelin, 1791)	75	rock, gravel	inshore/offshore (to 50 m)	Abbott and Dance, 1986; Kuroda et al., 1971
C. gloriosa (Reeve, 1852)	75	?	offshore	Abbott and Dance, 1986)
C. rosealbus (Scarlato)	90	silty-sand with pebbles, rocks (rarely sand, shells)	inshore/offshore (13-2030 m)	Silina and Pozdnyakova, 1990
C. nobilis (Reeve, 1852)	118?	rocks	inshore (to 20 m)	Kuroda et al., 1971
INDIAN OCEAN				
C. ruschenbergerii (Tyron, 1869)	75	?	offshore	Abbott and Dance, 1986
C. senatoria (Gmelin, 1791)	75	?	offshore	Abbott and Dance, 1986
C. townsendi (Sowerby, 1895)	150	?	inshore (to 20 m)	Abbott and Dance, 1986

[1]This is not a complete taxonomic listing. Bernard (1983) considers *Hinnites* to be a subgenus, however, because *Hinnites* spp. attach to the substrate by cementation rather than by a byssus this group has been excluded from analyses. In certain instances a species may occupy two geographic regions, however, in order to simplify the table the species is recorded for only one region. An exception was made in the case of *C. islandica*.

[2]Those species with maximum depth distributions of 30 m are considered inshore species. Note that this division is arbitrary and that not all deepwater occurrences are necessarily offshore.

[3]There is some debate over whether or not living *C. islandica* occurs in the eastern Pacific although it is reported to occur in the Arctic (Bernard, 1979; Lubinsky, 1980). Bernard (1979) considers *C. islandica* recorded from Point Barrow, Alaska (MacGinitie, 1959) to be *C. pseudislandica* while the more southerly occurring specimens from this collection he considers to be *C. rubida*.

[4]Although widespread on a variety of soft substrata, both juveniles and adults usually found attached by byssus to available solid objects, i.e. rocks, other bivalves, pier pilings (Young and Martin, 1989).

During the Paleozoic, bivalves were primarily restricted to nearshore habitats and it was largely after the Paleozoic that the bivalvia spread offshore to attain their present distributions, replacing the previously dominant articulate brachiopods (Stanley, 1972). From a survey of the habitats occupied by extant species within the genus *Chlamys*, it is seen that there is a high proportion (73%) of species with an offshore distribution, or at least ranging from shallow water to offshore depths (Table 2).

While there is limited ecological information on many of these species, particularly with respect to substrata associations, it would appear that members of the genus have radiated into a variety of habitat types. Substrata associations range from the undersides of shallow water boulders and coral reefs (e.g. subtropical and tropical species) to deepwater muds (e.g. *Chlamys septemradiata* Müller, 1776). Kauffman (1969) classifies byssate species of *Chlamys* as byssate fissure-dwellers. The typical habitats of this group are the under-

sides of rocks, crevices and fissures, reef tunnels, spaces inside root bundles of aquatic plants and similar niches with good water circulation, weak light and good protection from strong wave or current action. The occurrence of *C. septemradiata* on deep-water, flocculent muds (Allen, 1953) represents a unique substratum association within the genus. In fact, in this habitat, *C. septemradiata* serves as a stable settling surface for other sessile invertebrates which otherwise would be subjected to siltation.

Examining species-specific maximum sizes within the genus, it is seen that while most shallow water crevice species are small (< 60 mm), there are several very small (≤ 30 mm) species which are found distributed offshore to great depths (Table 2). The Iceland scallop is one of the largest species within the genus *Chlamys*, attaining a maximum size of about 100 mm in the Newfoundland regions although on the northeastern Grand Bank most scallops are between 60 and 80 mm in shell height (Naidu and Cahill, 1989).

The observed life habit orientation of *Chlamys islandica* on the northeastern Grand Banks is a fully exposed position. Because of the nature of the substratum (dense gravel, cobble), in most instances adult Iceland scallops must assume an epifaunal position on the exposed, upper surfaces of rocks. Only in the case of irregular occurrences of boulders would Iceland scallops be afforded the opportunity to assume a cryptic habit by attaching to the undersides. However, *C. islandica* could be compensated for this apparent lack of refuge through heavy biofouling by barnacles and soft corals in particular, which is often observed on the external surfaces of the upper valve (KDG, pers. obs.). While this may not decrease the risk of predation from chemosensory orienting predators (see Lake *et al.*, 1987), presumably it would be an advantage in the case of visually cueing predators, in particular, fish. Epizoic associations have been studied for several species. Epizoic sponge cover of the valves of *C. varia* (Linnaeus, 1758) and *C. asperrima* (Lamarck, 1819) is known to provide protection from predatory starfish (Forester, 1979; Chernoff, 1987; Pitcher and Butler, 1987). *Chlamys dieffenbachi* (Reeve, 1853) is almost invariably enveloped in living sponge (Powell, 1979) while *C. hastata* and *C. rubida* (Hinds, 1845) are regularly colonized by sponges that form thick coatings (Kozloff, 1983).

In summary, from the results of this study, and the observations of others, it would appear that *Chlamys islandica* is restricted to habitats with coarse substrata although this includes a range of sediment types from gravelly sand to gravel, cobble and shell mixtures. This would appear to be due to a requirement for byssus attachment at all life history stages. Within the genus, other species known to be byssally attached to substrates as adults include: *C. asperrima* (Young and Martin, 1989), *C. varia* (Rodhouse and Burnell, 1979), *C. irregularis* Sowerby, 1842, *C. squamata* Gmelin, 1791, *C. farreri* Jones and Preston, 1904 and *C. nobilis* Reeve, 1853

(Kuroda *et al.*, 1971). Frequency of byssal attachment to the substratum decreases with age in *C. tehuelcha* although the capacity to form a byssus is not lost in the largest individuals (Orensanz *et al.*, in press). While occupation of habitats with coarse substrata appears to be typical of members of the genus, there is at least one example *(C. septemradiata)* of radiation into a deepwater habitat characterized by flocculent muds, presumably with a consequential loss of byssus attachment.

ACKNOWLEDGMENTS

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