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BEACH CLAM FISHERIES

ANTON McLACHLAN,¹ JENIFER E.DUGAN,^{2,6} OMAR DEFEQ,³ ALAN D.ANSELL,⁴ DAVID M.HUBBARD,^{2,6} EDUARDO JARAMILLO⁵ & PABLO E.PENCHASZADEH⁷

¹Zoology Department, University of Port Elizabeth, PO Box 1600, Port Elizabeth 6000, South Africa.*

²Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106, USA.

³Instituto Nacional de Pesca, Constituyente 1497, Casilla de Correo 1612, 11200 Montevideo, Uruguay.

⁴Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, PO Box 3, Oban, Argyll, Scotland.

⁵Instituto Zoologia, Universidad Austral de Chile, Valdivia, Chile.

⁶Department of Marine Science, University of Otago, PO Box 56, Dunedin, New Zealand.

⁷INTECMAR, Universidad Simón Bolívar, Ap. 89000, Caracas 1080, Venezuela and Museo Argentino de Ciencias Naturales—CONICET, A. Gallardo 470, Buenos Aires, Argentina.

* Present address: College of Science, Sultan Qaboos University, PO Box 36, Al-Khod 123, Muscat, Sultanate of Oman.

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Abstract The biology, ecology, and fisheries of 15 species of clam from exposed ocean beaches are reviewed and contrasted. The species, representative of four families of bivalves, are *Tivela stultorum* and *Siliqua patula* from North America, *Tivela mactroides*, *Donax denticulatus* and *D. striatus* from the Caribbean, *Mesodesma mactroides* and *M. donacium* from southern South America, *Donax trunculus* from Europe, *D. serra* from southern Africa, *D. cuneatus* and *D. faba* from Asia, *Donax deltoides* from Australia, and *Paphies ventricosa*, *P. subtriangulata* and *P. donacina* from New Zealand. These clams tend to fall into two categories: generally larger temperate species that dominate the macrofauna community biomass on beaches of the dissipative type, and generally smaller tropical species, mostly donacids, found on reflective beaches. Some species have intertidal distributions, but most are centred in the swash zone or shallow subtidal. Vertical distribution appears to be related to latitude and temperature with lower temperatures leading to a more downshore distribution. Subtidal species are more difficult to exploit because of the protection afforded by high energy surf zones. All are filter feeders, playing important roles in the trophic structure of beaches. Most species have extended spawning, often with two peaks in the year. In many cases recruitment occurs in a different zone from the adult populations with subsequent migration up or downshore. Life spans range from 1–3yr for the smaller, warm water species to >20yr in the larger temperate species, but most species live for 2–8yr and have relatively rapid growth to maturity. Many populations exhibit resurgences—considerable fluctuations in abundance coupled to variable recruitment and/or mass mortalities. Exploitation of beach clams is sometimes constrained by the accumulation of toxins, such as those associated with blooms of toxic algae, that can render them unsafe for human consumption and may cause mass mortalities of the clams themselves. Many beach clam species support recreational, artisanal and commercial fisheries, but recreational fisheries are also mostly commercial and, with a few notable exceptions, most of the commercial fisheries are also artisanal. Recreational fisheries are notoriously difficult to manage since numbers of harvesters cannot usually be controlled and exploitation must be limited solely by recourse to size, bag and season and/or area restrictions. The recreational experience provided by clam fisheries on ocean beaches must be considered to be as valuable as the food value of the resource itself.

Introduction

Exposed sandy beaches dominate the ice-free shores of all continents and provide important recreational and commercial resources in many areas. Because the fauna of ocean beaches is cryptic and mobile it is easily overlooked and has tended to be neglected by ecologists. Nevertheless, many beaches, especially those of the dissipative type (Short & Wright 1983), support rich biotas of which clams are often an important component, especially in terms of biomass. On all continents at least one clam from exposed beaches is extensively collected as part of a recreational, artisanal or commercial fishery (Fig. 1). Large species from temperate areas are most often targeted, but there are exceptions.

For the purposes of this review we define a recreational fishery as collection for bait or food without sale or dependence on the resource; an artisanal fishery as collection for subsistence or sale by individuals or groups using traditional methods; and a commercial fishery as collection for sale by corporate or collective organizations. However, these distinctions are not precise; in many cases artisanal fisheries are also commercial (e.g. Chile, Uruguay) and recreational fisheries often also support commercial activities. Clam fishery catches, where available, are expressed as recorded landings. These are not generally based on stock size and they reflect a variety of influences, such as changes in market, economic and political climates, regulations, etc., and so must be interpreted with care.

The aim of this review is to summarize available information on beach clam fisheries, to contrast patterns in the biology, ecology and fisheries of the species involved in relation to beach type, geographical area and socioeconomic factors, and to assess the current status of clam fishery management on beaches that, in most cases, are also used for other recreational purposes. Fifteen species from exposed ocean beaches and surf zones are covered (Table 1, Fig. 2). All are heterodont eulamellibranchs except *Siliqua*, which is an adapedont. Not all potentially exploitable beach clams are included, only those species for which sufficient information is available to allow meaningful comparison. Even so, the 15 species have not been equally well studied; in some cases poorly researched species are included for comparison and because they are considered important in their region.

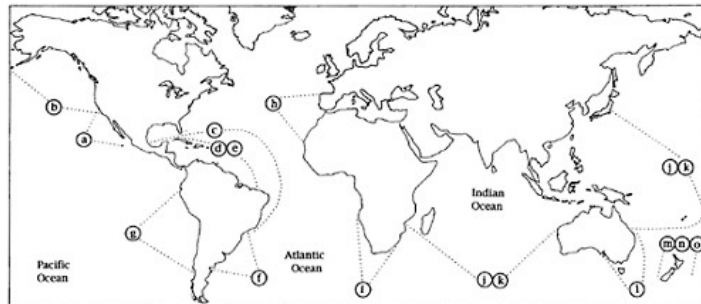


Figure 1 Geographical distribution of the species of beach clams considered in this review. North America: a, *Tivela stultorum*; b, *Siliqua patula*; Caribbean: c, *Tivela mactroides*; d, *Donax denticulatus*; e, *D. striatus*. South America: f, *Mesodesma mactroides*; g, *M. donacium*, Europe: h, *Donax trunculus*. Africa: i, *D. serra*; Asia: j, *D. cuneatus*; k, *D. faba*. Australia: l, *D. deltoides*. New Zealand: m, *Paphies ventricosa*; n, *P. subtriangulata*; o, *P. donacina*.

Table 1 Taxonomy and common names of the species dealt with in the text.

Geographical area	Species	Authority	Superfamily	Family	Common name
North America	<i>Tivela stultorum</i>	(Mawe)	Veneracea	Veneridae	Pismo clam
	<i>Siliqua patula</i>	(Dixon)	Solenacea	Solenidae	Pacific razor clam
Caribbean	<i>Tivela mactroides</i>	(Born)	Veneracea	Veneridae	guacuco (Venezuela);
	<i>Donax denticulatus</i>	(Linnaeus)	Tellinacea	Donacidae	beach clam (Jamaica)
	<i>Donax striatus</i>	Linnaeus	Tellinacea	Donacidae	chipi-chipi (Venezuela)
South America	<i>Mesodesma mactroides</i>	(Deshayes)	Maत्रacea	Mesodesmatidae	yellow clam
	<i>Mesodesma donacium</i>	(Lamarck)	Maत्रacea	Mesodesmatidae	macha
Europe	<i>Donax trunculus</i>	(Linnaeus)	Tellinacea	Donacidae	wedge clam
Africa	<i>Donax serra</i>	(Roding)	Tellinacea	Donacidae	white sand mussel
Asia	<i>Donax cuneatus</i>	(Linnaeus)	Tellinacea	Donacidae	
	<i>Donax faba</i>	(Gmelin)	Tellinacea	Donacidae	
Australia	<i>Donax deltoides</i>	Lamarck	Tellinacea	Donacidae	pipi, Goolwa cockle
New Zealand	<i>Paphies ventricosa</i>	(Gray)	Maत्रacea	Mesodesmatidae	toheroa
	<i>Paphies subtriangulata</i>	Wood	Maत्रacea	Mesodesmatidae	tuatua
	<i>Paphies donacina</i>	(Spengler)	Maत्रacea	Mesodesmatidae	tuatua

North America

Two species of beach-dwelling bivalves are harvested on beaches of the northeastern Pacific coast. These were among the largest beach clam fisheries in the world in terms of yield and also the most extensive in terms of shoreline length and latitude. No other beach clams are collected on any comparable scale in the USA.

The Pismo clam, Tivela stultorum (Fig. 2a)

Distribution

Tivela stultorum occurs on the Pacific coast of North America from Half Moon Bay, California to Isla Socorro in the Islas Revillagigedos, Mexico (Fitch 1950) (Fig. 1). Pismo clams can be rare to common on beaches in this range. The northern limit of the distribution of *T. stultorum* varies, expanding and contracting over time with episodic settlement events (Coe 1953). Populations of *T. stultorum* occur in a variety of sandy habitats including high intermediate to dissipative sandy beaches and the sandy entrance channels of bays, sloughs and estuaries (Shaw & Hassler 1989). *T. stultorum* can be found from the lower-mid to low intertidal and subtidally to depths of 25m (Shaw & Hassler 1989). The species is particularly prevalent in upwelling areas (Coe & Fitch 1950). In Monterey Bay, clams occurred on beaches with slopes of 1.1–4.6 degrees and not on those with steeper slopes (Nybakken & Stephenson 1975).

Biology and ecological role

T. stultorum is a broadcast spawner and fertilization is external (Coe 1947). The sexes are separate and similar in appearance, and hermaphrodites are rare (<1%) (Nybakken & Stephenson 1975). Males usually spawn first and the release of male gametes stimulates female spawning (Shaw & Hassler 1989). The reproductive cycle of *T. stultorum* is seasonal in Californian waters (Coe & Fitch 1950) and multiple spawnings may occur during a

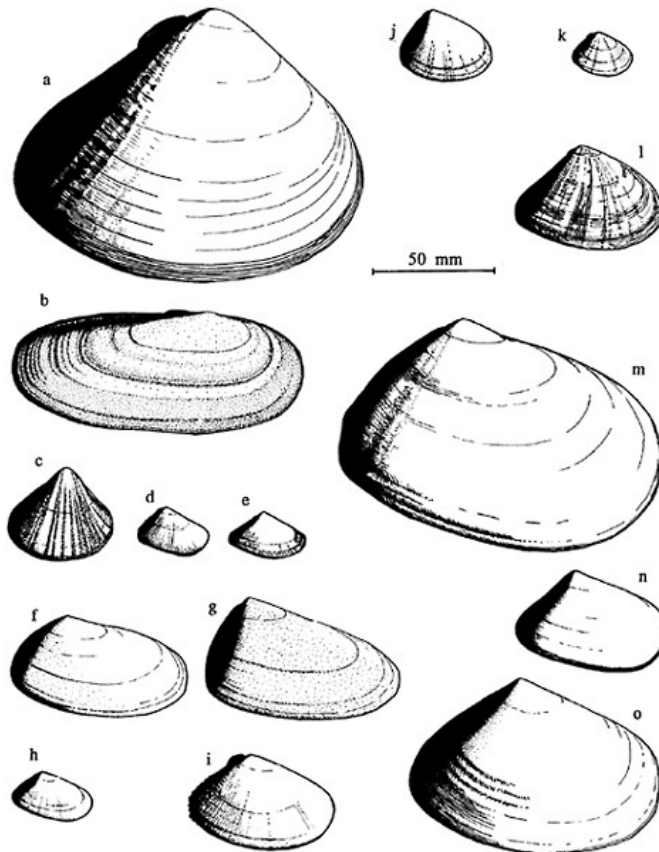


Figure 2 The species of beach clams covered in this review; key to species as in Figure 1.

season. Gametogenesis commences in March or April and ripe gametes are first evident in April and May. Spawning begins in late July or early August and continues through November (Coe 1947). Peak spawning occurs during September and October in Californian populations (Coe 1947, Nybakken & Stephenson 1975). The spawning season is extended in populations in Baja California (Coe & Fitch 1950). Fecundity increases with female size. In clams of legal size, 114mm or larger, fecundity ranges 11–20 million eggs and averages 15 million eggs per season (Coe 1953, Fitch 1950, 1961). The eggs are 74 to 81 μm diameter (Coe & Fitch 1950).

The larval biology of *T. stultorum* is not well known. Larval development is estimated to take 3 weeks (Coe 1947). Larvae reared in the laboratory are negatively buoyant (A. Hazeltine pers. comm) and it is suggested that they spend much of their larval life near the bottom, moving little in surface currents (Shaw & Hassler 1989). At metamorphosis and settlement the clam develops a foot and attaches to sand grains with a byssus (Shaw & Hassler 1989). As the clam grows the byssus disappears. Young clams occur in the mid to low intertidal zone of beaches. Settlement of *T. stultorum* has been observed in the intertidal, but it is not known whether settlement also occurs subtidally.

Pismo clams are suspension feeders, removing phytoplankton and detritus from the overlying water (Coe 1947). Because they have short siphons, feeding and undisturbed animals are buried close to the sand surface. The inhalant siphon has elaborate frills to reduce sand ingestion but the gut is often 50% full of sand (Fitch 1950).

T. stultorum is a bulky bivalve (114mm length, minimum legal size, weighs 350g live) with a large foot. Adult clams are not capable of much movement on the surface of the sand and have not been observed to migrate tidally (Fitch 1950), although small clams may be more mobile than large ones. The heavy shell appears to assist in burrowing and maintaining position in the sediments. Adult clams burrow to depths of 50–160 mm (Shaw & Hassler 1989). This species has been described as a slow burrower (Shaw & Hassler 1989) but, in a comparison of rates of burrowing in sandy-beach bivalves, the rate for *T. stultorum* was found to be intermediate relative to other species (McLachlan et al. 1995). A study of *T. stultorum* outplanted to intertidal and subtidal locations found animals planted subtidally occurred in subsequent intertidal surveys, indicating that subtidal animals moved into the intertidal zone (Dugan et al. 1995).

The shells of *T. stultorum* often carry a commensal hydroid, *Clytia bakeri*, and fishers may use the hydroid tufts to locate clams (Fitch 1950). A commensal pea crab, *Pinnixia* sp., occurs occasionally in the mantle cavity (Frey 1971). A larval cestode that matures in sting-rays and skates occurs in some clams and stops the sexual development of infected individuals (Warner & Katkansky 1969). Trematodes have been reported in some populations of clams (Coe & Fitch 1950). No diseases have been described in *T. stultorum* and incidents of mass mortalities are rare (Fitch 1950).

T. stultorum plays an important role in the filtering of large quantities of sea water and the conversion of surf zone primary production to secondary production. It is the dominant macrofauna species on some beaches, with high abundances and densities (>980 mature clams m⁻¹, Fitch 1950).

T. stultorum is an important prey item for a number of vertebrate and invertebrate predators and experiences considerable natural mortality at all ages. Skates, rays, surf fish, rock crabs, moon snails, gulls and sea otters prey upon *T. stultorum* (Miller et al. 1975, Haderlie & Abbott 1980). Most predation occurs at high tide with the exception of some of the gull predation. Moon snails, *Polinices lewisi*, drill the shells and prey on clams of up to 2yr (42–50mm) in age (Fitch 1950, Shaw & Hassler 1989). Rock crabs, *Cancer* sp., prey on clams up to 25mm in length by cracking the shell (Fitch 1950, Shaw & Hassler 1989). Gull predation on *T. stultorum* can be enhanced by the activities of human fishers that strand clams on the surface (Fitch 1950).

Some studies have implicated sea otter (*Enhydra lutris*) predation in recent (early 1970s) declines of pismo clam populations and fisheries in California (Stephenson 1977, Wendell et al. 1986). A sea otter was observed to eat 24 clams in 2.5h (Stephenson 1977). Wendell et al. (1986) estimated that one sea otter can consume 80 clams per day. In Monterey Bay, Miller et al. (1975) estimated that sea otters consumed 520000 to 700000 clams in a year.

Sea otters appear to feed primarily on clams that are 60mm in length or larger (Estes & Van Blaricom 1985). The average size of clam consumed by sea otters in Monterey Bay was 127mm (Nybakken & Stephenson 1975). Estes & Van Blaricom (1985) question the relative effects of sea otters on *Tivela stultorum* in the light of other influences on clam populations, including disturbance of clam beds by shellfish fishers, poaching, heavy motor vehicle traffic on clam bearing beaches, and the naturally high mortality of juvenile clams on certain beaches.

Population dynamics

Populations of *T. stultorum* have been extremely variable in time and space and were classed with those of *Donax gouldi* and other bivalves as resurgent by Coe (1953). This parallels the observation that settlement and recruitment of *Tivela stultorum* is extremely variable from year to year (Coe 1953). Existing data suggest that recruitment is independent of stock size (Tomlinson 1968). Detectable settlement events may occur once a decade or so and major settlement events occur episodically, at 18–28yr intervals, on California beaches (Estes & Van Blaricom 1985, Shaw & Hassler 1989). Recruitment of *T. stultorum* also varies significantly between beaches in any one region, e.g. Pismo Beach and Astascadero beach in the early 1970s (Wendell et al. 1986). As a result of the infrequent recruitment success and the long life of this species, populations of *T. stultorum* are often skewed towards large old animals. Fitch (1965) described a subtidal population where all but one clam was older than 13yr and only 2.5% were smaller than 118mm ($n=200$).

Tivela stultorum is a long-lived species, often living beyond 20yr and attaining sizes of 150mm or greater (Fitch 1950) (Table 2). The largest clam reported was 187mm long, weighed 1589g and was estimated to be 26yr old (Carriquiriborde et al. 1981). Gillilan (1964) estimated the age of one individual from Zuma beach, California to be 53yr. For the first 2 yr on the beach, pismo clams grow 21–25mm yr^{-1} (Coe & Fitch 1950). Growth rates decline with increasing age and 3 to 6-yr-old clams grow at rates of 10–18 mm yr^{-1} . Data

Table 2 Summary of key features of beach clam fisheries reviewed in the text. Under habitat I=intertidal, S= subtidal. Under fishery type A=artisanal, C=commercial, R=recreational and *=no longer operational. Lengths in mm and landings in tonnes live weight per year. $\Phi' = \log_{10}(K) + 2\log_{10}(L_{\infty})$ (approximate average values for each species are presented).

Species	Habitat	Length at maturity	Lifespan	Legal size	Max length	Fishery type	Maximum landings	Φ'
<i>Donax deltooides</i>	I & S	36	3.5	none/35	60	C & R	unknown	3.70
<i>Mesodesma mactroides</i>	I	43	3.5	50	85	A, C & R	1078 (1953)	3.71
<i>Mesodesma donacium</i>	S	50	15	50–60	100	A & C	18000 (1989)	3.74
<i>Tivela stultorum</i>	I & S	25	>20	114–127	187	R & C	24000(1945)	3.71
<i>Siliqua patula</i>	I & S	100	5–19	85–114	170	C & R	3600 (1915)	4.02
<i>Donax serra</i>	I & S	44	>5	58	80	R & C*	20 (1968)	3.57
<i>Donax trunculus</i>	I & S	8	1.5–>6	30 (Spain)	44	R & A	unknown	3.08
<i>Tivela mactroides</i>	I & S	20	1.5	–	35	C & R	354 (1992)	2.33
<i>Donax denticulatus</i>	I	10	1.5	–	23	A	226 (1990)	3.24
<i>Donax striatus</i>	I	10	1.5	–	35	A	unknown	3.15
<i>Donax cuneatus</i>	I	12	<3	–	23	A	unknown	2.55
<i>Donax faba</i>	I	10	<3	–	27	A	unknown	2.64
<i>Paphies ventricosa</i>	I	40	>10	100	160	R* & C*	185 (1940)	3.83
<i>Paphies subtriangulata</i>	I & S	unknown	>5	none	85	R & C	131 (1993)	3.30
<i>Paphies donacina</i>	I & S	unknown	17	none	109	R & C	5 (1992)	3.47

from Fitch (1950) allow an estimate to be made of the growth rate index ϕ^f values and pay less attention to individual values of K and L_∞ . Legal harvest size (114mm or 127mm) for *T. stultorum* is reached in 5–8yr in California (Coe & Fitch 1950).

Growth of *T. stultorum* varies seasonally and geographically, and slows markedly during the winter months (Coe & Fitch 1950) in California populations. However, slower winter growth was not observed in *T. stultorum* inhabiting beaches in Baja California (Searcy Bernal & Saavedra Rosas 1988). In general, faster growth of *T. stultorum* is observed in southern California populations than in northern California populations (Coe & Fitch 1950). Within a region, growth rate of clams can vary from beach to beach (Herrington 1929, Coe 1947, Coe & Fitch 1950). Pismo clams mature at shell lengths of 17–30mm (Coe 1947). Sexual maturation occurs during the first full summer in populations on southern California beaches but only during the second summer in populations near the northern limit of its range (Shaw & Hassler 1989).

The age and growth rates of *T. stultorum* are usually determined by examination of annuli or growth rings on the shell (Fitch 1950, Searcy Bernal et al. 1989, Shaw & Hassler 1989). These rings are usually formed in the fall or winter months in California and can be seen externally and internally in cross-sections of valves. External annuli are more easily distinguished on clams less than 5yr-old and become less distinct as growth slows (Fitch 1950). Searcy Bernal et al. (1989) suggest that analyses combining internal and external rings result in the most accurate age and growth rate determination in this species.

Sources of mortality other than predation for *T. stultorum* include natural events, fishing and pollution. Storm surf events can cause significant mortality in clam populations (Fitch 1950). Tomlinson (1968) estimated fishing mortality of *T. stultorum* of all ages as 0.8yr^{-1} . Occasional large mortalities, particularly of juvenile and young clams, have been attributed to heavy freshwater runoff, extreme cold and petroleum oiling (Fitch 1950).

Fishery

T. stultorum has been consumed and used by humans for thousands of years. The clams occur in middens of the coastal Chumash Indians, who used the shells as ornaments and tools (Frey 1971). Pismo clams are highly prized as delicacies in California but are not for sale in markets. In the USA, products of the now closed commercial fishery included fresh clams, canned clam meat and livestock food. The USA commercial fishery for *T. stultorum* lasted from 1916 to 1947 and occurred primarily at California beaches near Morro Bay, and at Pismo Beach, Oceano and Monterey Bay (Shaw & Hassler 1989). USA landings peaked in 1918 (302t) and declined thereafter despite management and restoration efforts (Fig. 3). Pismo clams were one of the most important commercial littoral invertebrate species in Baja California until the early 1980s (Searcy Bernal & Saavedra Rosas 1988). Between 1935 and 1947 up to $24000\text{t}\text{yr}^{-1}$ were imported to the USA from Mexico for canning to supplement declining California landings (Shaw & Hassler 1989). Shipping was discontinued in 1947

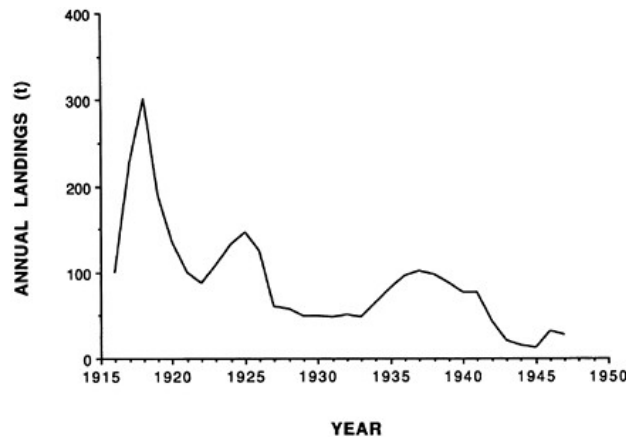


Figure 3 Commercial fishery landings of *Tivela stultorum* in California from 1916–47. (After Shaw & Hassler 1989).

due to high costs and the closure of the California fishery. Landings of *T. stultorum* in Baja California from 1977 and 1978 exceeded 1000yr^{-1} (Searcy Bernal 1983) and commercial harvesting continues in Baja California, Mexico, primarily at beaches near San Quintin.

The extent of recreational harvest of *T. stultorum* in Mexico is unknown. Recreational harvest occurs throughout the USA range of the species and affects both intertidal and subtidal populations. The total recreational landings for California are not known but thousands of people participate in clamming. Landings are variable and have declined in recent years despite some significant recruitment events. For example, in 1972 the largest settlement of *T. stultorum* in 30yr was observed at Atascadero Beach, California (Wendell et al. 1986) and landings did not increase.

To illustrate the pattern seen in many areas, recreational landings for Pismo Beach for 1975–83 are given in Figure 4. The decline in landings at Pismo Beach and other northern clamming areas seen in the 1970s and early 1980s were attributed to the expansion of the sea otter's range by some investigators (Miller et al. 1975, Stephenson 1977, Wendell et al. 1986). Southern California clam landings also declined precipitously in the early 1980s, this being attributed to catastrophic storms associated with the 1982–83 El Niño Southern Oscillation (ENSO) event (P. Haaker, California Dept of Fish and Game, pers. comm.). A series of good recruitment years in the late 1980s have revived the collapsed recreational fishery for *T. stultorum* on central and southern California beaches through the early 1990s (J.E. Dugan pers. obs.).

The failure of the commercial harvest in the USA and the high variability of the recreational harvest attest to the difficulty of sustainable management of *T. stultorum* fisheries with conventional approaches. Harvests of *T. stultorum* are apparently based on the strength of occasional, unpredictable strong year classes. Once a strong cohort or group of cohorts is fished down or affected by natural events or catastrophes, the harvest collapses until the next period of strong recruitment. Recreational landings from Pismo Beach vary considerably over time but illustrate that point (Fig. 4).

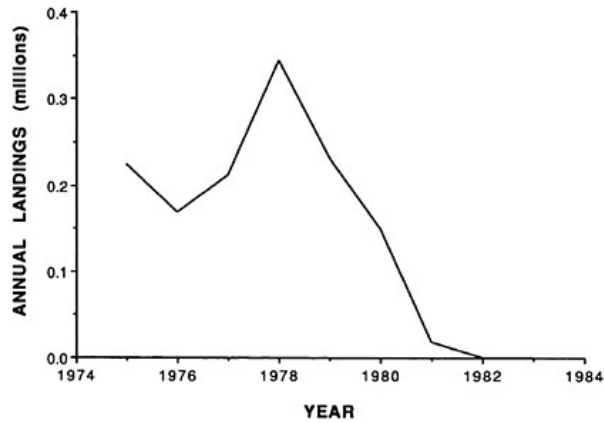


Figure 4 Recreational fishery landings of *Tivela stultorum* at Pismo Beach 1975–83. (After Wendell et al. 1986).

In California, early efforts to manage the fishery included bag limits, size limits, area closures and transplants of brood stock (Fitch 1950). The bag limit was reduced from 200 clams in 1911 to 50 clams in 1915, to 10 clams in 1948 (Fitch 1950). The minimum legal size is smaller in southern California (114mm for San Luis Obispo County and south) than in northern California (127mm for Monterey County and north) (Shaw & Hassler 1989) (Table 2, p. 168). Fishing gear is restricted to hand tools, e.g. a six-pronged potato fork, rakes, hands and feet. Divers locate siphons then excavate subtidal clams. None of these regulations have restored the *T. stultorum* fisheries to anything resembling the pre-1920 levels nor have they resulted in sustainable harvests.

The difficulty of controlling recreational harvest effort is well illustrated by the *T. stultorum* fishery in California. Anyone can purchase a clam fishing licence; therefore only season and area closures, and bag and size limits can be used to manage the fishery. Recreational fishing pressure can be great; for example, over 4million clams were removed in a 10-wk period from a 6.4-km stretch of beach (Frey 1971). On one weekend on Pismo Beach, an estimated 150000 clam diggers visited the beach and removed 341 of clams (Fitch 1950). Incidental mortality of undersized clams, which are often discarded on the surface and fall prey to gulls, desiccation and thermal stress, is a problem in this fishery (Shaw & Hassler 1989).

Although pismo clams can accumulate PSP (paralytic shellfish poisoning) toxins produced by blooms of certain dinoflagellates, no cases of human PSP poisoning were reported during the height of the fishery (Fitch 1950). Seasonal shellfish closures, known as quarantines, are imposed throughout California to prevent any human consumption of toxic shellfish during the summer season when toxin-producing phytoplankton blooms are known to occur.

A traditional fishery model (yield per recruit) developed by Tomlinson (1968) using unfished populations, suggested that the survival of *T. stultorum* increased with age. The current minimum size limit of 114mm in Southern California compared well with age at entry for maximum yield. Recruitment was independent of total mortalities in this model, which used an instantaneous fishing mortality of 0.8yr^{-1} for all ages but recognized that it was possibly an under-estimate of present fishing mortality.

The Pacific razor clam, Siliqua patula (Fig. 2b p. 166)

Distribution

S. patula occurs on the eastern Pacific coast of North America from Pismo Beach, California to the Aleutian Islands, Alaska (Lassuy & Simons 1989) (Fig. 1, p. 164). In British Columbia the clams are abundant only at Long Beach on the west coast of Vancouver Island, and near Masset on the northeastern coast of Graham Island (Queen Charlotte Islands). Populations of *S. patula* inhabit stable, open coast sand beaches, occurring primarily on fully exposed dissipative type beaches that are broad, flat, hard and composed of fine sand (Lassuy & Simons 1989). Large adult clams are densest in the low intertidal zone but subtidal populations can be substantial in some locations. Juvenile clams occur both intertidally and subtidally (Lassuy & Simons 1989). Adults are usually buried in the sand at depths of 300mm or more (McMillin 1924) and juveniles at about 50mm (Lassuy & Simons 1989).

Biology and ecological role

S. patula is a broadcast spawner and fertilization is external. The sexes are separate and the sex ratio of adult clams is 1:1 (Nickerson 1975). The eggs are *c.* 90µm in diameter (Breese & Robinson 1981) and are negatively buoyant (Weymouth et al. 1925). The peak spawning period varies geographically: in the late spring or early summer in Oregon and Washington (Lassuy & Simons 1989), and in August in Alaska (Weymouth et al. 1925). Some spawning may occur year-round and be related to food availability (Lassuy & Simons 1989). The initiation of spawning in *S. patula* may be related to water temperature, a rapid increase in water temperature, food availability, upwelling, the tidal cycle or some combination of those factors (e.g. Weymouth et al. 1925, Bourne & Quayle 1970, Nickerson 1975, Breese & Robinson 1981, Lassuy & Simons 1989).

The larval development of *S. patula* spans 5–16 wk at temperatures of 11–15°C, with the following stages: appearance of a veliger at 10 days, metamorphosis to a clam-like shape after 3wk, a distinct foot at 5wk, at 8wk loss of the velum and the shell becoming opaque, followed by settlement after 10wk (McMillin 1924). It has been suggested that razor clam larvae are negatively buoyant and spend much of their time in sand, thus limiting larval dispersal (McMillin 1924, Weymouth et al. 1925). However, recent observations indicate that the larvae are not negatively buoyant and do not occur primarily in the sand (D.Simons, pers. comm.). Settlement of *S. patula* can apparently occur intertidally and subtidally (Lassuy & Simons 1989). Large numbers of juvenile clams have been observed in both habitats (McMillin 1924, Rickard et al. 1986).

Adult razor clams are rapid burrowers, capable of vertical rates of movement of 230–305mm min⁻¹ (McMillin 1924, Lassuy & Simons 1989). *S. patula* displayed the highest burrowing rate index values of 12 species investigated by McLachlan et al. (1995). Adult razor clams show little lateral movement but juvenile clams are capable of some lateral movement (Bourne & Quayle 1970). The southern limits of *S. patula* distribution may be related to water temperatures and climate. In the laboratory, lethal temperatures for razor clams in sea water ranged from 27.5–22.5°C for exposure times of 1–4h, respectively (Sayce & Tufts (1971).

A commensal nemertean, *Malacobdella grossa*, 25–50mm in length, occurs inside the mantle cavity and siphon of *Siliqua patula* and a commensal pea crab, *Pinnixia* sp., is regularly found in the mantle cavity (Lassuy & Simons 1989). An infectious gill disease appeared in *Siliqua patula* populations in 1983, causing major mortalities and resulting in the closure

of the Washington fishery in 1984 and 1985 (Lassuy & Simons 1989). The disease was identified as nuclear inclusion X (NIX) by Elston (1986) and was unknown prior to that outbreak. It is caused by a prokaryotic, intranuclear bacterium that affects the gills, resulting in serious tissue damage to the gill epithelia and secondary bacterial infections (Elston 1986, Ayres & Simons 1994).

Pacific razor clams are filter feeders and can form a dominant component of the sand-beach community. Surf-zone phytoplankton, particularly the principal diatom involved in surf-zone blooms, *Chaetoceros armatum*, probably compose the bulk of the diet of *Siliqua patula* (Lewin et al. 1979a). Lewin et al. (1979b) suggest that dense populations of razor clams may play an important role in surf-zone nitrogen cycles through the excretion of ammonium. Juveniles and new recruits are consumed by birds (sandpipers, glaucous-winged gulls, surf scoters, ducks and crows), fish (English sole recruits, sturgeon and surf perches) and young Dungeness crabs (*Cancer magister*) (McMillin 1924, Tegelberg & Magoon 1969, Hogue & Carey 1982, Lassuy & Simons 1989). Sea otters, *Enhydra lutris*, prey upon adult clams throughout their range, particularly in Alaska (Estes & Van Blaricom 1985).

Population dynamics

Recruitment variability in populations of *Siliqua patula* may be related to currents and climatic events (Lassuy & Simons 1989). Populations of *S. patula* are somewhat resurgent (*sensu* Coe 1953) in the southernmost portion of the species range as a result of the high recruitment variability in that region. Juvenile clams have been observed to reach high densities ($>16000\text{m}^{-2}$) in the intertidal zone but generally occur in densities of $0\text{--}1076\text{m}^{-2}$ in the lower third of the intertidal zone (Lassuy & Simons 1989). A subtidal density of juvenile (1–15mm) razor clams of 38000m^{-2} was estimated in one study (Rickard et al. 1986).

Some workers have estimated the ages and growth rates of *S. patula* by counting the number of growth rings on the shell (Lassuy & Simons 1989). Each growth or check ring represents an annual ring or annulus, although the presence of other rings or checks formed during spawning or disturbance has also been noted (McMillin 1924, Weymouth & McMillin 1931, Hirschhorn 1962). The appearance and spacing of annuli can vary geographically in *S. patula*. Annuli in populations of razor clams in Alaska were more distinct, numerous and closely spaced, relative to those in Washington populations (McMillin 1924, Weymouth et al. 1925). Tegelberg (1964) suggested that the formation of distinct annuli in *S. patula* is dependent upon a period of slow growth in the winter, a phenomenon that may not occur in some populations. Growth rings or annuli are not considered reliable for use in age determination in razor clam populations in Washington State (D. Ayres pers. comm.).

S. patula is relatively long lived and has indeterminate growth. The growth rate, maximum length (120–170mm), maximum age (5–19yr), and population structure of *S. patula* vary geographically and with fishing pressure (Lassuy & Simons 1989) (Table 2, see p. 168). Growth rates are higher and maximum lengths, size at maturity and life spans are lower in southern populations (Lassuy & Simons 1989). For example, at Pismo Beach, California, at their southern distribution limit, razor clams grow to 127mm, live up to 5yr and have growth rates Φ' is lower (3.78) than in the southern population.

The growth of *S. patula* varies with tidal height; higher growth rates occur in clams living

near the low tide line and lower growth is found in those living higher on the beach (Tegelberg 1964, Bourne & Quayle 1970, Quayle & Bourne 1972). Growth rates of *S. patula* also vary seasonally; growth is usually slowest in the late fall and winter months and increases with the warmer water of spring (Weymouth et al. 1925, Hirschhorn 1962, Tegelberg 1964).

The age at maturity of *S. patula* varies geographically (Weymouth et al. 1925), ranging from 2–4yr and increasing with increasing latitude (Weymouth et al. 1931). At the southern end of the species' range, Pismo Beach, California, clams mature at 2yr. In Alaska, near the northern end of the species' range, clams mature at 3–4yr. In general, sexual maturity occurs at a shell lengths of c. 100mm (Lassuy & Simons 1989) (Table 2, p. 168).

Natural mortality of juvenile razor clams from predation by marine and terrestrial predators such as birds, fish, and crabs is high. Other significant sources of mortality to *S. patula*, especially younger clams, may include the scouring effects of winter storms, vehicle traffic on beaches, flood events and siltation (McMillin 1924, Tegelberg & Magoon 1969, Bourne & Quayle 1970, Nickerson 1975, Lassuy & Simons 1989). Natural mortality of adult clams is probably lower than that of juveniles. Sea otters prey on adult clams but their impact on populations has not been documented as it has on populations of *Tivela stultorum* in California (Wendell et al. 1986). McMillin (1924) estimated that the mortality of *Siliquapatula* was up to 99% in the first 8 months. Annual survival estimates increased with age, 9% for years one and two, 30% for years two and three, and 40% at greater ages (Nickerson 1975). Link (1980) found the opposite trend in his tagging study: highest survival (15.5%) occurred at age 0 with lowest survival (0.1%) in clams older than 3yr, but he had low returns of the latter.

Fishing is a significant source of mortality in populations of *S. patula*. Instantaneous mortality rates (Z) of *S. patula* in Oregon were estimated as 2.52yr^{-1} and 2.34yr^{-1} by Hirschhorn (1962) and Link (1980). Fishing mortality (F) was estimated as 1.78yr^{-1} and natural mortality (M), including wastage, as 0.74yr^{-1} by Hirschhorn (1962). Nickerson (1975) estimated M (not including wastage) as $0.33\text{--}0.50\text{yr}^{-1}$ for Alaskan populations of razor clams. Wastage of undersized clams is a significant source of fishery-associated mortality in *S. patula* populations (Lassuy & Simons 1989). Early studies estimated wastage to be equal to landings (McMillin 1924).

Epidemic levels of NIX disease resulted in significant mortality in *S. patula* populations, especially in Washington, in the early 1980s (Elston 1986). Disease-associated mortality rates of *S. patula* were dependent upon the prevalence and the intensity of NIX infection. The prevalence and the intensity of NIX infection in razor clams varied geographically and temporally, as did the mortality rates. Razor clam populations experienced 95% mortality in 1983–84 along the central coast of Washington where the prevalence of NIX was high (100% between June 1983 and June 1985) (Elston 1986). To the north and south of central Washington, the prevalence and intensity of NIX decreased. NIX was not observed in razor clams at the Queen Charlotte Islands or further north. A high prevalence of NIX was observed in razor clams on some Oregon beaches but the intensity of the infections was low and mortalities were not significant (Link 1986). LeClair & Phelps (1994) suggest that variation in the susceptibility of different populations to NIX may have a genetic basis. In Washington during 1987–93, NIX was widespread in razor clams, prevalence was high (c. 100%), intensity ranged from 2% to >40%, averaging about 20%, but no major mortality was detected (Ayres & Simons 1988, 1989, 1992). The intensities of NIX infection have generally increased over the last 10yr (Ayres & Simons 1994).

Fishery

Razor clams were harvested by native Americans and the shells are known from middens (Lassuy & Simons 1989). The modern fishery was initiated as early as 1894 in Oregon and spread north to Alaska (Nickerson 1975). By 1915, up to $3630\text{t}\text{yr}^{-1}$ were harvested commercially in Washington alone (Lassuy & Simons 1989). Size and season restrictions were imposed first on commercial harvest, recreational harvest being unrestricted until the 1920s, when restrictions on size, bag limits, and season were first imposed (Lassuy & Simons 1989). The fishery has shifted from commercial to recreational in Washington and Oregon and the recreational harvest now far exceeds the commercial harvest in the Pacific Northwest (Lassuy & Simons 1989). Up to 1940, 80% of Oregon take was commercial (Link 1980); after that time the recreational take increased. Commercial harvests of *S. patula* occur in Alaska, British Columbia, Washington and Oregon (Fig. 5) but not in California (Schink et al. 1983). Traditional fishery models for *S. patula* are not available in the literature.

In Alaska, commercial landings of razor clams exceeded 2200t in 1917, but have fluctuated considerably in subsequent years (Schink et al. 1983, Estes & Van Blaricom 1985). From 1960 to 1974, landings declined, ranging from a high of 210t in 1960 to a low of 5t in 1966 (Fig. 5). Annual landings averaged 134t for 1960–63, but after the earthquake in 1964, annual landings averaged 23t for the period through 1974 (Estes & Van Blaricom 1985). In recent years, most of the commercial harvest of razor clams comes from scattered locations on the Alaska Peninsula, Cook Inlet, Prince William Sound, Kodiak and the Copper River Delta. That harvest is used primarily as bait for the Dungeness crab fishery. The razor clam resources of Alaska are not fully utilized because of the distance from markets, supply fluctuations and shellfish toxin concerns.

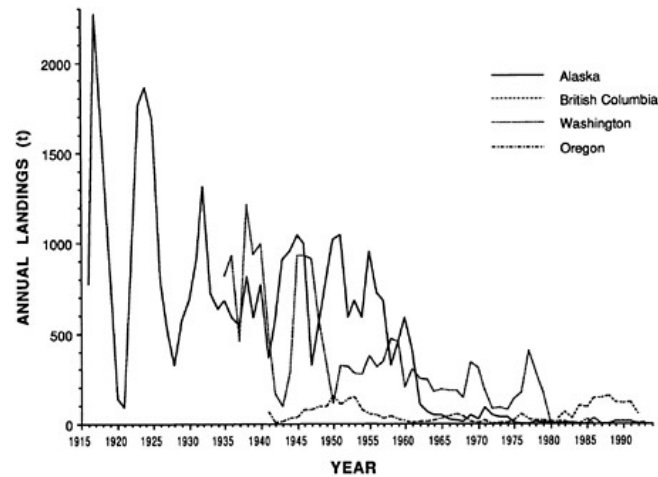


Figure 5 Commercial fishery landings of *Siliqua patula* in Alaska (1916–80), British Columbia (1981–92), Washington (1935–93) and Oregon (1942–86) (After Schink et al. 1983, Estes & Van Blaricom 1985, Lassuy & Simons 1989, Ayres & Simons 1992, 1994, Bourne pers. comm.). Landings for Alaska from 1975–80 are for Kodiak and Prince William Sound only. Landings for Washington from 1980–93 do not include the Quinault Indian Reservation.

In British Columbia, the commercial harvest of *S. patula* occurs only at Massett in the Queen Charlotte Islands (Estes & Van Blaricom 1985). Commercial harvest of razor clams began in 1924, producing canned clams, but the canneries shut down in the late 1960s and the commercial fishery harvest is now primarily used for Dungeness crab bait. Since 1970, commercial landings have ranged from 18–155t yr^{-1} (N.Bourne pers. comm., Estes & Van Blaricom 1985) (Fig. 5).

In Washington, commercial harvest of *S. patula* has fluctuated dramatically since 1915 and declined in recent years (Fig. 5). The commercial fishery is now relatively small and limited to beaches in the Willapa Spits in Willapa Bay and on the Quinalt Indian Reservation (Schink et al. 1983, Lassuy & Simons 1989). This is used primarily for Dungeness crab bait although some is sold for human consumption. Between 1950 and 1979 annual landings ranged from 77 to 467t (Schink et al. 1983, Lassuy & Simons 1989). Since 1980, off-reservation annual landings have not exceeded 35t and averaged less than 10t when the beaches were open for commercial harvesting (harvest figures from the Quinalt reservation are not available for that period). The annual value of the harvest to fishers has ranged from US\$4000 to US\$89000 since 1980 (Lassuy & Simons 1989). In Oregon, limited commercial harvest primarily occurs on beaches between the Tillamook Head and the Columbia River (Estes & Van Blaricom 1985). Most of the commercial harvest is marketed as fresh meat for human consumption. Annual commercial landings have declined since the mid 1950s and during recent years have fluctuated considerably, ranging from 45–55t (Estes & Van Blaricom 1985, Lassuy & Simons 1989). The mean annual landings for 1977–86 were 12t (142000 clams) with a mean total value of US\$35300. The highest harvest of that period occurred in 1985 and was 26t (303000 clams) with a value of US\$115000. The lowest harvest in that period occurred in 1983 and was 45kg (1000 clams) with a value of US\$100 (Lassuy & Simons 1989).

The market price of razor clams is generally high and stable (Lassuy & Simons 1989). Retail value of razor clams range from US\$2–5kg $^{-1}$ unshucked and up to US\$14kg $^{-1}$ shucked (Lassuy & Simons 1989). The wholesale value of commercial landings varies considerably between years and locations, ranging from US\$2–4.55kg $^{-1}$ (Lassuy & Simons 1989).

Recreational harvest of *S. patula* occurs throughout the species range but the intensity varies. Recreational harvest landings of *S. patula* are greatest on the Washington coast (Fig. 6). The recreational value of razor clams is high and the open season draws many participants, both resident and non-resident to clamming beaches (Lassuy & Simons 1989). Recreational harvest of razor clams may have considerable indirect value to coastal communities including increased revenue from housing and feeding of clammers during the season. Important sport harvest of razor clams occurs in the Clam Gulch area of the Kenai Peninsula and in Prince William sound in Alaska (Schink et al. 1983, Estes & Van Blaricom 1985). Annual landings are relatively low and did not exceed 900000 clams between 1969 and 1975 (Schink et al. 1983) (Fig. 6). Levels of recreational harvest are poorly documented in British Columbia. The major recreational harvest is at Long Beach on Vancouver Island.

The most intensive recreational harvest of *S. patula* occurs in Washington and landings fluctuate considerably. Between 1949 and 1976, landings ranged from 1.5–3.5 million clams (Ayres & Simons 1992). Between 1977–86, the average sport harvest was 6.4 million clams per year, the highest harvest during that period was 13 million clams, c.585t (1979) and the lowest when the fishery was open was 3.2 million clams (1986) (Lassuy & Simons 1989). The fishery was closed in 1984 and 1985 due to NIX disease. The fishery has recovered since then and, despite closure due to high levels of shellfish toxins, annual landings have averaged over 2.7 million clams since 1986 (Ayres & Simons 1988, 1989, 1992, 1994) (Fig. 6). Land-

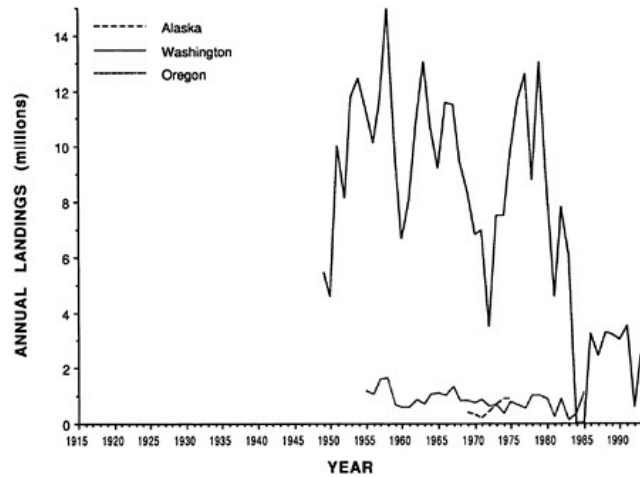


Figure 6 Recreational fishery landings of *Siliqua patula* in Alaska (1969–75), Washington (1949–93) and Oregon (1955–85). (After Schink et al. 1983, Lassuy & Simons 1989, Ayres & Simons 1992, 1994, Ayres pers. comm.).

ings for 1994 exceeded 4 million clams (D.L. Ayres pers. comm.).

A less intensive recreational harvest of Pacific razor clams occurs in Oregon where annual landings average less than 2 million clams (Schink et al. 1983) (Fig. 6). Recreational harvest between 1977–86 averaged 683000 clams per year, the highest harvest during that period being 1131000 (1985), the lowest 117000 (1982–83 ENSO event) (Lassuy & Simons 1989). In California recreational harvest of razor clams occurs primarily in the northern part of the state, between Humboldt Bay and the Smith River (Estes & Van Blaricom 1985). Recreational landings are small and the fishery is considered to be fairly stable (Schink et al. 1983).

Regulations concerning the harvest of *S. patula* vary between regions and between commercial and recreational harvest. In Alaska the commercial size limit is 114mm (Schink et al. 1983). In British Columbia the commercial fishery has a size limit of 85mm and no bag limit while the recreational fishery has no size limit and a bag limit of 12–75 clams (Bourne et al. 1987). The small recreational fisheries are not closely regulated in Alaska or British Columbia. In Oregon the commercial size limit is 95mm and seasonal closures are enforced (Schink et al. 1983) (Table 2, p. 168). The recreational fisheries in California and Oregon are controlled by regulations on bag limits, seasons and areas.

Both commercial and recreational seasons and landings of razor clams are regulated in Washington. The recreational and commercial seasons are staggered to prevent illegal sales of recreationally harvested razor clams as commercially-harvested clams (Ayres & Simons 1992). The recreational bag limit has been reduced from 36–24 to 18–15 clams of any size per digger in Washington (Ayres & Simons 1992). Commercial diggers have no bag limits. In the past, a commercial licence to harvest razor clams could be obtained for US\$5, but many recreational diggers bought commercial licences to avoid the recreational bag limits (Ayres & Simons 1992). Commercial licences now cost US\$130 to US\$185 and commercial

diggers must have a Washington State Health Permit, cost US\$250. The minimum size for commercial harvest is 114mm shell length and there is no minimum size limit for recreational fishers (Lassuy & Simons 1989). The autumn and spring harvest seasons are separate and season lengths vary between years and locations (Lassuy & Simons 1989). Closures of razor clam fisheries due to disease or shellfish toxin accumulation are frequent.

Recreational harvest with minimum size limits produces high associated mortality and wastage of improperly replanted undersized and injured razor clams (Schink et al. 1983, Lassuy & Simons 1989). In the Washington and Oregon recreational fisheries a regulation requiring that all razor clams must be kept, regardless of size or condition, has reduced the incidental mortality of undersized clams (Lassuy & Simons 1989). Wastage was high, up to 28% of the harvest in 1949, and has been reduced to levels of 5–10% (Lassuy & Simons 1989, Ayres & Simons 1992). Despite the new regulations, wastage continues to be a management concern in the razor clam fishery and has led to the implementation of emergency closures in some areas (Lassuy & Simons 1989). The primary gear used for recreational and commercial harvest of *S. patula* is a narrow-bladed shovel called a clam gun (Fig. 7); no motorized mechanical harvest is allowed (Lassuy & Simons 1989). Spring low tides are the best time for intertidal harvest so clamming seasons and enforcement efforts are concentrated around those tides.

In Washington, population assessments of *S. patula* using mark-recapture and stratified random digs are performed at each of the four major recreational clamming beaches three times per year (Ayres & Simons 1992). Abundance and size structure of populations are assessed before individual beaches are opened to harvest and these data are used to set the length of the season at each beach. Digger numbers, catch per unit effort, catch per mile of beach and estimates of wastage are made at each beach during the harvest seasons (Ayres & Simons 1992). The prevalence and intensity of NIX disease in razor clam populations was monitored periodically until 1993 (Ayres & Simons 1992, D.L.Ayres pers. comm.).

Accumulations of phytoplankton toxins in the tissues of razor clams have caused emergency fishery closures and affected fishery landings and economics throughout the range of the species. Pacific razor clams are tested regularly for the accumulation of toxins, such as PSP and, more recently, domoic acid in many areas. The commercial razor clam fishery has been closed by high PSP levels in Alaska on occasion (Orth et al. 1975) and high levels of PSP occurred in several razor clam populations in 1985 and 1987 (Richard Barrett, in Lassuy & Simons 1989). In 1984 high levels of PSP were observed in razor clams in Washington. However, the fishery was already closed due to NIX disease (Lassuy & Simons 1989). High PSP levels also caused fishery closures on some Washington beaches in fall 1992 and spring 1993 and led to reduced landings. In 1991 the standard PSP testing revealed domoic acid in razor clam tissue for the first time and the fishery was closed in Washington (Ayres & Simons 1992, Drum et al. 1993). The Washington razor clam fishery was also closed due to high domoic acid levels for all of 1992, parts of the fall of 1993 and the spring of 1994 (Ayres & Simons 1994, D.L.Ayres pers. comm.). Periodic closures of the razor clam fishery due to high levels of PSP and domoic acid have occurred in Oregon. Annual shellfish harvest closures, known as quarantines, occur throughout California to prevent human consumption of toxic shellfish during the season when toxin-producing phytoplankton blooms may occur.

A number of enhancement efforts have been made on the razor clam resource. Hatchery rearing and release of juvenile razor clams on clamming beaches occurred in Washington from 1980 to 1989 (Lassuy & Simons 1989). Juvenile razor clams were collected on beaches with high recruitment and transplanted to beaches with poor settlement in 1966–67 (Tegelberg & Magoon 1969). Rickard & Newman (1986) described collecting juvenile

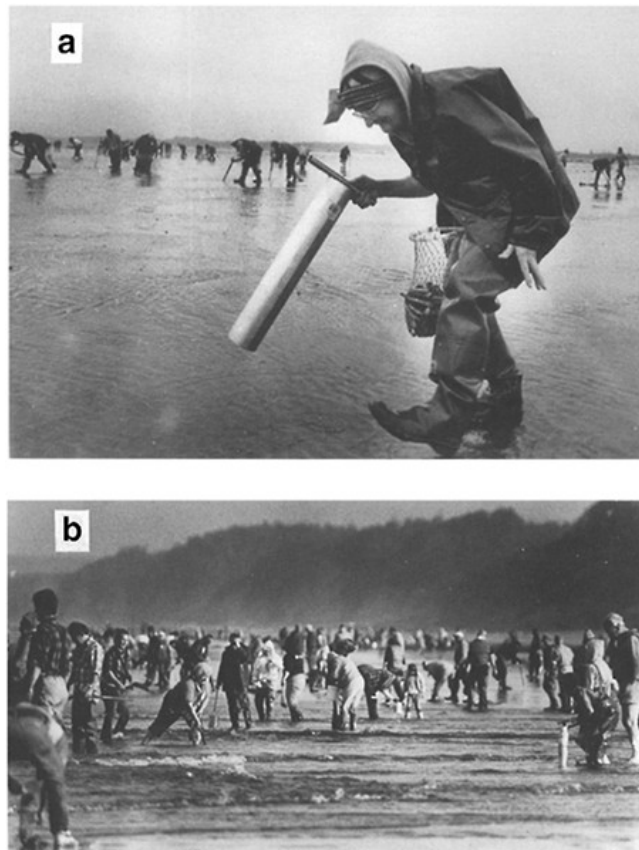


Figure 7 a, Collecting *Siliqua patula* with a “clam gun” in the Pacific Northwest; b, The recreational fishery for *S. patula* in the Pacific northwest where fishers number up to 1000 per mile of beach on spring low tides. (Photographs courtesy of the *Aberdeen Daily World*).

clams from the subtidal and transplanting them on to beaches to enhance the fishery. In 1985, 127 million juvenile razor clams were transplanted from the subtidal to the intertidal zones of beaches (D.L.Ayres pers. comm.).

The Caribbean

Several relatively small tropical species are collected in artisanal fisheries, based on intermediate to reflective beaches in this area.

The guacuco, Tivela mactroides (Fig. 2c, p. 166)

Distribution

T. mactroides is distributed on Caribbean and Atlantic coasts from Mexico to Brazil, including several islands of the West Indies (Fig. 1, p. 164), but it is in Venezuela where the species has a true commercial value and activity, as a result of the presence of very dense banks of clams in the upper subtidal of fine-grained sandy beaches. Rodriguez (1957) reported such banks for the Maracaibo area (Zulia); Rodriguez (1959), Etchevers (1976) and Prieto (1980b, 1983, 1987), for Margarita Island (Nueva Esparta) and Eastern Venezuela (Sucre); Brito (1984), Ruiz (1983) and Rincón (1986) for the Barlovento Region in Central Venezuela (Miranda); and Almeida (1974) for the beaches of Tucacas and Boca de Aroa (Falcon; Golfo Triste area). A number of reports indicate a very high abundance of this clam in the Golfo Triste area (Almeida 1974, de Mahieu 1984, de Mahieu & Gamba 1980, Penchaszadeh et al. 1979, 1983, Penchaszadeh 1983a, Penchaszadeh & Losada 1987). *T. mactroides* occurs in dense populations near the mouths of rivers, particularly where large amounts of particles of terrigenous origin are transported in suspension, or in areas where disturbance of the sediment carries large amounts of material into suspension. Ruiz (1983) reports mean grain size of the sediments from *T. mactroides* beaches of 0.145 and 0.195mm (fine sands).

There are probably geographical differences in vertical distribution of *T. mactroides* related to differences in the tidal regime; on the Atlantic coast of Brazil, *T. mactroides* (known locally as “sapinho” or “sapinhagu”) occurs in the intertidal (Narchi 1972) whereas in the Caribbean, the vertical distribution is predominantly subtidal, to depths of 3m. Here, however the influence of the small tidal range is insignificant when compared with wind-generated changes in nearshore sea level. Where it co-occurs on Caribbean beaches with *Donax denticulatus* and *D. striatus*, *Tivela mactroides* is found deepest in the sublittoral zone, *Donax denticulatus* most superficially and *D. striatus* intermediate and showing a small overlap with the other two species (Etchevers 1975).

Biology and ecological role

Tivela mactroides is dioecious. Sexual differentiation starts at a shell length of about 12mm and at 20mm length all individuals are sexually mature, with a 1:1 sex ratio (Brito 1984). Mature gametes are found throughout the year, and there may be many spawning episodes (Prieto 1983). At Playa Guiria, Sucre, Venezuela, the most intense periods of gonadal maturation were found to be from July–December and April (1974–5) while most spawning activity took place in October–November and January–February (1982–3) with a minor

spawning period also in April–May (Prieto 1987). There are monthly variations of the dry weight of the soft parts, mainly associated with reproductive activity; dry weight for a “standard animal” of 30mm shell length decreases between October–November and January–February, which are important spawning periods (Prieto 1980a). The larval development has not been investigated.

T. mactroides is a suspension feeder, and is often the dominant macrofaunal component of open sand beach communities. The morphological features associated with this habit have been described by Narchi (1972) and include adaptations of the siphons, ctenidia, labial palps and stomach that enable the clam to exclude sand particles and to cope with large amounts of material in suspension in the water drawn into the mantle cavity.

T. mactroides are eaten by a variety of predators. Prieto (1987) reported that, at Playa Guiria (Venezuela), juveniles are eaten by the polychaetes *Glycera* sp., *Lumbriconereis* and *Sthenelais boa*, and the hermit crab *Isocheles wurdemanni*, while adults are eaten by the gastropod *Natica cayenensis* and several fishes including *Cathorops spixi*, *Caranx hippos*, *Trachinotus carolinus* and *Menticirrhus martinicensis*. In surveys at Higuero beach, Central Venezuela in 1987, remains of *Tivela mactroides* were found in the stomachs of nine species of fishes; *Cathorops spixii*, *Trachinotus carolinus*, *Polydactylus virginius*, *Menticirrhus littoralis*, *Ophioscion punctatissimus*, *Umbrina coroides*, *Sphoeroides testudinalis*, *Eucinostomus* sp. and *Selenopsis* sp., reflecting the importance of this bivalve in the beach food chain (P.E.Penchaszadeh, A.D.Ansell, R.N.Gibson unpubl. obs.). Part of this predation involved non-lethal “grazing” as evidenced by the presence in the fish stomachs of the severed tips of siphons from the bivalve.

In the Caribbean, living *Tivela mactroides* shells are used as the substratum for attachment of their egg capsules by *Prunum prunum* (Gastropoda; Marginellidae) (Rincón 1986, Penchaszadeh & Rincón 1996). Similarly, on Atlantic beaches the living shells are used as a substratum for the attachment of the eggs of *Lintrricula auricularia* (Gastropoda; Olividae) (Narchi 1972). Narchi (1972) found large numbers of hydrozoan polyps, probably *Eugymnanthea cirrhifera*, attached to the labial palps, ctenidia and visceral mass.

Population dynamics

Populations of *Tivela mactroides* can reach high densities with a correspondingly high biomass. Prieto (1983) reported mean densities at Playa Guiria, of 788–1024 ind.m⁻² with a maximum biomass of 1229 gm⁻² shell free ww. Brito (1984) found maximum densities of 220 ind.m⁻² at Higuero, and 80 ind. m⁻² at Paparo. In Playa La Guardia (Margarita Island) the width of the bank of *T. mactroides*, as well as the density within the bank, has been found to vary throughout the year (Etchevers 1976). In general, the bank occupies a sublittoral strip, approximately 70m wide, stretching beyond the beach trough with maximum densities of *T. mactroides* in an intermediate fringe located between 20 to 45m from the shoreline. Total biomass (WW of whole animals with shells included) varied from 5.92 kgm⁻² in November to 12.24 kgm⁻² in April. Total production for 8.3km of beach was estimated as 3291t, of which some 10% was “non-commercial”, i.e. with shell height measuring less than 22mm. Prieto (1987) calculated the productivity for Playa Guiria as about 130.07 gCm⁻²yr⁻¹. At Playa Guiria, recruitment of *T. mactroides* (<8mm) occurred in November–December 1982 and January, March and June, 1983 (Prieto 1987). This population component also showed rapid growth (3.5mm month⁻¹) during the first months of life.

T. mactroides has a short life span and rapid growth in those populations that have been studied. The clams grow to a mean shell length of 25mm in 9 months at Higuero (Brito

1984) while at Playa Guiria they reach 30mm in 12 months, with a life span of 18 months (Prieto 1987). Growth may be described by the von Bertalanffy growth equation: for Higuerote, size frequencies analysis gave values of L_{∞} and K of 32 mm and 0.23yr^{-1} , respectively (Brito 1984), while for Playa Guiria L_{∞} was 36mm and $K=0.15\text{yr}^{-1}$ (Prieto 1987). Φ' values thus ranged between 2.28 and 2.38 (average=2.33: Table 2, p. 168).

Natural mortality is very high; it is common to see many dead and decaying large individuals in the upper surf zone causing the whole beach to smell. As a consequence of high natural mortality, the majority of the adult population is renewed annually, beginning in July. Using the Van Sickle method (Van Sickle 1977), Prieto (1987) calculated instantaneous total mortality rates (Z) of 1.56yr^{-1} (70% annual) for 1974–75 and 2.41yr^{-1} (91 % annual) for 1982–83. From surveys during 1982–83 of empty shells in which the ligament was still intact (indicating recent mortality), Prieto (1987) estimated an annual mortality of 55%.

Fishery

In common with many other edible molluscs inhabiting shallow waters, *T. mactroides* has been eaten since pre-Columbian times. Some cultures also used the shells for ornaments and trade. Nowadays, a popular dish in Venezuela is “crema de guacuco”, a kind of clam chowder made with *T. mactroides* meat. Harvesting of *T. mactroides* in Venezuela is both recreational and commercial but there are no reliable statistical records for either of these activities. Data collected by the Dirección de Control de Producción of the Servicio Autónomo de Recursos Pesqueros y Acuícolas (SARPA) for the last 10 years show a generally increasing harvest with a maximum in recorded landings of 3541 in 1992 (Fig. 8). These data almost certainly under-estimate the real production, but are the only available source of information.

Beach clams or chipi-chipi, *Donax denticulatus* and *D. striatus* (Fig. 2d, e, p. 166)

Distribution

D. denticulatus and *D. striatus* are distributed on Caribbean and western Atlantic shores from Cuba in the north to Brazil in the south (Wade 1967b, Abbott 1974, Rios 1975, among others) (Fig. 1, p. 164). Both are found in well sorted sand on open sea beaches exposed to wave action, but *D. denticulatus* occurs on more beaches and is generally more abundant (Wade 1967b), although *D. striatus* can dominate and reach high densities in some areas (Etchevers 1975, Farache 1980, De Mahieu 1984). On the beaches of Barlovento (Venezuela), for example, which are influenced by discharge from the River Tuy, *D. striatus* is by far the dominant *Donax* species, reaching a large size (P.E.Penchaszadeh unpubl. data). *D. striatus* is a very variable species in colour, shape, and sculpture of the shell and this has led to some taxonomic confusion in the past (Wade 1967b).

Caribbean beaches have only a small tidal range, seldom exceeding 0.5m, and the vertical distribution of beach clam populations is determined by the physical conditions at the water's edge. Etchevers (1975) reported that *D. striatus* occupies a belt between the upper beach with *D. denticulatus* and the subtidal *Tivela mactroides* population, but in other areas the distributions of the two *Donax* species may show more overlap, or coincide (Fluck 1906, Wade 1967b, De Mahieu 1984). For *D. denticulatus*, most of the population is distributed in the wash zone, with only a few individuals in the surf zone, and none in the spray zone.

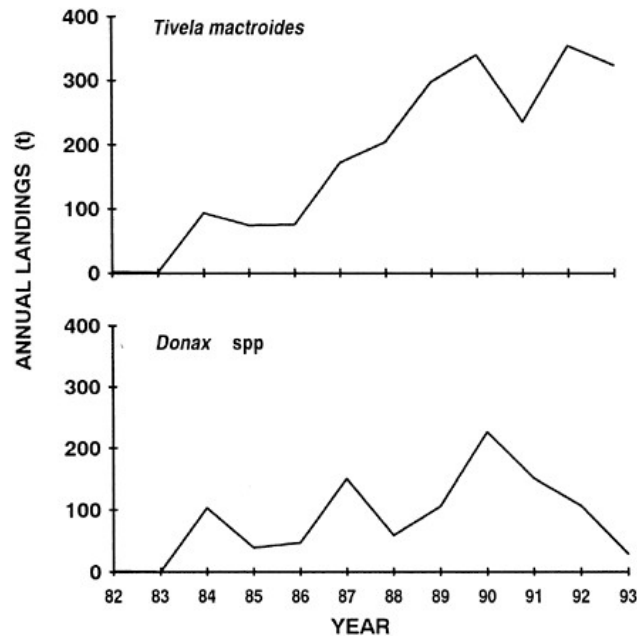


Figure 8 Fishery landings of *Tivela mactroides* and *Donax* spp. (*denticulatus* and *striatus*) from Venezuela (1982–93)

There is also a pronounced sorting by shell size in the wash zone with adults being confined almost entirely to the saturated zone, and only small individuals being found in the unsaturated zone. These distributions are maintained throughout the tidal cycle and during wind-generated changes in water height by tidal migration (Wade 1964, 1967a,b, Trueman 1971, Ansell & Trueman 1973).

Biology and ecological role

Both *D. denticulatus* and *D. striatus* are dioecious. For *D. denticulatus*, Velez (1985), studying a population on Araya beach, Venezuela, reported that approximately 3% of juveniles of shell length 7–9 mm showed signs of gametogenesis although it was difficult to determine the sex of individuals smaller than 11 mm. The number of sexually mature individuals increased progressively to the 17–19 mm group, in which 98% could be sexed. Juveniles and adults showed a 1:1 sex ratio. In this Venezuelan population, reproduction continued throughout the year although with some seasonal variation in the proportion of mature and spawning stages in the population. There was greater reproductive activity during July–December. For the populations of *D. denticulatus* he studied in Jamaica, Wade (1968) concluded that reproduction was seasonal, with ripe gonads being found mainly between August and January.

Wade (1968) found veliconcha stages of *D. denticulatus* in the plankton throughout the year in Jamaica, but they were especially abundant from November to January. Settled spat were found in every month over a period of nearly 2yr, but, nonetheless, a very well defined peak of settlement could be observed beginning in November. Similarly, Vélez (1985) reported monthly recruitment of *D. denticulatus* (of spat measuring 0.1 to 4.0mm) with minimum densities from January to June, and maximum densities from July to December. During this period there were peaks in September, October and December 1974, coinciding with observed gonadal changes. Wade (1968) reported that veliconchas of *D. denticulatus* taken from the plankton and reared in the laboratory lived for up to 3wk during which they sometimes doubled their size. He figured a late veliconcha of *D. denticulatus* but did not describe the larval development in detail.

Both *D. denticulatus* and *D. striatus* are important in the beach food chain as abundant primary consumers of phytoplankton and detritus. In turn these clams are eaten by a wide range of predators throughout the range of distribution. In the West Indies, Wade (1967a) lists portunid (*Araneus cribarius* and *Callinectes exasperatus*) and ocypodid (*Ocyopode albicans*) crabs, and birds (the sanderling *Crocethia alba*), as predators on *Donax denticulatus* together with the pig: "The pig's appetite for *Donax* is immense, and it seems that one pig in a day may devour more than what all other predators consume in one month". In Venezuela, *D. denticulatus* is eaten by a variety of fishes including *Menticirrhus littoralis*, *Conodon nobilis*, *Trachinotus carolinus*, *T. goodei* and *Umbrina coroides* (Penchaszadeh 1983b, Riera 1995, A.D.Ansell, R.N.Gibson & P.E.Penchaszadeh, unpubl. data), and by ghost crabs *Ocyopode quadrata* and the gastropods *Prunum prunum* and *Olivella verreauxi*. *Menticirrhus littoralis* and *Trachinotus carolinus* were found to have eaten both entire *Donax* and in some cases only the siphons.

Wade (1967a) recorded a low level of infestation of a bucephalid cercarian trematode *Cercaria caribbea* XLII in *Donax denticulatus* from Port Henderson and Green Bay, Jamaica. Parasitic castration had occurred in all the affected clams that appeared otherwise healthy. The shells of *D. denticulatus* are also used as a substratum for attachment by hydroids and algae (Wade 1967a).

Population dynamics

Population densities of *D. denticulatus* and *D. striatus* are variable both between locations and at different times at one site. For *D. denticulatus*, Wade (1967a) recorded densities ranging from 10 to 4120ind.m⁻¹ of beach on 22 beaches in the West Indies. At one site, Farquhar's Beach, Jamaica, the population density fell from 4120 to 360ind.m⁻¹ over an 18 month period. Recorded maximum population densities for *D. denticulatus* on beaches in Venezuela range up to 2150ind.m⁻² for populations consisting mainly of juveniles and up to 509ind.m⁻² for adults (Farache 1980, Penchaszadeh et al. 1983, Diaz et al. 1987, Pauls et al. 1990). Etchevers (1975) evaluated the biomass of *D. denticulatus* in Playa La Restinga, Margarita Island, Venezuela and estimated 14.2t (ww including shells) in 18km of beach.

For *D. striatus*, Wade (1967b) reported a density of 3000ind. m⁻¹ for a beach in Trinidad. In Venezuela, Farache (1980) reported a mean density of between 3.6 and 208ind.m⁻² with a maximum of 496 ind. m⁻² and De Mahieu (1984) found a maximum number of 1264ind.m⁻² at Tucacas beach, Venezuela, where Pauls et al. (1990) reported a maximum adult density of 198 ind.m⁻², and a juvenile density of 509ind.m⁻².

Age and growth for *D. denticulatus* were estimated by Velez et al. (1985) from size frequency distributions of clams collected from a beach of the Araya Peninsula, Venezuela.

A similar recruitment pattern occurred in both the years studied, 1974–75. Recruits, i.e. juveniles less than 4mm total length, appeared continuously through the year, but were most abundant between July and December. A distinct juvenile cohort (modal length 8–9mm) could be identified in June 1974 and remained clearly identifiable in the subsequent histograms for that year. August–September recruits first became noticeable in the juvenile size classes of the October–December 1974 histograms. By January 1975, the cohort of September 1974 recruits had become the dominant component in the population. Its decline by November 1975 to February 1976 suggested a life expectancy of only 13–16 months. Individual cohorts were less distinct in 1975–76 than in 1974–75 but in general, there was a dominance of juveniles from January through July and a dominance of adults from August through December. The rate of increase in total length was relatively high ($4.2 \text{ mm month}^{-1}$) during the first 2–3 month post recruitment. It fell to 1mm per month during the next 4 months and after 7 months appeared to be negligible. The mean maximum length did not exceed 19mm in this locality.

The von Bertalanffy growth equation calculated for this population of *D. denticulatus* (Vélez et al. 1985) was:

$$L_t = 18.5 (1 - e^{-0.43(t+0.058)})$$

where L_t is shell length in mm at time t in months and t_0 value (0.058) is the theoretical age when the mean clam had zero length. The maximum size reached by *D. denticulatus* in different populations varies greatly depending on conditions on different beaches. Wade (1967a) reported maximum sizes ranging from 12–23 mm for different populations in Jamaica.

Population densities for the population studied by Velez et al. (1985) ranged over approximately one order of magnitude during the 2 years of study, from 212 to 2435 ind.m^{-2} . Population density of individuals 4mm or less in shell length increased markedly from March to July principally from growth of recruits during November to December while mortality resulted in decrease in density of individuals of 4mm or more in shell length from August to November.

Estimated daily production ranged from 31 to 466 mgm^{-2} , with standing dry biomass values of 4 to 40 gm^{-2} . Integration of daily production over both years gave annual production estimates of 37.6 gm^{-2} and 77.4 gm^{-2} for 1974–75 and 1975–76 (equivalent to 181 and 372 kcalm^{-2}).

For *D. striatus*, Farache (1980), found two recruitments, one in March–April, and another in August, during a 9-month period of sampling at Tucacas and surrounding beaches in Venezuela. The growth rate at these beaches was very rapid during the first months after the recruitment, the clams reaching 50% of their asymptotic size in 2½ months, 66% in 4 months and 90% in 8 months. The mean monthly growth rate was 2.04mm. The von Bertalanffy growth curve for *D. striatus* at Tucacas (where La =the distance from the umbo to the end of the anterior part of the shell) was:

$$La = 20.2 (1 - e^{-0.286 (t-0.30)})$$

As with *D. denticulatus*, the maximum size reached by *D. striatus* varies greatly between areas and at different beaches in the same area (Wade 1967b). The maximum size of clams in the population studied by Farache (1980) was relatively small.

Fishery

The official statistics of landings of *Donax* in Venezuela probably greatly under-estimate the catches and do not discriminate between *D. denticulatus* and *D. striatus*. Adult individuals of *D. striatus* generally reach a larger size, however, and consequently this is the preferred marketable species. Data on landings (expressed as kg weight including shell) for the 12 years 1982–93 are given in Figure 8 (p. 183). Recorded landings have been variable with a maximum of 226t in 1990.

Additional studies of *D. denticulatus* and *D. striatus* are necessary to provide information on geographic and among-year variation in density, growth and production, and the effect of exploitation. At this time insufficient data are available for long-term fishery management decisions. Specifically, stock recruitment assessments would help to determine the susceptibility of the *Donax* populations to over-exploitation. Based on the results of Vélez et al. (1985) and Vélez (1985), however, there is the possibility that population stability could be sensitive to fishery exploitation of commercial-size individuals during the peak period of reproduction. Thus, Vélez et al. (1985) recommended that fishing should be limited to the period November–April in Venezuela.

Southern South America

A number of sandy-beach bivalves are exploited through recreational, artisanal and commercial fisheries on both the Atlantic and Pacific coasts of South America. Only the two most important species are covered here.

The yellow clam, Mesodesma mactroides (Fig. 2f, p. 166)

Distribution

M. mactroides is an intertidal bivalve distributed along the warm-temperate Atlantic coast of South America, from Sao Paulo State, Brazil (24°S) to the south of the Buenos Aires Province, Argentina (41°S; Fig. 1, p. 164). This range includes hundreds of kilometres of sandy beaches in Brazil, 22km in Uruguay and beaches of the Buenos Aires Province in Argentina (Olivier & Penchaszadeh 1968a). This review is based mainly on the yellow clam population in Uruguay, which has been the most extensively studied.

Yellow clam populations prosper primarily in the intertidal zone of dissipative beaches (*sensu* Short & Wright 1983) characterized by gentle slope, fine sand and heavy wave action (Olivier et al. 1971, Defeo 1985a, Defeo et al. 1986). A decrease in clam abundance is frequently observed near estuarine zones or freshwater discharges (Defeo et al. 1986) and on sheltered beaches (Defeo et al. 1992a). The beach that *M. mactroides* inhabits in Uruguay is microtidal dissipative (slopes 3/100, fine to very fine sands) with high wave energy and a wide surf zone. It is characterized by high primary production by surf diatoms (Defeo & Scarabino 1990) that allows the beach and surf zone to function as a semi-closed ecosystem (*sensu* McLachlan 1980).

M. mactroides presents a marked longshore distribution in the 22-km beach; abundance is highest in the central zone and declines towards both ends. Freshwater inflows, coarser and poorly sorted sands (negatively skewed and high kurtosis values), the dominance of erosional

processes, and a selective winnowing of fine sediments, contribute to a reduction of the stock towards the ends of the beach (Defeo 1993a). Salinity is positively correlated with clam abundance, largely explaining the alongshore distributional pattern.

The intertidal and vertical distribution of *M. mactroides* varies seasonally (Coscarón 1959, Olivier et al. 1971, Defeo et al. 1986). In winter, adults (ages 1–4) are found 30–40cm deep in the sediments and below the swash zone, while in summer they are located close to the sand surface and almost exclusively above the swash zone. In spring and autumn, intermediate situations are commonly observed. Water temperature and correlated factors (e.g. chlorophyll concentration, gonadal development) appear to be important in determining the intertidal distribution and depth stratification of *M. mactroides* adults. Recruits are mainly concentrated at upper intertidal levels (Defeo 1985a, Defeo et al. 1986). These spatial gradients for recruits and adults suggest a differential capability of each population component to select the desirable microhabitat. Whereas recruits appear to be more dependent on passive transport (waves, tides), seasonal variability in the zonation of adults may be the result of an active process which involves a certain level of mobility and a complex set of behavioural adaptations (e.g. burial depth with an anchoring system; see Narchi 1981) to variations in environmental factors such as temperature, sand desiccation and food availability (Olivier et al. 1971, Defeo 1993a).

Temporal variations in the mean clam bed width (CBW) can be explained for adults and recruits by an asymptotic function of density (Defeo 1993a). Asymptotic values of the mean CBW were close to 13m. Oliver et al. (1971) also mention a clam bed width ranging from 4m to greater than 20m, depending on the beach face slope. Distribution is aggregated and patch characteristics show a clear trend toward ellipses, with the major axis parallel to the shore (Defeo et al. 1986, Defeo 1993a). Within each patch, a concentric gradient may arise from (a) passive transport and sorting by the swash (e.g. recruits), (b) similar reactions to environmental factors, and (c) active selection of a suitable microhabitat to avoid predators or to search for localized food concentrations (e.g. adults).

Distinct aggregation of all ages occurs throughout the year. Results obtained from the analysis of the variance: mean ratio (even within a year) showed the capacity of *M. mactroides* to develop high densities. The patchy distribution among recruits and the inverse relationship between individual size and density (Defeo 1993a), suggest that the clams tend to space themselves as a function of an increasing area of influence needed for filtering activities (see also Hall 1983).

Biology and ecological role

A 1:1 sex ratio and two spawning periods were observed for Uruguayan (Defeo 1985b, Masello 1987) and Argentinian populations (Olivier et al. 1971): one between October and December and a second one from February to April (late summer). Sexually ripe individuals of 2–4 yr are responsible for the former, while newly mature individuals of age 1 (from 40mm to 45mm) spawn in late summer (Masello 1987). Gonadal development is controlled by temperature, with spawning taking place when the temperature is close to 20°C. *M. mactroides* has a high fecundity, producing about 5.3 million eggs per female. The mean size at first maturity is 43 mm (age 1; Masello & Defeo 1986). Settlement occurs in the intertidal zone from January to May.

M. mactroides has been commonly described as a suspension feeder (Olivier et al. 1971, Narchi 1981, Gianuca 1983, Defeo 1985a). Diatoms such as *Asterionella glacialis*, the basic food source (Gianuca 1983; Defeo 1985a), *Skeletonema costatum*, *Thalassionema nitzschoides* and *Coscinodiscus* spp. constitute the bulk of the stomach contents. Laboratory and field observations (Defeo & Scarabino 1990) showed that it also has a deposit-feeding mechanism.

Some special features of the adaptive morphology of the species (Narchi 1981), attributed to an adaptive divergence of the superfamily Mactracea (Stanley 1970), could support the deposit-feeding habit (Defeo & Scarabino 1990).

Mesodesma mactroides is the dominant suspension feeder in the intertidal macrofauna assemblages of dissipative sandy beaches in Uruguay (Defeo et al. 1992a), Brazil (Gianuca 1983) and Argentina (Olivier et al. 1971). Another potentially exploitable bivalve, the wedge clam *Donax hanleyanus* (Philippi), is sympatric and subdominant to *Mesodesma mactroides* in those beaches (see also de Alava 1993). *Donax hanleyanus* is numerically dominant on the reflective beaches with coarse sediments and sharp slopes along the Atlantic coast of South America, from the state of Espiritu Santo (Brazil) (Narchi 1978) to Punta Mogotes, Buenos Aires Province (Argentina) (Penchaszadeh & Olivier 1975). This intertidal filter feeder has a maximum adult size of 35mm, and rarely lives for more than 3yr (Penchaszadeh & Olivier 1975).

Competition between *Mesodesma mactroides* and *Donax hanleyanus* has been indicated by a long-term study in Uruguay (de Alava 1993, Defeo & de Alava 1995). Spatio-temporal variations in recruitment success and population levels of *D. hanleyanus* were inversely correlated with the magnitude of fishing effort exerted on *Mesodesma mactroides*. This human impact caused a reduction of *M. mactroides* stock and a consequent release of space that enhanced recruitment of *Donax hanleyanus*. Thus, even though *Mesodesma mactroides* is a suspension feeder, it may be a keystone species in the sense that fluctuations in its magnitude can generate cascade effects affecting the structure and abundance of the sympatric species.

The main predators of *M. mactroides* are the gastropods *Olivancillaria vesica auricularia* and *Buccinanops duartei*, fishes like *Micropogonias furnieri*, *Paralichthys brasiliensis*, *Mustelus schmitti* and others of the genera *Raja* and *Psammobatis*, and birds such as the oystercatcher *Haematopus ostralegus* and *Rinchoris nigra* (Olivier et al. 1971). The large cirrolanid isopod *Excirrolana armata* has been observed feeding on damaged, stranded or unburied clams.

Population dynamics

The yellow clam population in Uruguay displays temporal “stock-dependent recruitment” (*sensu* Hilborn & Walters 1992). A significant over-compensatory relationship between spawning stock and recruitment of *Mesodesma mactroides* was modelled for the first time in an exposed sandy beach population by Defeo (1993a). Two definite trends emerged: (a) larger adult densities produced extremely low recruitment and (b) maximum recruitment densities occurred from moderately low and medium sizes of spawning stock. The proposed mechanism of pre-settlement, density-dependent mortality is the filtering of larvae out of the water column by the adult stock.

The relation between stock and recruitment varies with the scale: even though over-compensation exists at a macroscale, transect and site analyses show a consistent pattern of alongshore distribution common to adults and recruits: the central portion of the habitat is more densely populated than the margins, whereas zones with low adult density receive fewer recruits. Higher mortalities before and after settlement because of adverse environmental effects (i.e. lower salinities), could account for this variability. At a quadrat scale, high densities of recruits never coincided with high densities of older clams. Recruitment success appears to be highly inhibited in quadrats with high density and biomass of adults. The recognition of a certain maximum width of the clam bed suggests a limitation of avail-

able space at an adult density close to 120m^{-2} . This value is consistent with those suggested by the spatio-temporal analysis of the stock-recruitment relationship (Defeo 1993a).

The yellow clam is a fast-growing ($K \sim 0.8$; $\phi' = 3.71$), short-lived species (Table 2, p. 168). Maximum observed length ranged from 78mm (Uruguay) to 80–85 mm (Argentina: Carcelles 1939, Olivier et al. 1971). Growth parameters have been estimated by methods that use age or length data in Uruguay. Age structure, determined by the interpretation of growth rings and by shell sectioning techniques, suggests a life span of ≈ 3.5 yr (Table 2). Rings of different periodicity are identified: “winter rings”, formed during late fall and winter, coinciding with the period of null growth determined by length-frequency analysis; and secondary rings during the main period of gamete production, considered as “reproductive rings” (Defeo et al. 1988a). Growth rates are higher during the summer season, dropping between fall and winter, and increasing from September (austral spring) (Defeo et al. 1992b). A 14°C difference between minimum and maximum mean monthly values of temperature in the study area (de Alava & Defeo 1991) accounts for the seasonal variation in growth rates. Density-dependent growth rates were demonstrated in a long-term study (Defeo 1993a).

Olivier et al. (1971) did not report seasonal variations in growth for clams in Argentina, but estimated lower growth rates (i.e. $K \approx 0.25\text{--}0.29\text{yr}^{-1}$) and greater longevity (≈ 8 yr) than for studies in Uruguay (Defeo 1993a). The lack of seasonality was probably due to the growth model employed (von Bertalanffy 1938), whereas lower growth rates could be attributed to the assumption of annual periodicity in the formation of rings (without this being corroborated by any other method). However, differences in growth rates may be a response to dissimilar environmental characteristics. Defeo (1993a) reported lower sizes at marginal, less favourable sites, with a virtual absence of clams of 40mm length. Considering these effects over 22km, growth rate differences within the geographical range of the species are likely.

Estimates of the instantaneous rate of total mortality (Z) were obtained by means of catch curves drawn according to the age-length key, and had values of 1.81yr^{-1} and 2.55yr^{-1} for 1983 and 1984, respectively. From age 2 on, the clams were fully available to the catch (Defeo et al. 1992b). The increase in Z for 1984 could be attributed to an increase in density-dependent natural mortality (i.e. greater densities for the 1984 cohort), or fishing pressure or both. However, a high variability in mortality rates among years implies that the above values must be treated with caution (see below).

The instantaneous rate of natural mortality (M) varied. For the closed fishing season 1988–90 an M value of 1.64yr^{-1} was obtained from changes in abundance of the cohort over time. Based on the unexploited fraction of the population (1–50mm) for years 1983 to 1987 and 1990, when the fishery was open, M ranged from 0.90yr^{-1} (1990) to 3.17yr^{-1} (1985). M was highest in the densest cohorts, which also exhibited lowest growth rates under intense fishing pressure (Defeo 1993a). M also varied spatially, according to the quality of the site, the extent of adult-recruit interactions and the heterogeneous allocation of fishing effort. A long-term study between 1983 and 1990 detected potential incidental mortality in the young-of-the-year, produced by damage and sediment disturbance during harvesting activities: M was significant and positively correlated with the amount of fishing effort and catches observed per fishing ground (Defeo 1993b). Fishing mortality values ranging from 0.62yr^{-1} for 1983 to 1.27yr^{-1} for 1984 were obtained by subtracting M from Z . A cohort analysis was useful to determine the extent of fishing mortality per age group (Defeo et al. 1988b).

Fishery

Information on the *M. mactroides* fishery in Brazil is scarce, and it can be considered an open-access system. The yellow clam can almost disappear at the end of each summer season around every important seaside resort, where it is consumed as food and utilized as bait (Gianuca 1983). In Argentina, exploitation of *M. mactroides* has been carried out since the 1940s, concurrently with the development of the canning industry (Olivier et al. 1971). Landings peaked in 1953 at 1078t, then declined; a total closure of the fishery has been implemented since 1958 (Olivier & Penchaszadeh 1968b). To date, even with the fishery closed, the stock has diminished due to illegal extraction, including that associated with summer tourist activity (Bastida et al. 1991).

In Uruguay, the yellow clam constitutes an important artisanal fishery. The clams are collected by hand-gathering techniques and marketed either for bait or human consumption, mainly during the summer months and in the seaside resorts. Prices paid to fishers range US\$0.5–1kg⁻¹, and market value for consumers is near US\$5kg⁻¹ (including valves). The enhanced demand for the clams caused a fast growth in landings during the 1980s, ranging from 62t in 1981 to a peak of 219t in 1985 (Fig. 9). Thereafter landings decreased rapidly. A temporal closure of the fishery was imposed between April 1987 and December 1989.

An overall catch quota, the first management measure implemented, was unsuccessful; rapid collection and stockpiling of organisms meant that the catch quota was quickly reached, leading to a deterioration in the product. A minimum profitable catch volume per fisher, differential fishing quotas per season and rotation of areas were therefore recommended as tools for the management of the fishery (Defeo 1989). For the implementation of such strategies, habitat heterogeneity, which accounts for spatial and temporal variations in resource abundance and in the fishing effort exerted, was considered. A minimum legal size of 50mm (\approx 1.5yr) for commercial harvest, based on the length at first maturity, is also used as a regulatory measure (Defeo 1987).

Management of the Uruguayan stock was improved through experimental procedures that included natural repopulation of depleted areas, rotation of areas and the allocation of indi-

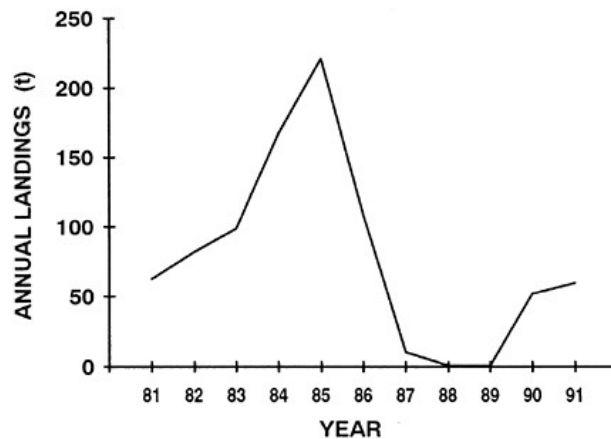


Figure 9 Time series of *Mesodesma mactroides* landings, 1981–91. (After Defeo et al. 1993).

vidual quotas per fisher through a catch per month per fisher. This number was determined as the ratio between the net value of the overall quota and twice the annual minimum salary (Defeo 1993b). To implement the spatial management plan, fishing grounds with lower productivity were used as exploitation units when demand for clams was low (i.e. austral autumn and winter), whereas the central sections, with highest stock and recruitment densities, were used in spring and summer (Defeo et al. 1991). This period maximizes the biomass of the cohort available for harvesting (Defeo et al. 1992b). Rotation of fishing areas also maintains space and a certain level of adult density to enable recruitment success at desirable levels.

The wide range of levels of fishing effort achieved by experimental management provided a range of variability in the spawning stock size, and allowed determination of population patterns and processes that were obscure before closure, for example the exact shape of the recruitment curve. The spatially disaggregated analysis of the resource and the fishery constituted a useful approach in interpreting the behaviour of this exposed sandy-beach population (Defeo 1993a). Results of the long-term study in Uruguay demonstrated that quantitative models developed for exploited populations from sandy beaches must take into account density-dependent, or area-specific variations in growth, recruitment and fishing and natural mortality (Defeo et al. 1993).

Simulation of alternative management strategies (Defeo 1993a) suggested that, if the population is closed to fishing activities for a long period, high adult density could inhibit recruitment success and hence the magnitude of the stock available for fishing. However, a closed season of 2 years could promote successful recruitment in the short term, and an increase in population growth above that observed under an exploited scenario. Fishing pressure acts as a source of disturbance, but also as a way of releasing space, thus enabling the recolonization of disturbed patches. Harvesting activities within certain levels may diminish the magnitude of pre-settlement natural mortality and promote successful recruitment. Because of very low levels of the unit cost of effort, bioeconomic equilibrium occurs at high levels of fishing intensity, which in turn increases the risks of exhausting this highly vulnerable sedentary species.

The macha, Mesodesma donacium (Fig. 2g, p. 166)

Distribution

M. donacium is distributed along the Pacific coast of South America, from Bahía Sechura (Perú, c. 5°S) to Isla de Chiloé (c. 43°S) (Tarifeño 1980) (Fig. 1, p. 164). This species inhabits the swash zone to about 15–20m deep off exposed high-energy intermediate and dissipative sandy beaches (Tarifeño 1980, 1984). It has also been found in sheltered sites in the outlets of estuarine areas of south central Chile (E.Jaramillo unpubl. data). The across-shore distribution of *M. donacium* is patchy and adult clams are primarily confined to the surf zone, while the vast majority of juveniles occur in the swash zone (Tarifeño 1980, Jaramillo et al. 1994).

The longshore distribution of *M. donacium* is highly variable (Tarifeño 1980, Jaramillo et al. 1994). For example, in a sandy beach stretching approximately 1800m, several surf clam beds were clearly distinguished; patches of surf clams are usually separated by areas with very low densities or by vacant areas whose lengths can reach several hundreds of metres (Jaramillo et al. 1994). The discontinuous distribution of this species might be related to longshore differences in grain size (Tarifeño 1980) and/or variability in compactness of the substratum (E.Jaramillo unpubl. data).

Biology and ecological role

Populations of *M. donacium* usually have a sex ratio of 1:1 (Salgado & Ishiyama 1979, Tarifeño 1980, Peredo et al. 1987). Studies of the reproductive cycle of *M. donacium* in Peruvian and Chilean waters have shown differences in the timing of gametogenesis and spawning periods along this latitudinal gradient. These differences may be related to local variability in environmental factors such as water temperature and food availability (Tarifeño 1980, Peredo et al. 1987). Surf clams matured in Peru ($\approx 16^\circ\text{S}$) between late winter and late spring (August–November), while the spawning period lasted from late spring to midwinter (December–July), the last stage being most frequent during summer months (December–March) (more than 85%) (Salgado & Ishiyama 1979). In latitudes close to 33°S , ripe animals peaked (95%) in midwinter (August), while spawned surf clams were more frequent in September, with less than 20% in this stage until late summer (March) (Tarifeño 1980). Surf clams collected further south ($\approx 37\text{--}38^\circ\text{S}$) were mature during winter, while the spawning season was primarily during late spring (November–December) (Tarifeño 1984); Tarifeño also mentioned a second spawning period (late summer; February–March). Clams of south central Chile ($\approx 39^\circ\text{S}$) had a maturation period during winter and spring (from June through November), ripe animals being most abundant in November (Peredo et al. 1987) and spawning extended from summer to early autumn (December to April). Further south ($\approx 40^\circ\text{S}$), *M. donacium* has two main periods of spawning: one during spring (October–November), and the second one during late summer (López 1976). The duration of larval stages is unknown, as are the dynamics of recently settled larvae and recruits. However, in central and south central Chile, recruitment takes place primarily at sheltered sites near estuarine outlets (Tarifeño 1980; E. Jaramillo unpubl. results).

Size at first maturity (Table 2, p. 168) also varies geographically in *M. donacium*, but there is no clear latitudinal pattern. Maturation occurred at 35–70mm shell length (mean 56mm) in Peru ($\approx 16^\circ\text{S}$) (Salgado & Ishiyama 1979), and at 16–18mm in central Chile ($\approx 33^\circ\text{S}$) (Tarifeño 1980). Further south, maturity occurred at 28–76mm (mean 49.1mm) (Tarifeño 1984), while López (1976) mentions a range of 47–57mm.

Population dynamics

Age and growth of *M. donacium* have been studied by analyses of length-frequency histograms and growth rings on the shell (Alarcon 1979, Tarifeño 1980, 1984, Arntz et al. 1987). Comparisons of results showed that growth rates vary with latitude (Table 2, p. 168). In Perú (12°S), Arntz et al. (1987) calculated a maximum shell length of 110–124mm and annual growth rates Φ' value for the species throughout its entire distribution range was close to 3.74.

Fishery

Landings of *M. donacium* in Peru showed a steady increase from 1964 (36t) to 1977 (597t), reaching an impressive peak between 1978 and 1979, when catches were seven-fold higher ($\approx 4000t$; see Fig. 10). This happened during the period preceding the ENSO event of 1982–83. The decline from 1980 to 1985 may be a combined result of resource over-exploitation (1980–81) and negative effects of ENSO on *M. donacium* populations (Castilla & Camus 1992). Arntz et al. (1987) pointed out that from March 1983 onwards, no live surf clams were found in shallow waters south of Lima and reported no recovery up to 1986. Landings from 1986 to 1989 showed a recovery of the resource, but never reached the landing levels of 1978–79 (see Defeo et al. 1993).

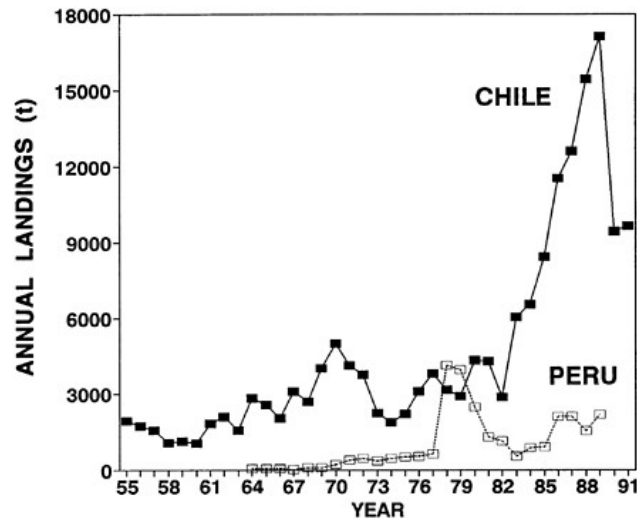


Figure 10 *Mesodesma donacium* landings in Chile (1955–91) and Peru (1964–89). (After Defeo et al. 1993).

In Chile, surf clams are primarily harvested by artisanal fishers operating from the beach and entering the surf zone during low tides. However, most of the catch is ultimately sold on commercial markets. The fishers operating from the beach, called “macheros”, collect the clams by twisting their feet and using their body weight to excavate the sand until clams emerge at the sediment surface to be picked up by hand. In some areas (especially during very calm days) *M. donacium* is also harvested by hookah divers from boats located behind the surf zone.

The exploitation of *M. donacium* is regulated only by a minimum size of 50 mm shell length in south central Chile ($\approx 38\text{--}42^\circ\text{S}$) and 60 mm shell length in the rest of the country. Landings data gathered from Government sources (Servicio Nacional de Pesca, SERNAP) between 1965 and 1991 show a marked increase from 1983 onwards (Fig. 10), as a response to a strong trend towards diversification in the export of Chilean shellfish products (Defeo et

al. 1993). Landings peaked in 1989, reaching *c.* 18000t, and declined thereafter (1990–91) down to 9000t (Fig. 10), probably due to over-exploitation and/or fluctuations in market demand. Indeed, a trend of the foreign market (i.e. Spanish market) towards the selection of clam sizes lower than the legal marketable size, has been observed (Defeo et al. 1993). According to these fishery statistics, areas located in south central Chile account for the majority of the landings. However, not all the catch is reported to SERNAP; often the macheros use the catch for their own consumption, or else sell it directly to consumers.

A daily set of data on the fishery of *M. donacium* was collected from May 1992 to October 1994, on a 2-km stretch of beach in south central Chile (Mehuín, *c.* 39°S). During this period, the maximum numbers of macheros working in a single day were 73, 23, and 20 (February, April 1993, and March 1994, respectively). The average maximum number of fishers was three macheros per day. Open harvesting seasons for other species (primarily “loco” *Concholepas concholepas*) influenced the number of fishers collecting surf clams during some stages of this study. The maximum number of working days (up to 90% of the whole month) occurred during the austral summer months of January–March, whereas during winter and early spring months few days were worked (less than 40% of the whole month), primarily because of rough surf-zone conditions. The total catch ranged from 58–6558kg per month, and peaked during summer months. Lowest harvests occurred during winter months, for example less than 100kg per month during July-August 1994. However, the mean catch of surf clams per machero remained fairly stable, (i.e. 10.5 kgday⁻¹).

Europe

Only one species of clam is widely harvested on exposed sandy beaches in Europe, although many are utilized on tidal flats and in estuaries.

The wedge clam, Donax trunculus (Fig. 2h, p. 166)

Distribution

D. trunculus is distributed along the Atlantic coasts of Europe and North Africa, from the Bay of Douarnenez, Brittany, France (Guillou & Le Moal 1980) to Senegal (Fischer et al. 1981), and throughout the Mediterranean and Black Seas (Fig. 1, p. 164). Within this range of distribution, abundant populations are found in areas of high productivity often, but not exclusively, associated with the discharge of rivers. Distribution is limited to moderately-exposed or exposed beaches of clean, well sorted sand with median particle sizes in the range 190–370µm (Mazé & Laborda 1988, Guillou & Bayed 1991). For beaches along the coast of Morocco, there is a close correlation between the maximum density of adults found and the distance from the coast to the 30-m depth contour, indicating dependence of density on hydrodynamics which is controlled by the gradient of the sea bed inshore of this critical depth at which wave energy begins to be dissipated (Guillou & Bayed 1991). Hydrodynamic conditions also account for differences in population density along the length of beaches (Mouéza & Chessel 1976).

The vertical distribution of *D. trunculus* varies in different parts of its range. In the essentially tideless Mediterranean Sea, *D. trunculus* occupies a relatively narrow zone in depths of

a few centimetres to 1m (Massé 1971, 1972, Amouroux 1972, Degiovanni & Mouëza 1972, Geldiay & Uysal 1972, Mouëza 1972a, Bodoy & Massé 1979, Salas-Casanova 1987) with a second smaller species of *Donax*, *D. semistriatus*, occupying a similarly narrow zone in slightly deeper water (Massé 1971, 1972) and a third species, *D. venustus*, yet deeper. On the tidal Atlantic coasts, *D. trunculus* occurs in the intertidal zone (Salvat 1968, Chassé 1972, Gruet 1974, Guillou & Le Moal 1978, 1980, Ansell & Lagardère 1980, Guillou 1982, Otero 1982, Bayed & Guillou 1985, Guillou & Bayed 1991) usually with the size classes partially segregated; juveniles occupy the higher levels while increasingly larger individuals are found closer to low water; the largest individuals occur near low water mark of spring tides.

In the northern parts of its range on Atlantic coasts, the distribution of *D. trunculus* overlaps the southern part of the range of a second smaller species, *D. vittatus*. Here the vertical distributions of the two species also overlap, but the latter reaches its greatest population density subtidally (Guillou & Le Moal 1978, 1980, Ansell & Lagardère 1980, Guillou 1982). Near the southern part of the range of *D. trunculus*, *D. venustus* occupies a similar essentially subtidal zone (Guillou & Bayed 1991). In the Bay of Malaga, Spain, just within the Mediterranean Sea, four *Donax* species are all present in the same area with overlapping vertical distributions; here *D. trunculus* are the most superficial, *D. vittatus* and *D. semistriatus* slightly deeper, and *D. venustus* the deepest (Salas Casanova 1987).

Biology and ecological role

In *D. trunculus* the sexes are separate and the sex ratio does not differ significantly from 1:1 (Lucas 1965, C.Tirado & C.Salas, pers. comm.). There is no sexual dimorphism of the shell, but males and females can be readily distinguished on dissection by the colour (white and green, respectively) of the gonad, except during the inactive period of the annual reproductive cycle.

The reproductive cycle of *D. trunculus* shows essentially the same characteristics throughout its range of distribution (Lucas 1965, Mouëza & Renault 1971, Badino & Marchionni 1972, Poli 1972, Mouëza & Frenkiel-Renault 1973, Ansell & Bodoy 1979, Ansell et al. 1980b, Bayed 1990). Following an "inactive period" or "resting stage" of variable duration depending on the geographical area, gametogenesis begins either in the autumn or winter. Spawning first takes place in the spring and this is followed by further spawning(s) before the reproductive cycle is completed in late summer or autumn and animals have returned to the resting stage. During the resting period, the gonad is regressed and the sexes are indistinguishable macroscopically. There may be two major spawnings during the year; in June/July and September/early October on the Camargue coast of France (Ansell & Bodoy 1979) and in spring and summer on the Moroccan coast (Bayed 1990), or spawning may be more evenly distributed throughout the summer, as on the Algerian coast (Ansell et al. 1980b). On the coast of Málaga, southern Spain, spawning was found to be continuous from April to October but with peaks in May and August (C.Tirado & C.Salas pers. comm.). The start and duration of the different stages shows some regional variation related to differences in the annual cycle of seawater temperature (Bayed 1990), or with the cycle of phytoplankton production (C.Tirado & C.Salas pers. comm.).

The tissue weight and the biochemical composition of the tissues show characteristic seasonal changes associated with the reproductive cycle and with the associated cycle of storage and utilization of reserves in the tissues (Ando et al. 1976, Ansell & Bodoy 1979, Ansell et al. 1980b, Dowidar & El-Nady 1984). On the coast of Algeria (Ansell et al. 1980b), the dry

tissue content is low in winter and rises rapidly in the spring and early summer as the gonad increases in size. Dry tissue content then fluctuates depending on the balance between gametogenesis, storage of reserves and spawning, but falls again at the end of the reproductive period. The nitrogen (protein) and lipid content reflect these changes. On the Camargue coast of France (Ansell & Bodoy 1979), the cycle is similar to this in many respects but there is a rise in tissue content in late autumn, following the fall that marks the end of the reproductive period, probably reflecting a higher food (phytoplankton) availability at this time in this area.

For *D. trunculus* from the coast of Málaga, Southern Spain, where there are two peaks of spawning, C. Tirado & C. Salas (pers. comm.) estimated that fecundity (total number of oocytes contained in the ripe gonad) ranged between 58900 and 641000 for females collected in May and between 33245 and 361000 for females collected in August and September. At the time of spawning, the gametes are released into the water where the eggs are fertilized. Development has not been described in detail for *D. trunculus* but Otero (1982) reared larvae through to settlement in the laboratory and his results indicate that development is similar to that described in more detail for *D. vittatus* (Frenkiel & Mouëza 1979). The spherical eggs (70–80 µm diameter after fertilization) develop through free-swimming blastula and trochophore stages to produce a D-larva (86–95 µm length × 78–85 µm height in *D. vittatus*) after 48h. Mouëza (1975) figured a fertilized egg of 76 µm diameter and a D-larva of 100 µm length × 80 µm height for *D. trunculus*, but did not succeed in rearing larvae to settlement. Otero (1982) figured a D-larva of 110 × 90 µm. Further development is typically planktotrophic. Growth of the veliger larva is presumably dependent on sea water temperature and the availability of suitable microalgae as food as in other bivalves. Settlement and metamorphosis takes place at the pediveliger stage that, in *D. vittatus*, is reached at a shell length of 250–350 µm after some 31 days at a temperature of 16–18°C. For *D. trunculus*, metamorphosis took place after 19–23 days at 21°C (Otero 1982). Neither settlement behaviour, nor post-settlement redistribution of juveniles has been studied in *D. trunculus*, but there is a strong supposition from the patterns of distribution of juveniles found on beaches that some active process of habitat selection is involved, perhaps mediated by the use of byssal thread flotation (Sigurdsson et al. 1976).

Like other *Donax* species, *D. trunculus* is relatively shallow burrowing, maintaining contact with the sand surface by means of separate inhalant and exhalant siphons through which the respiratory and feeding current is drawn. The siphons are sensitive to vibrations and other disturbances that cause them to close and withdraw but with little delay before extension and re-opening occurs. Unlike many other *Donax* species (Ansell 1983), *D. trunculus* shows no directed tidal migration. Its rapid burrowing movements, however, allow it to maintain its superficially-buried position in the sand during disturbance by wave action. These movements, combined with some surface movement by crawling or “leaping” probably result in redistribution of a proportion of individuals on each tide as is the case in *D. vittatus* on Scottish beaches (Ansell 1994). In the longer term they lead to the size segregation of the population seen on Atlantic beaches. The characteristic vertical and geographical distribution of *Donax* species on European beaches are related to different tolerances to environmental temperature extremes (Ansell et al. 1980a).

D. trunculus is reported as the host of a variety of parasites including trematodes (Pelseneer 1896, 1906, Lucas 1965, Mouëza 1975), gregarine sporozoans and nematodes (Mouëza 1975), and a species of *Rickettsia* (Comps & Raimbault 1978). Where they infest the visceral mass and gonad, some parasites may cause parasitic castration of the host (Pelseneer 1896) but none has been studied in any detail.

Where it occurs in high densities, *Donax trunculus* is often the dominant filter-feeding macro-invertebrate on Atlantic beaches or in the shallow subtidal of the Mediterranean Sea, feeding on suspended organic material, predominantly phytoplankton (Plante Cuny & Bodoy 1987). Its morphological adaptations to this role have been well documented (Mouëza & Frenkiel 1974, 1976a,b, 1979, Mouëza 1976, Pichon et al. 1980). Beaches dominated by *D. trunculus* have not been extensively studied at community level and no synthesis of its role in the food chain can be made. *D. vittatus* populations, which occupy a similar ecological niche on UK beaches, are subject to predation by a variety of epibenthic marine predators, including drilling gastropods (naticids), crustaceans (shrimps, portunid and other crabs), and fishes (particularly flatfishes). Predation may be lethal, resulting in the death and ingestion of the whole bivalve, but in many instances is non-lethal, often involving the loss of only one siphon tip. This non-lethal (grazing) predation plays a major role in the nutrition of juvenile flatfishes like plaice, dab, and flounder that use sandy beaches as nursery grounds (Ansell & Gibson 1990). It is likely that a similar suite of predators affect *D. trunculus* populations. George (1965) and Neuberger-Cywiak et al. (1989, 1990), for example, report predation by naticid gastropods occurring in Mediterranean populations.

Population dynamics

Aspects of population dynamics of *D. trunculus* have been studied in Mediterranean (Bodoy & Massé 1979, Dowidar & El Nady 1984, Neuberger-Cywiak et al. 1990) and Atlantic (Degiovanni & Mouëza 1972, Mouëza 1972b, Guillou & Le Moal 1978, 1980, Ansell & Lagardère 1980, Bodoy 1982, Guillou 1982, Otero 1982, Fernandez et al. 1984, Bayed & Guillou 1985, Mazé & Laborda 1988, Le Moal 1993) populations. Several authors provide data on population densities of *D. trunculus* in different areas (Atlantic: Degiovanni & Mouëza 1972, Mouëza 1972a, Guillou & Le Moal 1978, 1980, Ansell & Lagardère 1980, Bodoy 1982, Guillou 1982, Otero 1982, Fernandez et al. 1984, Mazé & Laborda 1988, Le Moal 1993; Mediterranean: Neuberger-Cywiak et al. 1990).

The maximum size reached by *D. trunculus* lies between 30mm and 44mm shell length. Maximum size varies among different populations, depending on both the growth characteristics and on the extent of exploitation of the larger size groups (see later). Both the life span and the growth rate vary among populations from different geographical areas, between different beaches in the same geographical area, and among different cohorts from the same beach. At the northern limit of the geographical range in Brittany, up to six annual cohorts may be present in the population at any time, indicating a maximum life span in this area of more than six years (Guillou & Le Moal 1980, Guillou 1982). Here, growth is restricted to the summer months and the shells bear well marked annual growth checks that provide a reliable basis for growth measurements. Clear growth checks are also found in shells from further south on the French Atlantic coast (Ansell & Lagardère 1980). In Algeria, the maximum sized individual found by Mouëza (1972b, 1975) was 34mm shell length. The population here showed numerous modal classes, but apparently few individuals survive for more than 16–18 months. The life span is also short in other Mediterranean populations and at the southern end of the range in the Atlantic. Growth and life span in other Atlantic populations lie between these two extremes, Φ' ranging between *c.* 2.90 and 3.25 (average \approx 3.08, Table 2, p. 168).

Most authors have not attempted to estimate mortality or overall production. Ansell & Lagardère (1980) provided a “provisional” estimate of mortality and production based on mean size-frequency distributions (equivalent to “catch curves”) for two populations at Ile

de Oleron, French Atlantic coast. These indicate a gradually increasing rate of mortality from year one to year four with few individuals surviving into their fifth year. On the two beaches studied the mean estimated rate of production was similar, a lower mean population density on one being compensated for by a higher productivity per individual resulting from a higher growth rate.

Fishery

The major commercial shellfisheries that exploit natural populations of intertidal or shallow subtidal soft sediments in European waters all centre on sheltered sand flats or estuaries rather than on the more exposed beach habitats that form the subject of this review. *D. trunculus* is the closest analogue on European coasts to the beach clams of the other geographical areas discussed and is included here for that reason. *D. trunculus* is exploited in most European countries although generally only as a recreational fishery for individual consumption or as an artisanal commercial fishery supplying local markets. In some countries, there is a more extensive fishery; in Italy, for example, *D. trunculus* is fished on the east coast from Tuscany to the southern part of the Napoli area, and on the Adriatic coast in the north (Friuli, Venezia Giulia) and south (Puglia) (D. Del Piero pers. comm.). *D. trunculus* has been heavily exploited in some areas of Italy, notably the Tyrrhenian Sea coast. Dowidar & El-Nady (1984) report that *D. trunculus*, known locally as “Om El-Kholool”, is the most popular edible clam along the Mediterranean coast of Egypt where it is caught commercially using a “special dredge, dragged by man or animal power” (Aleem 1969). There are no published official statistics for any *D. trunculus* fishery.

The techniques of harvesting *D. trunculus* vary from country to country and from region to region; they mostly involve methods of manual collection by individual fishers. Otero



Figure 11 Hand dredge in use for collecting *Donax trunculus* in Portugal. (Photograph courtesy of Simon Grosset, photo-journalist.)

(1982) described the “small rasca”, a sickle-like device used by fishers in Galicia, Spain, to bring *Donax* to the sand surface. Along the coast of the Algarve, Portugal, fishers use individual dredges drawn backwards in shallow water, with a harness worn round the waist, and rocked to and fro by means of a wooden post attached at the front of the dredge (Fig. 11). On the French Mediterranean coast, a somewhat similar small dredge known as a “tellinière” is pulled by hand or, in some cases, by a horse. Hydraulic dredges, normally employed in fisheries for *Chamelea gallina* (Veneridae) and *Ensis minor* (Solenaceae), were used in Italy to harvest *Donax trunculus* but are now prohibited (D. Del Piero pers. comm.). In some areas local regulations have been introduced to help conserve the stocks of *D. trunculus* and other exploited bivalves in shallow coastal waters; local regulations in Andalusia, Spain, for example, define a minimum size of 30mm shell length and a closed season for the fishery extending from 1 April to 30 September (Dr Carmen Salas pers. comm.).

Africa

This section covers a single species that occurs on sandy beaches in South Africa and Namibia. Other species may support artisanal fisheries elsewhere in Africa but this is the only species for which published information is available and it is probably also the only species that is, or has been, utilized commercially.

The white sand mussel *Donax serra* (Fig. 2i, p. 166)

Distribution

D. serra occurs around the southern African coastline from the Transkei coast of South Africa in the east through to the Kunene River at the border between Namibia and Angola in the west (Fig. 1, p. 164). Its distribution thus covers three biogeographic provinces: the warm temperate south coast and the temperate Namaqua and Namib upwelling regions along the west coast (Bally 1986, Donn 1990a). Intertidal distribution varies considerably between the warm temperate south coast province and the cold temperate west coast provinces.

The intertidal distribution presents a distinct size-specific zonation that differs between regions. In the east and south the species is entirely intertidal with adults being centred on the midshore, although spat may settle in the surf zone and migrate upshore as they grow (McLachlan & Hanekom 1979, Donn 1990a, Lastra 1994). On the west coast this reverses and juveniles occur in the intertidal with adults on the lower shore and in the surf zone (de Villiers 1975a, Bally 1983, Donn 1990a). However, in northern Namibia intertidal distribution switches back to the south coast pattern, with adults in the intertidal (Bally 1986, Donn 1990a). This is probably due to increasing water temperature north of the upwelling region in Namibia and parallels the seasonal shifts in distribution of *Mesodesma mactroides* in South America.

Donax serra is not the only donacid inhabiting South African beaches; *D. sordidus*, a smaller tidal migrant species, occurs lower on the shore on the south coast. There is no indication of any competition between the two species and distribution of the latter is centred on the surf zone, whereas *D. serra* is entirely intertidal except for new recruits that settle in the surf zone.

Distribution and zonation are not constant and this species, like most inhabitants of exposed beaches, undergoes migrations. In contrast to most other *Donax* species, however, *D. serra* does not undergo tidal migrations, but rather shows small semi-lunar movements up and down the shore coupled to changes in beach water tables during spring and neap tides (McLachlan et al. 1979, Donn et al. 1986). These movements have been recorded only in south coast stocks; west coast populations do not appear to undertake any tidal or semi-lunar migrations. It has been suggested that the large size of *D. serra* and the low water temperatures on the west coast make rapid burial difficult, precluding any migrations or intertidal existence, hence the subtidal adult stocks (Donn 1990a, Donn & Els 1990).

Another distribution pattern described for *D. serra* is a longshore size-specific segregation around log-spiral bays in the eastern Cape. Donn (1987) suggested that spat recruit more abundantly near river mouths but are subsequently transported eastwards by longshore currents, thereby creating a size specific longshore zonation in these populations: juveniles are most abundant near river mouths, whereas adults become more prolific eastwards. Dugan (1994) subsequently attempted to test for longshore migration in adults by tagging, but failed to detect any significant movement. Furthermore, juvenile distribution was patchy with no clear size gradient as postulated by Donn (1987).

Biology and ecological role

Both south and west coast stocks of *D. serra* have a poorly-defined breeding cycle and exhibit extended spawning with, typically, more than one peak in the year. On both coasts these peaks generally span the periods late summer and late winter. Sexes are separate and hermaphrodites have not been recorded; the sex ratio is 1:1 and they are external fertilizers (de Villiers 1975b, McLachlan & Hanekom 1979, van der Horst 1986). Females produce large numbers of small (45µm) eggs (van der Horst 1986) but fecundity has not been quantified.

Seasonal changes in biochemical composition of adults have been linked to the reproductive cycle (McLachlan & Hanekom 1979). *D. serra* on the south coast undergoes a substantial drop in tissue mass in winter and spring and a smaller drop in summer, corresponding to the two spawning seasons. The tissue comprises 66% protein, 15% carbohydrate and 4% lipid.

A free-swimming planktotrophic larva develops through trochophore and veliger stages before settling as spat (Brown et al. 1989) but the duration of larval life is not known. Recruitment is to the surf zone on the south coast but probably to the intertidal on the west coast. Settlement can occur throughout the year but may peak in late summer and early autumn for the 2–3 mm length class on the south coast where spat appear to settle selectively in patches of fine sand in the surf zone (Lastra 1994). De Villiers (1975b) recorded peak recruitment to a length of 3–5mm during spring and summer, following the extended major spawning period starting in winter.

D. serra, which is the largest member of the genus, is a successful suspension feeder and the dominant contributor to macrofaunal biomass on many South African beaches (McLachlan et al. 1981, Donn 1986). The biology of the species has been reviewed by Brown et al. (1989). *D. serra* positions the tips of its siphons level with the sand surface and takes in swash and surf water including phytoplankton and detrital material. The inhalant siphon has a fringe of tentacles to exclude sand grains. It feeds in pulses and is capable of filtering a wide range of particles from 40µm down to bacteria, but extracts particles in the size range 4–7µm most efficiently (Stenton-Dozey 1989, Matthews et al. 1989).

The siphons bear ciliated tufts on their surfaces that may be primary receptors responding

to light, tactile or chemosensory stimuli (Hodgson & Fielden 1984, Hodgson 1986). *D. serra* has a large blade-shaped foot and muscles plus the pedal haemocoelic cavity are used to extend the foot and aid in burrowing (Brown et al. 1989). It is a rapid and powerful burrower (Trueman & Brown 1985) and burial time increases with size and lowered temperatures (McLachlan & Young 1982, McLachlan et al. 1995). It also surfs in the swash, smaller individuals doing so more frequently. The energetics of locomotion have been reviewed by Brown et al. (1989).

D. serra is relatively tolerant of heat stress, surviving for extended periods at temperatures of 25–30°C. Size classes that occur highest on the shore show the greatest temperature tolerance on both coasts (Ansell & McLachlan 1980, Stenton-Dozey 1989, Stenton-Dozey & Brown 1994). *D. serra* is also moderately tolerant of lowered salinities (McLachlan & Hanekom 1979) and could thus penetrate a short distance into estuaries if other conditions were suitable.

Considerable attention has been paid to respiration in *D. serra* and published information is summarized in Brown et al. (1989). The gills are not especially large in relation to body size, oxygen uptake is proportional to body weight to the power 0.7–0.75 and animals display flat rate-temperature curves. They are oxyconformers, uptake increasing in proportion to ambient partial pressures. Metabolism during withdrawal into the shell under unfavourable conditions is anaerobic, the animal incurring an oxygen debt. An energy budget compiled for this species indicates that scope for growth is greatest when it is fed on algal rations and lower when fed on detritus (Brown et al. 1989, Matthews et al. 1989). No parasites or commensals have been recorded on *D. serra*. With high fecundity, rapid growth and unspecialized feeding, *D. serra* is clearly a typical *r*-strategist species

D. serra is the dominant suspension feeder among the benthos on both south and west coasts of southern Africa. Its standing stock can run into kilograms of dry flesh mass per linear metre of beach and it constitutes up to 98% of intertidal biomass. Its position in the ecosystem is best understood in the eastern Cape sector of the south coast where food webs, trophic relations, energy flow and nutrient cycling in beach and surf-zone ecosystems have been well studied. Trophic dynamics of the beach and surf-zone ecosystem in this area have been summarized in reviews by McLachlan & Bate (1984), Cockcroft & McLachlan (1993) and Heymans & McLachlan (1996).

This beach and surf-zone ecosystem is fuelled by intense accumulations of surf diatoms, *Anaulus australis*. Within the macrofaunal trophic assemblage, zooplankton and benthos constitute approximately equal biomass and *D. serra* makes up 70% of the latter biomass. It has a P:B ratio of about 0.6yr⁻¹ (McLachlan & Hanekom 1979, Donn 1986, Schoeman 1996). Production by this species constitutes about 10% of all production in the macrofauna assemblage and is taken by swimming crabs *Ovalipes trimaculatus* (30%), birds, especially oystercatchers and gulls (40%), and a variety of benthic feeding fishes, including batoids (30%) (du Preez 1984, McLachlan et al. 1980, du Preez et al. 1990). Predation is both lethal, for example sandsharks preying on juveniles in the surf zone and skates, oystercatchers and gulls taking adults in the intertidal, and sublethal, with sanderlings nipping siphons in the intertidal and some fishes doing this in the subtidal. Damaged siphons can be regenerated within a few weeks (Hodgson 1986).

As well as its contribution to energy flow, *Donax serra* is also a regenerator of nutrients, principally ammonia, which represents a significant source of nitrogen to phytoplankton (Prosch & McLachlan 1984, Cockcroft & McLachlan 1993). Its shells contribute to the calcium carbonate fraction on these beaches.

The above scenario applies to the eastern Cape sector of the south coast where exposed inter-

mediate to dissipative beaches are characterized by high surf-diatom production. Elsewhere the role of white sand mussels may differ; on intermediate to reflective beaches it is much less abundant or absent. On the west coast, surf zones are characterized by upwelling, high detrital inputs from kelp beds and the absence of surf diatoms. The great biomass of sand mussels in the surf zones of the more dissipative beach types suggest that they must play an important role as consumers of water column particulates and as food for fishes and crabs. The consumption of adults by birds is restricted to the south coast where adult white sand mussels occur intertidally.

Population dynamics

The population dynamics of *D. serra* have been examined in two areas, on the west coast north of Cape Town and on the eastern sector of the south coast near Port Elizabeth. The west coast studies (de Villiers 1975a) could only clearly distinguish two age groups on the beach because slowing of growth with age resulted in a unimodal frequency band of adults and this was compounded by the migration of adults into the subtidal below the limits of sampling. Recent stock assessments (Tarr 1994) at four west coast sites indicated mean population sizes on the beach and shallow subtidal of 150–4272 per linear metre (m^{-1}), with a maximum of 7884 m^{-1} , and populations up to 4.3 million km^{-1} shoreline. On the south coast, populations have been studied by McLachlan & Hanekom (1979), Donn (1986) and Schoeman (1994, 1996). Most work has concentrated on two exposed beaches (24km and 40km long) where abundances are high, ranging from 1000–7000 m^{-1} (mean 2300 m^{-1}) and shell-free dry biomass values up to 7 kgm^{-1} (mean 1600 gm^{-1}) have been recorded. Abundance shows interannual fluctuations, mainly due to varying recruitment, adult stocks being remarkably stable.

Growth is rapid, to 32–35mm in the first year in the intertidal, and to 48–50mm in the second year, on the south coast (McLachlan & Hanekom 1979, Donn 1986, Schoeman 1996). Thereafter growth rate decreases to a size of 67mm (maximum 80mm) after five or more years (Schoeman 1996). Empirical (McLachlan & Hanekom 1979), Gompertz (Donn 1986) and von Bertalanffy seasonally oscillating (Schoeman 1996) growth curves have been estimated, all in close agreement: K ranged 0.39–0.73 yr^{-1} , and L_{∞} 66–68mm. An approximate value of the growth index ϕ' was 3.57 (Table 2, p. 168).

On the west coast growth is slower but continues until a larger size is attained. De Villiers (1975a) was able to obtain growth ring readings of sufficient reliability to compile a growth curve that corresponded well with curves from length-frequency analyses. De Villiers (1975a) estimated an empirical growth curve with lengths of 22mm, 43mm, 58mm, 64mm and 68mm after their first five years on the beach and sexual maturity at 37–54 mm or 1.5–2.5 years. West coast specimens can grow to 80mm shell length. This species does not usually have distinct and usable growth rings on the south coast.

There was remarkable consistency in these three studies and P:B ratios were found to be about 0.6 yr^{-1} and total mortality 0.5–0.85 yr^{-1} with fishery mortality ($F=0.07 yr^{-1}$) negligible (Schoeman 1996). Comparable production and mortality data are not yet available for the west coast. Sexual maturity is reached at a length of about 44mm on average (range 38–49mm), this being at an age of about 2yr after settlement or 1.5yr in the intertidal (McLachlan & Hanekom 1979, Schoeman 1996).

Donn (1990b) analyzed morphometric differences between west and south coast populations, finding the slightly smaller intertidal south coast specimens to have heavier valves, greater density and more wedged shapes than their colder water west coast counterparts. He suggested that these differences aided better movement and rapid burial in the swash in the case of south coast specimens.

Mass mortalities are a common phenomenon on the west coast and de Villiers (1975a) described one major mortality at Elands Bay. This was caused by red tides in the form of blooms of the dinoflagellate *Gonyaulax grindleyi*. This effect was greatest at lower tide levels and virtually all adult individuals perished; recovery was not evident within six years. Such red tides are a common occurrence on the west coast but only occasionally cause mass mortalities on the scale described by de Villiers (1975a). On the south coast minor mortalities have been recorded where many dead animals littered the drift line. It is not known what caused such mortalities but they generally affect less than 5 % of the population at any one time (A.McLachlan unpubl. data).

Fishery

Stone age peoples around southern Africa subsisted on sand mussels for millennia and their shells characterize middens along the coast. In recent times mussels have been collected in recreational and commercial fisheries for use as bait and food, but mainly bait. The west coast stocks have been subjected to both forms of fishery but only recreational fisheries exist on the south coast. A size limit of 38mm shell width (58mm length) has long been in force. Statistics of licensed landings for commercial collecting, recorded since 1966, show a clear decline (Fig. 12) coupled to both decreasing demand and reductions in annual quotas. All licences were revoked in 1988 and the issue of new licences has been limited pending the outcome of ongoing stock assessments (Tarr 1994). The problem of toxins accumulating in the tissues during red tides has inhibited the development of this industry on west coast beaches and landings are used primarily for bait. Although little further information is available on this fishery it is clear that these stocks are lightly utilized and could sustain a much greater harvest if it were not for the inhibiting effects of poisoning by red tides.

On the south coast, intertidal adults are widely collected in a recreational fishery. Although some interest has been expressed in establishing a small commercial operation near Port Elizabeth, there has been strong public opposition to what is seen as a danger to the wilderness quality of the beaches and no formal applications for permits for such a fishery have been submitted to date. Schoeman (1996) and Sims (1996) have monitored the recrea-

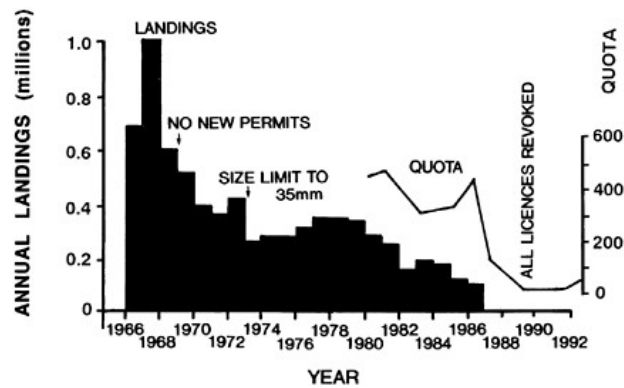


Figure 12 Annual commercial landings of *Donax serra* for bait. (After Tarr 1994.)

tional fishery on the beach supporting greatest sand mussel populations and found that collectors remove <2% of the population (<2% of biomass) per year. However, many collectors exceeded their quota of 50 mussels per day and collected animals below the size limit. The infringement of size limits is largely because the size limit of 58mm shell length, 14mm > than size at first maturity (Table 2, p. 168), is inappropriate for the south coast where adults are smaller than on the west coast and <10% of the population is above this minimum limit. *D. serra* appears to be under-exploited on the south coast and there is an as yet untapped potential for a commercial fishery. An ongoing study of possible harvesting impacts and a cost-benefit analysis of the feasibility of a commercial fishery for *D. serra* in St Francis Bay on the south coast have indicated that 10% of clams are damaged during harvesting, even using traditional techniques (spades), but that no ecological damage to the beach could be detected. These results indicate that a small commercial fishery is indeed viable (Schoeman 1996, Sims pers comm.).

There is a fundamental difference between the south and west coast stocks of *D. serra* in terms of fishery management. The intertidal situation of adults on the south coast makes them readily accessible to collecting and the absence of red tides allows utilization for food and bait. Careful control and management is thus needed on the south coast and quotas and collection methods (hand only) should be enforced. However, minimum legal size on the south coast could be reduced to about 45mm shell length, since this is above size at maturity; it could reduce incidental mortality and is more appropriate for a population that has a smaller individual size than on the west coast. On the west coast, however, the subtidal distribution of most of the adult stock renders them relatively inaccessible, red tides prevent their use for food at certain times and the considerable extent of the coast and low human population densities also limit impact. It is therefore doubtful whether any management or control is needed beyond quotas and size limits.

Asia

Numerous species of bivalve are harvested and utilized as food in tropical and subtropical countries around the Indo-Pacific region, but most of these fall outside the scope of this review as they are either subtidal in distribution, or from intertidal sand flats or estuaries. Sand beaches in this region commonly support populations of mostly small-sized donacid, mesodesmatid and venerid bivalves; only the few larger species are exploited in some areas by mainly artisanal fisheries, although the commercial potential of other species has been explored in some countries (Mwaidseje 1982, Parulekar et al. 1984).

The wedge clams Donax cuneatus and D. faba (Fig. 2j, k, p. 166)

Distribution

D. cuneatus is distributed on tropical coasts from east Africa, throughout the Indo-Pacific region to Japan and Australia, and eastward in the Pacific Islands to Fiji (Fig. 1, p. 164). Typically it is found on intermediate or dissipative beaches (Ansell 1985). The closely related species *D. faba* has a similar geographical distribution, but is typically found on more reflective beaches of relatively coarse sand (Smith 1975, Ansell 1985). Populations of both species undergo some tidal migration (Smith 1975, Ansell 1985) and may also show some

vertical separation in the distribution of juveniles and adults on the beach (Alagarwami 1966). The two species may sometimes have been confused in the past as both are variable in colouration and shell shape, although there are clear and consistent taxonomic differences (Ansell 1985).

Biology and ecological role

As in other *Donax* species, in both *D. cuneatus* and *D. faba* the sexes are separate. The sex ratio does not differ significantly from 1:1 in *D. faba* (Alagarwami 1966), but Nagabhushanam & Talikhedkar (1977a) found a 1.1:0.9 ratio in favour of females in *D. cuneatus*. In both species, first maturity is reached in less than a year from settlement; in *D. cuneatus* at about 10–11 months and a length of 12–13mm (Nayar 1954, Talikhedkar et al. 1976) and *D. faba* at 6–7 months and 10–11 mm (Alagarwami 1966) (Table 2). Where they have been studied, the two species show very similar reproductive cycles, with distinct seasonal peaks in spawning that are reflected in seasonal peaks in settlement and recruitment to the beach populations. In India, where the two species have been most studied, the seasonality in the reproductive cycle is related to changes in temperature and particularly salinity brought about by the seasonal monsoon cycle. In *D. cuneatus*, at Ratnagiri on the east coast of India, development of the gonads began in March and by July the whole population was in a fully ripe condition that was maintained from July to September; spawning extended from October to January, reaching a peak in November–December (Nagabhushanam & Talikhedkar 1977a). Differences in the timing and duration of development and spawning stages of *D. cuneatus*, however, have been reported for other localities (Nayar 1954, Rao 1967, Talikhedkar et al. 1976). In *D. faba*, from the Gulf of Mannar on the south-east coast of India, development of the gonads took place between August and late October, by which time all individuals in the population were ripe; spawning began in November and most individuals were spent by the end of that month—although some spawning continued into December; a further development of the gonad then took place through the period January to April with further spawning from March through June (Alagarwami 1966). Changes in tissue weight and the biochemical composition of the tissues are related to the gonadal cycle (Alagarwami 1966, Nagabhushanam & Talikhedkar 1977b).

D. cuneatus and *D. faba* are both rapid burrowers. In *D. cuneatus* the BRI increased from <5 to >15 over the range 15–26.5°C (Ansell 1985) indicating that it burrows more rapidly than any of the other beach clams reviewed here for which this index has been determined (McLachlan et al. 1996). *D. faba* had a lower burrowing rate index at 25°C than *D. cuneatus* (Ansell 1985).

Both species can develop large populations where they occur on productive beaches, becoming dominant benthic filter feeders (Harkantra & Parulekar 1986), Smith (1975) recorded densities of up to >2000m⁻² for *D. faba* on Tanzanian beaches. Hughes (1966) reported that *D. faba* are heavily predated by the ocyppid crab *Ocyppode ceratophthalma* on beaches in Mozambique and Smith (1975) showed that this crab selectively attacked different colour morphs in populations on the coast of Tanzania, East Africa. Smith also reported predation by the sanderling, *Crocethia alba* in the same area.

Population dynamics

Relatively little information is available on the population dynamics of either *D. cuneatus* or *D. faba* over most of their geographical range. Nayar (1954) and Talikhedra et al. (1976)

studied the growth rate of *D. cuneatus*, and Alagarwami (1966) that of *D. faba*, in India. Shell growth is rapid, more or less constant and steady during the initial growth period of about one year, but then slows (Alagarwami 1966) or stops after sexual maturity is reached, although there may be further short periods of renewed growth thereafter (Nayar 1954). *D. cuneatus* can potentially reach a larger size than *D. faba*, although Alagarwami (1966) recorded a maximum length of 27mm for *D. faba*, and Nayar (1954) only about 23mm for *D. cuneatus* (Table 2, p. 168), however, in both species the maximum shell length reached can vary greatly among populations in different localities. The maximum life span probably does not exceed 3yr (Table 2).

Fishery

Wedge clams in India are exploited by the coastal fishing communities, but do not form the basis of a large commercial fishery. Both Nayar (1954) and Nagabhushanam & Talekhedkar (1977b) stated that *D. cuneatus* is exploited mainly at times when general fishery conditions are poor and other shellfish difficult to obtain, for example particularly during the monsoon season when the sea is rough. Elsewhere, as in the Phillipines (Talavero & Faustino 1933), artisanal fisheries exploit local populations of *D. faba*. In some parts of India (Chari & Unny 1947) and in the Phillipines (Talavero & Faustino 1933) the shells have been used in the production of quicklime.

Australia

Only a single clam, the donacid *Donax deltoides*, is widely utilized on sandy beaches in Australia. It has not been well studied and the limited information available is summarized here. Hopefully this will encourage further study since this appears to be the only species of beach clam in Australia with commercial potential.

The pipi or Goolwa cockle, Donax deltoides (Fig. 2l, p. 166)

Distribution

D. deltoides occurs along the south and east coasts of Australia from the Adelaide area up to southeastern Queensland, and including Tasmania (Fig. 1, p. 164). Juvenile clams are located in the intertidal and adults on the lower shore and in the surf zone, but their distribution is probably centred on the low tide swash zone area (Dakin & Bennett 1987, Saenger & Keyte 1990, McLachlan et al. 1996). It is possible that juveniles undergo tidal migrations but unlikely that the adults do so. In many respects, including appearance and distribution, this species is very similar to *D. serra* in South Africa.

Biology and ecological role

Almost nothing is known of the reproductive biology of *D. deltoides*. In South Australia spawning can occur throughout the year but is most marked in spring. Sexes are separate and pipi are probably broadcast spawners. There is a 6 to 8 week larval phase before settlement (Saenger & Keyte 1990).

D. deltooides develops large populations on high energy dissipative beaches where surf diatom blooms occur, e.g. Goolwa (McLachlan & Hesp 1984). Here they are the dominant benthic filter feeders, for example making up 73% of macrofauna numbers and 85% of biomass on Goolwa beach (McLachlan et al. 1996), and thus occupy a key position in the beach and surf-zone food web. Their predators, besides man, include beachworms (*Onuphis* sp., Dakin & Bennett 1987), seabirds and fishes.

Population dynamics

Donax deltooides is said to exhibit resurgent populations but supportive data are lacking. River discharge and calm periods without vigorous wave action are considered possible causes of widespread mortalities (Saenger & Keyte 1990), but no studies have been published on the population dynamics. There are a handful of estimates of density, with values ranging up to 345m^{-2} (juvenile densities can exceed 1000m^{-2}). Growth is rapid; clams reach 36mm shell length and sexual maturity in 13 months. Growth continues to a maximum length of about 60mm in 3.5yr (Saenger & Keyte 1990, unpublished data from the South Australian Fisheries Department). Only one empirical growth curve has been determined for South Australia stocks of *D. deltooides* (Saenger & Keyte 1990), which rendered preliminary estimates of the growth parameters L_{∞} and K close to 56mm and 1.59yr^{-1} , respectively, giving a value of the growth rate index ϕ' of 3.70 (Table 2, p. 168).

No information is available on recruitment or mortality for *D. deltooides*.

Fishery

In the past, *D. deltooides* was a staple item in the diets of coastal aboriginal populations (Godfrey 1988). The fishery for pipi in Australia consists of both recreational collecting, mostly by anglers for bait, and commercial harvest for eating. This is undertaken in South Australia and New South Wales and possibly also Victoria. No reports are available on landings. However, Saenger & Keyte (1990) failed to detect any significant reduction in pipi densities at beaches where they were subject to commercial exploitation in comparison with unexploited populations in northern New South Wales. There is no management of this resource other than size and quota limits: 50 clams of any size per person per day in New South Wales, a 5–1 bucket of clams of any size per person per day in Victoria and any number of clams above 35mm length in South Australia.

New Zealand

Three species of clams of the genus *Paphies* have supported traditional, recreational and commercial fisheries on New Zealand sand beaches. The taxonomic history of these species is complicated; there have been more than 30 names applied to *P. subtriangulata* since 1828 (Beu & De Rooij-Schuilting 1982). The recent division of the tuatua species into *P. subtriangulata* and *P. donacina* by Beu & De Rooij-Schuilting (1982) has been supported by electrophoretic and morphometric studies by Richardson et al. (1982) and Smith et al. (1989).

*The toheroa Paphies ventricosa (Fig. 2m, p. 166)**Distribution*

P. ventricosa is endemic to New Zealand and populations occur at scattered locations throughout the country (Fig. 1, p. 164). Historically, the largest populations were found on three, long, northwestern coast beaches on North Island: Ninety Mile Beach (89km), Dargaville Beach (72km), and Muriwai Beach (48km). Elsewhere on North Island, substantial populations have also been found at Mitimiti and on the Wellington west coast beaches, particularly Hokio and Waitarere (20km total), and small populations have been reported from the northeastern coast. On South Island, significant stocks are found on the southern coast at Oreti Beach (17km) and Te Waewae Bay (11km), and small populations have occasionally been reported on the southeastern coast (Redfearn 1974).

Populations of *P. ventricosa* are found intertidally on wide, fine sand beaches (Redfearn 1974). The largest populations occurred on dissipative beaches with prevailing onshore winds and regular surf-zone diatom blooms on the west coast of North Island (Cassie 1955). Large *P. ventricosa* at these sites were aggregated in dense beds. Redfearn (1974) observed adult aggregations and higher densities of recruitment in “bays” adjacent to rip currents. Street (1971) reported that populations at Te Waewae Bay did not occur in distinct aggregations.

Intertidal zonation of *P. ventricosa* is associated with size (Redfearn 1974, Street 1971). Large clams (>75mm shell length) are generally aggregated in beds from the mid to low intertidal. Smaller clams are usually found on the upper beach or in separate single-aged beds in the mid intertidal, but may also occur in a layer between large clams and the sand surface. Dense bands of newly recruited clams have been found just below the high tide line (Redfearn 1974). Although Cassie (1955) proposed that subtidal stocks must exist to explain fluctuations in stock estimates and missing small cohorts in size frequency distributions, no subtidal stocks have been documented despite numerous attempts (Street 1971). Toheroa, *P. ventricosa*, occur from just beneath the sand surface to depths of 20cm (Redfearn 1974). In good conditions, toheroa can be located by siphon holes visible on the sand surface at low tide (Cassie 1955).

Biology and ecological role

Reproduction of *P. ventricosa* is by broadcast spawning, and fertilization is external. Sexes are separate and have a ratio of close to 1:1 (Redfearn 1974). Sexual maturity occurs at small sizes. Redfearn (1974) reported that some juveniles had fully developed gonads at 10-mm shell length, the majority of individuals matured in their first year, and all individuals were mature by 15 months (47mm). The main spawning season on Dargaville beaches occurred from September to February, but individuals with ripe gonads were found throughout the year (Redfearn 1974). Fecundity varies with female size; 15–22 million eggs, 60–66µm in diameter, may be produced in a single spawning in the laboratory (Redfearn 1982).

Larvae of *P. ventricosa* have been reared successfully in the laboratory with development being completed within 22 days at 25°C (Redfearn 1982). Settlement occurred in the laboratory at lengths of 270–300µm (Redfearn 1982).

The siphons of *P. ventricosa* are the longest in the genus in New Zealand, and allow toheroa to feed while deeply buried. The siphons are held close to the level of the sand surface when feeding. Adult *P. ventricosa* dig rapidly when disturbed, reaching depths of

200mm (Redfearn 1974). For juvenile *P. ventricosa*, the average burrowing rate index (BRI) was 4 at 15°C (J.E.Dugan & D.M.Hubbard unpubl. data), a value intermediate between those of juvenile *P. subtriangulata* (BRI=7) and juvenile *P. donacina* (BRI=3) (McLachlan et al. 1995). Redfearn (1974) observed small clams, and occasionally larger ones, surfing in the swash. Aggregations of toheroa may move during disturbance events, and have been reported moving seaward by as much as 30m in a day in the absence of noticeable disturbance (Redfearn 1974), but some beds remain stationary for years (Rapson 1952). There is no evidence of tidal migration in *P. ventricosa*.

The condition of *P. ventricosa* varied seasonally at Dargaville and was lowest in the summer during the peak spawning season. Meat volume as a percentage of shell cavity volume ranged from maximum values of >70% in August and September to <50% in January and February (Redfearn 1974).

A variety of predators including birds, crabs and fish prey on *P. ventricosa*. Southern black-backed gulls, red-billed gulls, South Island pied oystercatchers and variable oystercatchers prey on toheroa during low tide. Southern black-backed gulls have been reported taking clams up to 120mm in length (Redfearn 1974). The effects of paddle crab, *Ovalipes catharus*, predation at high tides is probably significant only for small size classes of clams (Wear & Haddon 1987). Results of laboratory experiments suggest that individual *Paphies ventricosa* attain some refuge from *Ovalipes catharus* predation with increasing depth of burial, and mortality is reduced in dense aggregations. *Paphies ventricosa* are also preyed on at high tide by fish including snapper, *Chrysophrys auratus* (Rapson 1952).

Population dynamics

The earliest stock estimates available for *Paphies ventricosa* are from the 1930s, and were made after decades of commercial harvest and the collapse of at least one major stock at Muriwai in 1928 (Redfearn 1974). Stock estimates from most of the important fishery areas for *P. ventricosa* have declined to about 10% of their highest levels in the last few decades (Fig. 13). Maximum densities reported for the six major fishery areas are: 340ind.m⁻¹ at Ninety Mile Beach, 420ind.m⁻¹ at Dargaville, 310ind.m⁻¹ at Muriwai, 125ind.m⁻¹ at Hokio and Waitarere, 90ind.m⁻¹ at Te Waewae Bay, and 120ind.m⁻¹ at Oreti Beach (harvestable clams only). The only population that appears to have been relatively stable in recent decades is at Oreti Beach, South Island, which had an estimated density of 74 clams (>80mm)m⁻¹ in 1990 (Millar & Olsen, 1995). Population estimates available for *P. ventricosa* have large confidence limits, and stock estimates fluctuate considerably from year to year. Most of the available data on toheroa populations were obtained in efforts to assess harvestable stocks, and are likely to be biased against smaller clams both because of the sampling methods and locations (Street 1971, Redfearn 1974).

P. ventricosa are long-lived (>10yr) and have indeterminate growth. They have the fastest growth rate ($\phi' \approx 3.83$: Table 2, p. 168) and attain the largest size (160mm, >470g) of the *Paphies* species in New Zealand and reach legal size for harvesting (100mm shell length, 120g) in 4 to 5 years on North Island beaches (Cassie 1955), and 7 to 9 years on South Island beaches (McKinnon & Olsen 1994) (Table 2). Redfearn (1974) reported similar shell growth estimates using three methods: length frequency analysis, size at age from shell rings, and mark-recapture studies.

Size frequency distributions of *P. ventricosa* are not generally characterized by large numbers of young-of-the-year animals and decreasing numbers of older year classes (Cassie 1955, Redfearn 1974, McKinnon & Olsen 1994). Samples of *P. ventricosa* populations gen-

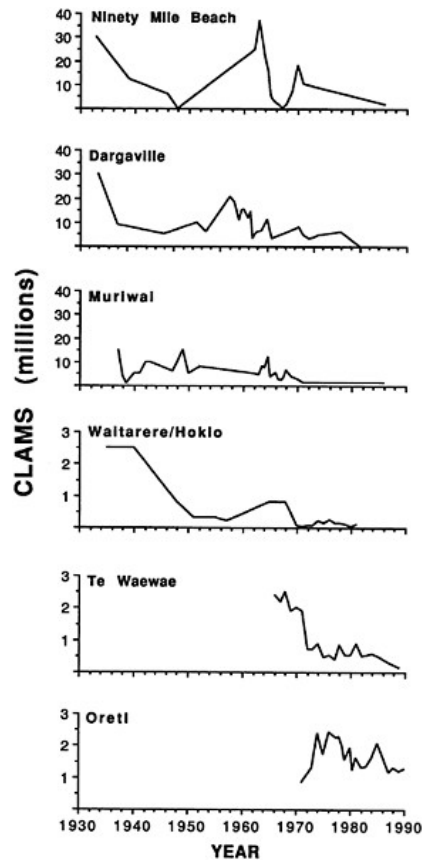


Figure 13 Population estimates for *Paphies ventricosa*. North Island (top 4 beaches), South Island (bottom 2 beaches). Some South Island estimates are for harvestable stocks only (>75mm 1971–78, >100mm 1979–90). Data are from Cassie 1955, Greenway 1969, Redfearn 1974, McKinnon & Olsen 1994, Millar & Olsen 1995, and unpublished MAF fisheries reports. Not all beaches were surveyed each year and effort varied between surveys.

erally have relatively few or no recruits, one or two small cohorts of intermediate size and a mode of larger animals presumably composed of several year classes (Redfearn 1974, McKinnon & Olsen 1994).

Recruitment of *P. ventricosa* appears to be sporadic (Street 1971, Redfearn 1974). Cohorts from strong recruitment years do not necessarily survive to make significant contributions to adult stocks (Greenway 1969, Street 1971, Redfearn 1974). Peak recruitment to the beach at Dargaville was in the summer, between November and March (Redfearn 1974), but newly settled individuals were found as late as August. Redfearn (1974) observed small clams (2mm) being transported up the beach by swash at all tidal phases, and concluded that this led to the formation of a concentrated band of recruits in the upper intertidal zone.

Population structures of *P. ventricosa* have changed on some beaches with the decline in harvestable stocks. For example, large clams (>100mm) have virtually disappeared from Ninety Mile, Dargaville, and Muriwai beaches. In 1986, samples from these sites had substantial modes of clams between 40 and 50mm and <1% clams longer than 100mm (MAF unpubl. data). Redfearn (1974) estimated mortality rates of *P. ventricosa* of about 50% per year, but was unable to determine what proportion was due to harvesting.

Fishery

Toheroa have been subject to artisanal, recreational and commercial fisheries. Maori people harvested toheroa before the settlement of New Zealand by Europeans, and middens contain large deposits of *P. ventricosa*. Commercial harvest of toheroa occurred from about 1900 until 1969 (Stace 1991). Canning started on North Island in Dargaville in the 1890s (Redfearn 1974). Other canneries operated at various times at Waipapakauri at Ninety Mile Beach (1923–45), Muriwai (1946), the Wellington beaches, and on South Island at Te Waewae Bay. The last canning licence was issued in 1969, and the last cannery was closed in 1971 (Stace 1991). Long-term landings data are not available, but the production of toheroa products by canneries was summarized by Redfearn (1974). Maximum annual commercial production of *P. ventricosa* peaked at 77t canned in 1940 (Fig. 14). A conversion of production data to landings is approximately 20 clams per kg canned (using data from Dargaville, Redfearn 1974). This ratio varied due to seasonal and annual differences in the condition of the clams, size classes harvested, and the proportion of clams in the canned product (e.g. as soup or whole clams).

Toheroa were harvested commercially with flat pronged potato forks at low tide. Rapson (1952) reports that at Dargaville beaches, 1- to 2-m wide trenches were dug through dense beds, and the fishers deliberately left areas with high densities of clams along the outside of the trenches. Some canneries operated seasonally, and harvested when clams were at peak condition (Redfearn 1974). After 1962, quotas for the commercial harvest of *P. ventricosa* were based on annual surveys (Redfearn 1974). Live toheroa were difficult to market. Mestayer (1921) attributed the short shelf life of live *P. ventricosa* to the valve gape of market size clams. Canned whole clams and toheroa soup were produced for domestic sales and exports (Cassie 1955). Toheroa soup was typically bright green due to high concentrations of phytoplankton in the guts of the clams.

No long-term data on recreational harvests are available, but recent estimates indicate that they can make substantial impacts on stocks in a short period. Estimated recreational landings of *P. ventricosa* on Dargaville beach from 1966 to 1971 were between 160000 and 3700000 clams per season (Redfearn 1974). In 1974, 52000 toheroa (38% of the stock) were harvested in 11 days from an estimated harvestable population of 130000–136000 at Hokio

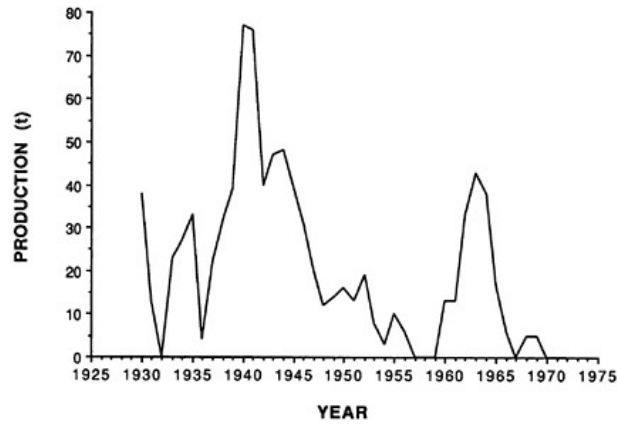


Figure 14 Commercial production (tonnes canned) of *Paphies ventricosa* from Ninety Mile Beach, Dargaville and Muriwai, 1930 to 1970. (From Redfearn, 1974).

on the Wellington west coast. In 1975, approximately 1 million clams (52% of the stock) were taken at Dargaville in a 14 day opening, leaving an estimated 926000 remaining on the beach. Legal recreational take was 76% of the stock in fisheries openings of one week duration at Wellington west coast beaches in 1978 (127000 of 167000 takeable clams from three beaches) and 1979 (60000 of 79000 from four beaches). An estimated 56500 *P. ventricosa* (6% of stock) were harvested in 9h at Oreti Beach in 1990 (McKinnon & Olsen 1994).

Recreational harvest of *P. ventricosa* was unregulated in 1921 (Mestayer 1921), and since then regulations on season, bag limit, size and methods have been increasingly restrictive as stocks declined in most areas. In 1932, a 2-month closed season, 50 clam per day bag limit, and minimum shell length of 76mm were imposed. A bag limit for Maori fishers of 80 clams per day was set in 1941. In 1953, harvest was restricted to a 2-month open season, and bag limits were reduced to 20 clams per fisher per day. The use of digging implements for *P. ventricosa* collection was prohibited in 1962. All North Island beaches were closed to toheroa harvest for the year in 1967. Open seasons were reduced to two weeks in 1972, 7 days in 1978, and 5 days in 1980. Minimum shell length for harvesting was increased to 100mm in 1979. *P. ventricosa* has been under total protection from all harvesting on North Island since 1980 (Haddon 1988).

The only two fishery openings since 1981 were single days at Oreti Beach on South Island (an 11-h opening in 1990 and a 9-h opening in 1993). Restrictions for the one day southern fishery recreational openings included: (a) a minimum stock projection of at least 1000000 legal sized animals remaining on the beach after the season at Oreti Beach and 450000 at Te Waewae Bay, (b) a closed reserve area at the south end of Oreti Beach, (c) a limit of five clams per person, and (d) no vehicles on the beach. The impact of illegal take on stocks of *P. ventricosa* is unknown, but may be significant.

The continued decline in toheroa stocks have been attributed to many factors over several decades: increased harvesting rates, illegal harvesting, changes in currents and phytoplankton production, mass mortalities, liquefaction of the sand by vehicular traffic, and sedi-

ment changes (Te Waewae Bay). Management efforts, including restrictions on harvesting season, size, bag limit, methods of digging, and closure of some fishery areas for over 20yr, have failed to restore stocks of this highly prized species to levels capable of sustaining fisheries.

The tuatua Paphies subtriangulata (Fig. 2n, p. 166)

Distribution

P. subtriangulata is endemic to New Zealand, and occurs on beaches on North Island, South Island, Stewart Island and in the Chatham Islands (Fig. 1, p. 164). Electrophoretic studies by Smith et al. (1989) suggest that there are three or four geographic groups of *P. subtriangulata* around New Zealand. Of these, the Chatham Island group is most isolated and has reduced heterozygosity. Shell morphology varies between beaches (J.E.Dugan & D.M. Hubbard unpubl. data).

Populations of *P. subtriangulata* occur across a remarkable range of beach types from high energy dissipative beaches to sheltered reflective beaches (J.E.Dugan & D.M. Hubbard unpubl. data). Adult *P. subtriangulata* generally occur from the low intertidal to shallow subtidal zones, but are occasionally found in dense beds in the mid intertidal (Grant 1994). Recruitment occurs in the intertidal zone, and individuals are reported to move to lower levels over time (Greenway 1969, Grant 1994).

Biology and ecological role

P. subtriangulata are broadcast spawners with separate sexes. The sex ratio is not significantly different from 1:1 (Grant 1994). Greenway (1981) reported that low condition index values for *P. subtriangulata* from Dargaville between October and December occurred during the spawning season. Grant (1994) found two major spawning periods at Little Omaha Bay, North Island, (October/November and February/March) and no resting period. Spawning was observed at high tide by Grant (1994). During spawning events clams extended their siphons beyond the usual distance from the bottom and expelled visible streams of gametes. Some individuals spawned for over 20minutes, and some aggregations exhibited spawning activity for up to 2h (Grant 1994). Female clams produced eggs that were about 60µm in diameter in the laboratory (Redfearn 1987), and larvae were reared successfully. Larvae settled at a size of 230µm after 17 days at 20°C (Redfearn 1987).

P. subtriangulata are suspension feeders with short siphons relative to *P. ventricosa*. In a study of Wellington west coast beaches, algae and hydroids present on the shells of *P. subtriangulata* were taken as evidence that they occupy shallower depths in the sediment than *P. ventricosa* and *P. donacina* (Richardson et al. 1982). *P. subtriangulata* have a burrowing rate typical of beach clams. McLachlan et al. (1995) reported that the BRI for juvenile clams was 7 at 20°C. Juvenile clams have been observed surfing in the swash zone with feet and siphons extended (J.E.Dugan & D.M.Hubbard unpubl. data). There is no evidence of tidal migration in *P. subtriangulata*. Predators on *P. subtriangulata* include birds, crabs and fish. *P. subtriangulata* form a considerable part of the diet of paddle crabs, *Ovalipes catharus* (Wear & Haddon 1987), but clams >40mm shell length may have some refuge in size. Sublethal predation in the form of siphon nipping by *O. catharus* has been observed during high tides (Grant 1994).

Population dynamics

Few studies have investigated the population dynamics of *Paphies subtriangulata*. Population structure of *P. subtriangulata* in the low intertidal and shallow subtidal was stable over 10 months (Grant 1994). Most individuals were between 30–65mm shell length, and the mean length of the dominant cohort was about 55mm (Grant 1994). Size structure and abundance of *P. subtriangulata* varied with beach morphodynamic type at 12 North Island sites. Clams from reflective beaches had larger average sizes than those from more dissipative beaches (J. E. Dugan & D.M. Hubbard unpubl. data).

Abundance of *P. subtriangulata* has been estimated for intertidal (Grant 1994, J.E. Dugan & D.M. Hubbard unpubl. data) and shallow subtidal areas (Cranfield et al. 1993, Grant 1994). Variability in abundance associated with beach type and harvesting pressure may affect the proportions of clams found in the two zones. Densities of *P. subtriangulata* were as high as 1400m^{-2} in the mid-intertidal at Ocean Beach in May 1992 (Grant 1994). Low intertidal and shallow subtidal densities averaged from 10 to 20ind.m^{-2} with maximum values of 55m^{-2} in adult aggregations at Little Omaha Bay (Grant 1994). Estimates of intertidal abundance at 12 North Island beaches were correlated with Dean's parameter and ranged from 25m^{-1} on a reflective beach to 495m^{-1} on a dissipative beach (J.E. Dugan & D.M. Hubbard unpubl. data). Much higher densities of *P. subtriangulata* have occasionally been reported: Grant (1994) estimated up to 6000m^{-1} at Ocean Beach in 1992. Estimated densities of larger *P. subtriangulata* from hydraulic dredge sampling in the subtidal ranged from $0\text{--}136\text{m}^{-1}$ (Cranfield et al. 1994), and biomass estimates were $0\text{--}1.3\text{kgm}^{-1}$. Intertidal biomass estimates from 12 North Island sites ranged $0.2\text{--}7.8\text{kgm}^{-1}$ and were not correlated with measures of beach state (J.E. Dugan & D.M. Hubbard unpubl. data).

P. subtriangulata attains a smaller maximum size and has a slower growth rate ($\phi' = 3.30$; Table 2, p. 168) than its New Zealand congeners, *P. ventricosa* and *P. donacina*. Grant (1994) estimated that clams reached 40mm shell length in 2yr, 50mm in 3yr and have a maximum age of more than 5yr. Large individuals reach lengths of $>80\text{mm}$, and weights of $>90\text{g}$. Greenway (1981) estimated that *P. subtriangulata* took 3 yr to grow to a size suitable for commercial harvesting.

Recruitment of *P. subtriangulata* is sporadic, and the abundance of cohorts from different years can vary greatly (Greenway 1969, Redfearn 1974, Grant 1994). Newly recruited clams can occur in high densities (up to 4cm^{-2}) in the intertidal (Greenway 1969, Grant 1994).

Fishery

P. subtriangulata have been harvested in traditional, commercial and recreational fisheries. Significant traditional harvest of *P. subtriangulata* is suggested by the large numbers of shells in coastal middens (Cranfield et al. 1994). Commercial landings of *P. subtriangulata* are substantial and have increased in recent years. The landings are primarily from north-western North Island, the area that formerly supported the commercial fishery for toheroa, *P. ventricosa*. Commercial fishery landings for *P. subtriangulata* averaged 53tyr^{-1} from 1974 to 1978, and 106tyr^{-1} from 1979 to 1984 (Greenway 1981, Haddon 1988). Recent landings were 83t in 1992, and 131t in 1993 (Fishing Industry Board unpubl. data). Fishers received a port price of $\text{US}\$600\text{t}^{-1}$ green weight in 1992, and $\text{US}\$480\text{t}^{-1}$ in 1993.

Tuatua are sold fresh, frozen and as prepared products including "toheroa-style soup" (Greenway 1981) for domestic and export markets. In New Zealand, *P. subtriangulata* is marketed in canned products, in jars, and as fresh whole and shucked clam meats for retail sales, catering and restaurants. In 1993, 26t (20% of landings) of chilled whole clams were

exported to the USA, and 4t (3% of landings) of frozen clams were exported to Reunion Island and Guam (Fishing Industry Board unpubl. data). The export price for frozen and chilled whole clams was US\$2.65kg⁻¹ in 1993 (Fishing Industry Board unpubl. data).

P. subtriangulata are harvested by hand at low tide. The number of permits issued for commercial take has decreased from 35 in 1981 to approximately six in 1994. There was a limit of three bags (c. 40kg) per fishers per day in 1981. In 1994, the limit was 300kg per fisher per day. Commercial harvest is prohibited in specified areas near access points for recreational fishers.

Data on recreational harvesting are not available, but landings are likely to be substantial in some areas. Recreational harvesting is unregulated except for a daily bag limit of 150 clams per person, and closed periods due to toxic algal blooms.

The tuatua Paphies donacina (Fig. 2o, p. 166)

Distribution

The second species of tuatua, *P. donacina*, is also endemic to New Zealand, occurring primarily along the west coast beaches of North Island, on sandy beaches of eastern South Island, and on Stewart Island (Fig. 1, p. 164). *P. donacina* is not known from northeastern North Island and is rare north of Auckland. *P. donacina* occurs on dissipative and intermediate beaches, and in some more sheltered locations including harbour mouths. Adult *P. donacina* are found in the low intertidal and in the subtidal to depths of 4m, but generally occur shoreward of the primary breaker zone (Cranfield et al. 1994).

Biology and ecological role

The sexes are separate in *P. donacina*, and occur in a ratio close to 1:1 (Dawson 1954). The eggs of *P. donacina* are larger than those of *P. ventricosa* and *P. subtriangulata*. Egg diameters of *P. donacina* are approximately 80µm (Dawson 1954) compared with 60–66µm in the other species.

P. donacina is a suspension feeder with short siphons that are held at the sand surface. *P. donacina* has slow burrowing rates relative to other beach clams (McLachlan et al. 1995). Juvenile *P. donacina* had a BRI of 3 at 15°C. Small clams have been observed surfing in the swash with feet and siphons extended. There is no evidence for tidal migration by *P. donacina*.

Predators of *P. donacina* include southern black-backed gulls, red-billed gulls, variable oystercatchers and South Island pied oystercatchers. Southern black-backed gulls have been observed diving in the shallow subtidal to extract buried clams of up to 100mm shell length, and opening them by dropping them on to the sand from a height (J.E.Dugan & D.M. Hubbard unpubl. data). Oystercatchers prey on smaller clams to about 50 mm shell length in the intertidal zone (J.E.Dugan & D.M.Hubbard unpubl. data).

Richardson et al. (1982) reported that the shells of *P. donacina* from Wellington west coast beaches were free of hydroids and algal growth, and suggested that they occur at greater depths in the sand than *P. subtriangulata*. This may vary geographically as shells of *P. donacina* from Otago beaches frequently bear hydroid clumps and algal growth (J.E. Dugan & D.M.Hubbard unpubl. data).

Population dynamics

High densities of *P. donacina* recruit to the intertidal where larger clams are rare. Small clams (mean length <10mm) were numerically dominant (>90%) in intertidal samples from ten Otago beaches (J.E.Dugan & D.M.Hubbard unpubl. data). Samples of *P. donacina* from the subtidal zone have length frequency distributions that are primarily composed of a substantial mode of large animals. These modes are probably composed of multiple year classes (Cranfield et al. 1993). The lengths of clams in these modes were mostly 50–80mm in samples dredged from Wellington west coast beaches, North Island, and 75–105mm in samples from Cloudy Bay, South Island (Cranfield et al. 1993). *P. donacina* sampled in the shallow subtidal at Warrington, South Island, had similar length frequency distributions with mean lengths of 71mm in February 1994, and 78mm in January 1995 (J.E.Dugan & D.M. Hubbard, unpubl. data). *P. donacina* sampled by Cranfield et al. (1993) reached larger maximum sizes on South Island beaches (95–109mm shell length at six sites) than on North Island (73–88mm shell length at four sites). The size structures of subtidal *P. donacina* populations were stable over time in nine samples from Cloudy Bay and eight samples from the Wellington west coast over 19 months (Cranfield et al. 1993).

Estimated biomass of subtidal *P. donacina* from 16 beaches across 11 degrees of latitude was 0–60kgm⁻¹ (Cranfield et al. 1994). Estimated biomass of *P. donacina* in the shallow subtidal at Warrington was 1.6kgm⁻² (J.E.Dugan & D.M.Hubbard unpubl. data).

Recruitment of *P. donacina* occurs across the entire intertidal zone (J.E.Dugan & D.M.Hubbard unpubl. data), with substantial variation in recruitment to different beaches. Estimates of recruit densities (2–12mm shell length) for east coast beaches of South Island (Otago) in 1994 varied from 0 to >3000m⁻¹, and beaches north of Cape Saunders had much higher densities of young-of-the-year clams (>900m⁻¹) than those to the south (<60m⁻¹) (J. E.Dugan & D.M.Hubbard unpubl. data).

Growth rates and maximum sizes (109mm shell length and 180g WW) for *P. donacina* are intermediate to those of *P. subtriangulata* and *P. ventricosa* (ϕ' growth rate index=3.47; Table 2, p. 168). Growth rates of subtidal *P. donacina* were estimated from a one year mark-recapture experiment at Cloudy Bay (Cranfield et al. 1993). No increase in length was measured for a large proportion of the clams with initial lengths >70mm. It would take 5yr for recruits to reach marketable sizes (approximately 75mm). Analysis of shell sections indicated that *P. donacina* reach ages up to 17yr. Cranfield et al. (1993) estimated *M* of *P. donacina* at 0.26–0.32yr⁻¹ for Cloudy Bay.

Fishery

Artisanal, commercial and recreational fisheries for *P. donacina* are smaller than those for the other beach *Paphies* species in New Zealand. The commercial fishery for *P. donacina* is currently very small, but there is potential for substantial landings if the surf-zone clam fishery develops further. One fisher is currently harvesting surf clams commercially by hydraulic dredge in central New Zealand, but total landings were less than 5tyr⁻¹ from 1990 to 1992 (Cranfield et al. 1994). *P. donacina* is one of several species harvested, and composed 20% and 29% of the estimated stock biomass at Cloudy Bay and Clifford Bay, respectively (Cranfield et al. 1994). Cranfield et al. (1994) estimated maximum constant yield [$MCY=0.25 (F_{0.1})$ (virgin biomass)] for *P. donacina* at two sites: 15.5tyr⁻¹ (1.4kgm⁻¹yr⁻¹) from Cloudy Bay (11km), and 25.8tyr⁻¹ (1.1kgm⁻¹yr⁻¹) from Clifford Bay (23.5km). No data are available on the recreational harvest of *P. donacina*, but harvesting rates are probably much lower than for *P. subtriangulata*. The recreational fishery for *P. donacina* is unregulated except for a daily bag limit of 150 clams per person, and closures due to toxic algal blooms.

Discussion

General

Several clear patterns and contrasts emerge from the foregoing review. Many of the species covered in this review are large (Table 2, p. 168) and found on temperate dissipative beaches in areas of high primary production, which is often in the form of surf diatom blooms. Species from warmer waters tend to be smaller, occupy a wider range of beach types and support artisanal fisheries, while large species in temperate areas support or have supported commercial fisheries.

The species covered all come from exposed ocean beaches but can be divided into intertidal and subtidal forms (Table 2), the latter with adults in the surf zones and the former with adults on the intertidal beach. In both cases juveniles tend to settle at different levels before migrating to the adult zone. A third zonation pattern is intermediate between these two extremes, with adults in the shallow swash, extending both into the intertidal and out into the surf zone. In the case of one species, *Donax serra*, an intertidal distribution occurs in a warm part of its range and subtidal distribution in a colder part. A similar temperature effect is seen in *Mesodesma mactroides*, which occurs subtidally in the cold winter months and intertidally in summer. This seems, at least in part, to match the other species patterns: there appears to be a good relationship between tide level occupied by a clam species and water temperature, those occurring in the warmest waters (*Donax denticulatus*, *D. striatus*, *D. faba*, *D. cuneatus* from tropical and *Mesodesma mactroides*, *Donax serra*, *D. trunculus*, *D. deltoides*, *Tivela stultorum* from warm temperate areas) being either intertidal or tidal migrants, whereas those from higher latitudes (*Siliqua patula*, *Mesodesma donacium*, *Paphies donacina*) are mixed or subtidal. The explanation for this may lie in Donn's (1990a) hypothesis that the subtidal shift in *Donax serra* populations in areas of lower water temperature is a consequence of slower burial rates at these temperatures and thus inability to maintain position in the dynamic swash conditions of the intertidal zone. Burial time increases with size in bivalves (McLachlan et al. 1995) and large species such as these may be extremely slow at low temperatures. This would make repositioning and burial on the beach face, an essential process on dynamic beaches, difficult or impossible.

Many of the species covered are large (>50mm) and, unlike many other beach animals, do not undergo tidal migrations. They thus differ from the small, highly mobile donacids and other species typical of reflective and intermediate beaches, especially in warmer climates. McLachlan et al. (1995) have shown that bivalves from ocean beaches can be separated on the basis of size, density and shape into forms typical of reflective, intermediate and dissipative beaches. Those from intermediate and dissipative beaches include large forms with low densities and variable shapes, in contrast to the small, dense, wedge-shaped forms strongly selected to cope with the turbulent swash conditions of reflective beaches. Donn (1990b) found intertidal populations of *D. serra* to have higher densities, and smaller, thicker, less-rounded and more wedge-shaped valves than subtidal populations. Some of the bivalves listed here clearly fall into the category of large species with low densities and subtidal distributions. The exceptions are probably *D. serra* on the south coast of South Africa, *D. deltoides* in Australia, and *D. trunculus* in Europe, which are intermediate between the bulky forms from dissipative beaches and the small, dense forms from reflective beaches such as those found in the tropics. This may explain the ability of these three species to colonize a fairly wide range of intermediate beach types and to maintain intertidal positions.

The species supporting substantial beach clam fisheries in temperate areas tend to be larger, longer-lived and with higher growth rates than many other beach bivalves (Table 2, p. 168). Many have life spans exceeding 5yr and can attain high biomass values, contributing significantly to biomass on the beaches where they occur. Most occupy central positions in beach food chains, often constituting the dominant prey of birds, fishes and crabs. But the impacts of clam beds on beach ecology may extend beyond their role in energy flow. Although competitive interactions have not been demonstrated in exposed sandy beaches, the presence of substantial numbers and biomass of large filter feeders may be expected to affect other species on the beach. Competitive interactions in sediments are generally not strong because of the three dimensional space and the effectiveness of predation in keeping numbers below carrying capacity (Peterson 1979). However, de Alava (1993) has shown in the case of *Mesodesma mactroides* that competition with *Donax hanleyanus* may occur since the latter exhibits recruitment fluctuations inversely correlated with both abundance of juveniles plus adults of *Mesodesma mactroides* and also the amount of fishing effort focused on the latter (Defeo & de Alava, 1995).

The role of density-dependent processes in structuring exploited sandy-beach populations must not be neglected. Defeo (1993a) demonstrated reduced recruitment under high adult density, presumably due to filtration of larvae on a microscale. The strength of a newly settled cohort could also be inhibited by density-dependent growth and mortality rates. Depression of growth rates at high density could also have an effect on subsequent recruitment events produced by these cohorts. For example, cohorts with lower growth rates would not achieve the size at maturity during the spawning season, thus affecting fecundity and possibly leading to recruitment failure (Defeo et al. 1992b). Conversely, at low adult densities growth rates may be higher and the consequent size at maturity may be achieved during the normal spawning season.

Population dynamics of species supporting beach fisheries are not particularly well studied and in many cases data on recruitment, stock size, mortality and growth are incomplete or absent. The two North American clams, *Tivela stultorum* and *Siliqua patula*, *Donax serra* from South Africa, *Paphies ventricosa* from New Zealand and *Mesodesma mactroides* from Uruguay, have been best studied in this regard. Recruitment is probably the least studied aspect of beach clam fisheries and has been quantified in only a handful of cases. It has been shown to be stock dependent on a macroscale in *M. mactroides* but may be independent in *Tivela stultorum*. Most species have rapid growth to sexual maturity and then slower but nevertheless indeterminate growth and various growth models have been successfully applied (Table 2, p. 168). Mortality rates vary considerably between species, beaches and years and total mortality can be high, ranging $0.5-3.1\text{yr}^{-1}$ in different situations. Fishing mortality makes up a significant proportion of this in some cases and associated incidental mortality (clams not taken but discarded on the surface to die) can be a major cause of mortalities. Survival probably increases with age in all cases, especially the long-lived species.

Human utilization of beach clams extends far back into pre-history on most coasts. Today beach clam harvests seem to be clearly divided into recreational and commercial fisheries, with a clash of interests between the two in many cases. The scenic nature and sporting potential of beaches renders them ideal for the development of recreational activities, and recreational fisheries have even replaced commercial fisheries (especially for species in areas with high human density, e.g. *Siliqua patula*, *Tivela stultorum*) as beach recreation becomes more popular and human population increases. Recreational activities on beaches, are not, in general conducive to coexistence with commercial fisheries, especially for intertidal species in warm climates (*Donax serra*, *D. deltoides*) where beach recreation is

extremely popular. For subtidal species this appears less of a problem since fishing effort is based below the intertidal beach. While all fisheries include some recreational components, artisanal fisheries predominate in South America and some tropical areas. Commercial fisheries, which in the past were strongly developed in the case of *Siliqua patula*, are still important only in the case of *Mesodesma donacium* in Chile. It appears that the tendency in beach clam fisheries is towards more recreational/artisanal fisheries and away from large commercial operations, although the former may have commercial interests.

Intertidal species are readily accessible and harvest incurs very low operating costs, thus they are particularly vulnerable to over-exploitation and require careful management. In contrast, subtidal species occupying high energy surf zones are relatively inaccessible and less management is required. In recreational fisheries, limits to the number of fishers are generally not possible and managers have made recourse to size and bag limits, restrictions on collecting gear and closed seasons and areas. However, for many of these fisheries research and management are limited or non-existent. In a few areas restocking or enhancement has been tried as a management tool but, on the whole, the idea of reseeding beaches has not been tested and in most cases little is known of larval biology. Only on the northwest American coast does management seem well developed.

Beach clams are used for food and bait. They obtain best prices as food and clams can reach US\$30kg⁻¹ in their shells. In areas with restricted access to markets, limited demand for clam meat, or high occurrence of toxic algal blooms, a significant proportion of the take goes to bait for crabs and fishes in other recreational or commercial fisheries.

A problem affecting commercial fisheries that target beach clams for eating is the tendency of several species to accumulate phytoplankton toxins produced by blooms of certain species of phytoplankton. High levels of toxins, such as PSP and domoic acid, are harmful to consumers of bivalves and pose health hazards to humans and other animals. This limits the potential utilization of many stocks in cooler waters and creates the need for careful monitoring and management. As human impacts on coastal waters continue, blooms of toxin-producing phytoplankton could affect beach clam fisheries more (e.g. Hallegraeff 1993).

In general it appears that beach clam fisheries are ubiquitous features of open coasts in all latitudes. Despite their extent they are relatively small in comparison with some commercial clam fisheries. For example the offshore fishery for “surf clams” (*Spisula solidissima*) and quahogs (*Arctica islandica*) off the east coast of the USA had landings of 56000t and a first sale value of US\$58 million in 1986 (Murawski & Serchuk 1989). Total beach clam takings for all species covered in this review is not known but is today certainly below this figure, although in the past landings of *Tivela stultorum* were comparable.

Future research needs

Based on this review, we suggest that a number of topics deserve special consideration in order to provide a sound scientific basis for management of beach clam fisheries.

Recruitment processes

Little is known about dispersive abilities of meroplanktonic larval phases of exposed sandy beach macrofauna (Efford 1970) and the mechanisms influencing larval distribution are still poorly understood. Research should focus on planktonic stages and the role of near shore hydrodynamics in settlement processes. This will determine the spatial scales at which population dynamics may be considered an open process, i.e. if it is more related to the arrival

rates of larvae than to post-settlement processes. Efford's (1970) hypotheses should be tested to determine whether exposed sandy-beach populations could be considered as self-sustaining, with relative isolation of the rest of the species distribution. The inclusion of physical-oceanographic information related to larval dispersal would be of importance in this context. In addition, potential mechanisms associated with over-compensatory processes in stock-recruitment relationships, such as passive filtering of larvae by adults, should be examined by field and laboratory studies.

Density-dependent processes Spatial and temporal variations in growth, mortality and recruitment rates in sandy-beach populations may be related in part to density-dependent processes in sandy-beach populations (Defeo, 1993a, J.E.Dugan unpubl. data), and hence could affect the clam stock available for exploitation (Defeo et al. 1992b). However, as these processes are relatively unknown for exploited beach clams, future work should emphasize scale-dependent experimental manipulations of resource abundance and population density.

Disturbance associated with harvesting and incidental mortality The natural mortality rates of the unharvested fraction of exploited sandy-beach populations may be directly related to the amount of fishing effort (Schink et al. 1983, Lassuy & Simons 1989, Defeo, 1993a), suggesting that harvesting activities constitute a source of sediment disturbance and incidental damage particularly in intertidal species. Furthermore, incidental effects (shell damage) of fishing pressure could affect harvested and unharvested populations in sandy beaches (Defeo & de Alava 1995, Sims pers. comm.). Such short-term effects need to be further tested through direct quantification of incidental damage and mortality, as in the *Siliqua patula* fishery where wastage is reported (Ayres & Simons 1992), and the effects of substratum perturbation (e.g. mortality of clams immediately after fishing manipulation versus control areas). In clam fisheries where harvesting produces significant incidental mortality, the reduction of minimum size limits may reduce losses of small clams (see Lassuy & Simons 1989). Such regulatory measures could be experimentally evaluated in vulnerable clam stocks. In order to evaluate the long-term effects of harvesting on the population dynamics of the target species and other species within the community, human exclusion experiments (see Defeo, 1993a) could be used.

Modelling and management Management must account for temporal and geographic variation in life history and population dynamics characteristic of fished stocks, e.g. *Mesodesma donacium* of Chile, *Donax serra* of South Africa. Since the allocation of fishing effort closely follows spatio-temporal variations in resource abundance, fishing effort and catches should also be obtained discriminately by homogeneous areas (see Defeo et al. 1993 and references therein). The spatially discrete analysis of sandy beach stocks, the surrounding environment, and the fishery, will be a useful tool for (a) the assessment of spatial dynamics of catch and fishing effort, (b) the detection of changes in length or age composition of the catch, and (c) monitoring changes in stock abundance and its composition by size and/or age, as well as in other population dynamics parameters and environmental variables. From the above, an integrated approach could be built to develop a comprehensive management scheme of the fishery (Defeo et al. 1993). Since aquaculture has not been feasible in most of the species reviewed, and considering their increasing demand, we recommend an experimental approach to management through rotation of fishing areas, creation of spawning stock refuges and restocking through direct seeding of juveniles or adults (Castilla 1988, Defeo 1993b, Dugan & Davis 1993). A spatial management scheme could complement these

strategies by accounting for spatial variation in the magnitude of recruitment, and thus protecting those areas with high probabilities of successful recolonization (Caddy 1989).

Future prospects

Although beach clams do not provide very large commercial catches they are ideally suited to recreational exploitation because of the popularity of beaches as recreational areas. Ready accessibility, large size and slow growth of several temperate species does, however, necessitate careful management to prevent unsustainable exploitation. The same may hold for tropical species, especially in areas where large numbers of poor people depend on these for subsistence. Unfortunately, beach clam stocks have often received limited attention by authorities and fisheries managers, as evidenced by the paucity of information reviewed. It is important that these stocks be seen as a valuable resource even where they do not support commercial exploitation. The value of recreational fisheries lies not only in the value of the meat but also in the recreational enjoyment of the whole experience. Thus the true value of beach clam stocks may include a small food component and a large recreational activity component. This must be recognized and managed so that beach clammers can be assured of a quality recreational experience even if their take is modest.

Over-exploitation by recreational and commercial interests is not the only threat facing beach clam fisheries. Any threat to beaches in general also threatens the stocks. Off-road vehicles, pollution, heavy recreational pressure, coastal engineering structures, beach erosion or replenishment programmes and coastal development all pose problems. With increasing global population and sea level rise, both directly impacting on ocean beaches, these stocks must be assumed vulnerable and the formulation of dynamic management strategies is essential.

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