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Review

Introductions: some biological and ecological characteristics of scallops

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Abstract

Several molluscs that have been introduced world-wide have become economically important for coastal communities. As far as it is known, at least four scallop species (*Argopecten irradians, Argopecten purpuratus, Patinopecten yessoensis, Pecten maximus*) have been moved between different biological provinces and it is possible there will be further such movements. Making an introduction involves responsibilities and so requires careful consideration. This is because there have been several unwanted impacts with movements of molluscs in the past. The International Council for the Exploration of the Sea's (ICES) 1995 Code of Practice on the Introductions and Transfers of Marine Organisms and recent revision provides a basis for undertaking such an action wisely. In this review, scallops that may be used in future cultivation or in fisheries as potential candidates are examined in relation to the first phase of an introduction—the prospectus. This prospectus should take account of the purposes and objectives of the introduction, including relevant biological, pathological and ecological conditions in the donor region and the potential impacts of the species in the expected range occupied in the recipient region. This may require a study visit to the donor region to evaluate concerns relating to potential hazards. The ecomorphology of five different scallop shell morphs is discussed in relation to their behaviour and occupied habitat. Such information may provide an indication of their interaction with native scallop species in advance of their introduction.

Résumé

Introductions : caractéristiques biologiques et écologiques des coquilles St-Jacques et pétoncles. Plusieurs mollusques qui ont été introduits de part le monde sont devenus importants économiquement pour les populations littorales. Au moins quatre espèces (*Argopecten irradians, Argopecten purpuratus, Patinopecten yessoensis, Pecten maximus*) ont été transportées entre différentes régions et il est probable qu'il y en ait d'autres. Introduire une espèce implique des responsabilités et demande quelques précautions. Précédemment, il y eut diverses conséquences indésirables, à la suite de transferts de mollusques. Le Code pratique des introductions et transferts d'organismes marins du Conseil international pour l'exploration de la mer (CIEM-ICES, 1995) fournit une base pour entreprendre cela prudemment. Les coquilles St-Jacques et pétoncles, qui pourraient faire l'objet d'élevage par la suite ou bien être pêchés, sont étudiés en relation avec la 1ère phase d'une introduction par une étude prospective. Cette étude prospective doit prendre en compte les raisons et les objectifs de l'introduction, y compris les conditions biologiques, pathologiques et écologiques de la région « donneuse » d'origine et les impacts potentiels de l'espèce dans la zone prévue de la région destinataire. Ceci peut demander une visite d'étude dans la région d'origine pour évaluer les risques potentiels. L'écomorphologie de cinq formes différentes de coquilles est discutée en relation avec leur comportement et l'habitat ; de telles informations peuvent fournir une indication de leur interaction avec les espèces autochtones, préalablement à leur introduction.

Keywords: Introductions; Management; Ecomorphology; Culture; Scallop

1. Introduction

Most managers will reflect on whether they have in cultivation the most suitable scallop species for their purposes and so will consider the possibility of introducing a scallop that is in cultivation from elsewhere in the world. Native species should be examined before any such decision is made. However, once a species is successfully hatchery reared, grown in culture or ranched attracts attention and this could lead to a plan to introduce that species (Minchin and

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Rosenthal, 2002). The carrying out of an introduction carries responsibilities, and the International Council for the Exploration of the Sea's (ICES) Code of Practice on the Introductions and Transfers of Marine Organisms (ICES, 1995) provides guidelines for such an introduction to take place. This code is updated from time-to-time with improved scientific knowledge as in the current draft (http://www.ices.dk). In this account some considerations, as required in the prospectus phase of the ICES code in advance of an introduction taking place, is examined and some ecomorphological features of scallops are discussed in relation to their habitat occupation and behaviour.

Molluscs are also spread unintentionally by shipping, either in ballast tanks or on ships' hulls (Carlton, 1992). Adult molluscs have been found attached to ships' hulls with mussel and oyster species occurring frequently (Gollasch, 2002). However, there are no known accounts of scallops carried by ships. This is despite their occasional heavy natural settlements on aquaculture equipment (personal observation). Introductions by ships should be of concern because pests, parasites and diseases could also be spread in this way (Minchin and Gollasch, 2002a).

Large consignments of molluscs, such as oysters, were deliberately introduced in the past without any quarantine measures and such actions should not be repeated. Such movements can include unwanted biota (Verlaque, 2001) and result in declines in production (Chew, 1990; Minchin, 1996; Carlton 1992). Fortunately the majority of unintentionally introduced species are benign and great numbers almost certainly remain cryptogenic (of "hidden-origin" as defined by Carlton, 1996). Rarely do unintended introductions become of economic benefit.

Nevertheless, transfers of large volumes of molluscs regularly take place in the course of culture practices (Grizel, 1994; Gruet et al., 1976) and with free-trade between countries (Jenkins, 1996). Unauthorised introductions including harmful species may now become rapidly spread with stock movements (Sindermann, 1993). Imported molluscs intended for direct human consumption may be held in the sea and so may release progeny or escape thereby expanding their range (Minchin and Gollasch, 2002b). *Bonamia ostreae*, a sporozoan parasite of oysters, probably increased its range in Europe in this way following transfers of *Ostrea edulis* (Hudson and Hill, 1991), although this protozoan may also have been spread by coastal craft (Howard, 1994).

Scallops are widely distributed from the intertidal area (*Mimachlamys varia*) to ~7000 m (*Hyalopecten*) (Waller, in Shumway, 1991). They can attain sizes >24 cm (*Patinopecten caurinus*), and occupy cold water areas with reduced salinity near the seaward end of glaciers (*Zygochlamys patagonica*) to sub-tropical and temperate estuarine bays (*Argopecten irradians, M. varia*) and tropical shallow seas (*Amusium japonicum*). They are widely regarded as a quality product and attain a higher market price than most other marine foods. Consequently they are likely to be introduced once culture techniques lead to economic successes. The ICES Code of Practice (ICES, 1995) provides a responsible way in which such an introduction may proceed and following this code can considerably reduce unwanted impacts.

1.1. The ICES code of practice

The ICES Working Group on Introductions and Transfers of Marine Organisms initially arose out of the necessity to manage parasites and diseases with importation of exotic species for culture, but later included ecological and genetic considerations (ICES, 1995). The code is updated from time-to-time, taking into account changes in technology and recent developments in the current revision includes issues relating to trade. In regions where there is a dependency on a small number of molluscan aquaculture species, alternative species, which may include introductions, should be considered and should take place with sufficient time so that molluscan production involving a "new" species does not become an urgent matter.

The main elements of this ICES code may be summarised as follows:

(a) A prospectus of the species to include a comprehensive account of the biology, ecology and its associated organisms, physiological expectations, reproductive capabilities and an evaluation of the likely problems for the species that may arise in culture, or should it escape or be released to the wild.
(b) An examination of earlier introductions of the candidate species elsewhere, and an evaluation of reasons for their success or failure.
(c) A critical examination of potential problems by a scientific forum, who may require further information from a study tour in the donor region.
(d) Introductions of the candidate species through a rigorous quarantine.
(e) Release of the F1 or subsequent generations, only if free of parasites and disease agents.
(f) Development of a pilot scale project with contingency measures to withdraw.

Compiling the prospectus is the first stage, the following account provides an approach to manage the elements (a) and (b) in part.

2. The biological and ecological characteristics of the scallop species candidate for introduction

2.1. Objectives of an introduction

Reasons for species introductions may include, biotechnology, food production, habitat modification, biological control, development of a recreational fishery or as food for other organisms. Generally molluscan introductions are intended for cultivation to provide a product for human consumption. To date four scallop species have been introduced to different world regions (Table 1). Not all of these introductions were via quarantine or were successful.

Table 1
Criteria pertinent to scallop species that have been introduced (Ht, shell height; L, shell length)

Species	*A. irradians*	*A. purpuratus*	*P. yessoensis*	*P. maximus*
Spawning	Protandrous hermaphrodite, at 25–30 °C in early summer	Protandrous hermaphrodite, mainly spring and autumn but all year spawning is possible	Dioecious, spawns with temperature rise in spring at 6–8.5 °C	Protandrous hermaphrodite May to September at >11 °C
Larval development	Eggs 55–65 µm, remain in plankton 10–19 days at 20–28 °C	In plankton for 35–40 days	22–35 days at 7–13 °C and 15 days at 17–19 °C	16–33 days at 15–20 °C, settle at 190–260 µm
Settlement	From 148–216 µm, at low temperatures may reach 260 µm	At about 240 µm	At 230–286 µm	June to September on hydroids, marine algae
Growth	Survives only 2 years	Attains 9 cm Ht in 2–2.5 years	Can attain 6 cm in 1 and 10 cm in 2 years in culture	3–6 years to attain 11 cm L
Natural collections	Hatchery reared	Hatchery reared	In large bays, industry based, larvae collected on collectors	In coastal bays, Scotland, Ireland
Hanging culture	Intensive hanging culture, using pearl and lantern nets	Intensive hanging culture using pearl and lantern nets	Intensive culture using different methods in suspension	Trays in frames on bottom, Lantern nets for juveniles
Sowing culture	No	No	Sown at 3 cm+, extensive method on plots on seabed	From 3–5 cm, depending on crab species present
Cultured to market size	Yes	Yes	Yes	Normally ranched
Benefits	Short larval life and easily cultured. Tolerant to handling, wide temperature range –3 to 30 °C, salinities 20–38%, has rapid growth	Cold water, fast growing, may be robustly handled, easily cultured	Cold water, rapid growing, tolerant of handling, culture methods well understood	Sown culture produces shells with little fouling
Disadvantages	Small size, high handling	Great variability of stock following hydrographic conditions	High handling, toxic algal blooms in some areas affect production	Sown scallops have weaker shells
Successful cultivation in native range	Partly	Yes	Very successful cultivation and sowing	Still being researched
Successful cultivation in introduced area	Large production based on intensive suspended cultivation	In part, in culture only	Successfully cultivated in west Canada, experimental and failures elsewhere	No
Reasons for introduction	Developmental project	Developmental project	Uninformed entrepreneur, business project, developmental projects	Uninformed entrepreneur, developmental project

2.2. Selection of a species

Usually a species considered for introduction is either fished or is in cultivation. Information on its biology, behaviour and pathology would normally be available. When compiling a prospectus this information must be compiled to include relevant information from laboratory reports or memos from the source region.

Some characteristics of known commercial scallops world-wide are summarised in Table 2. It is from these species, whose larval culture have been successfully achieved, that future introductions are likely to occur.

In some cases, the transfer of a genetically distinct population, that has specific characteristics, may be under consideration for culture within its natural or extended range. The numbers of individuals used in transfers should take account of expectations of survival and heterogeneity of the population. A knowledge of the handling of scallops in transport may greatly increase survival (Minchin et al., 2000) and so reduce the numbers required.

2.3. Potential habitat breadth

It is difficult to predict the potential range of a species in advance of an introduction. Yet it will be a requirement to determine whether the introduction is likely to result in competition with native commercial species. The substrata preferred and behaviour of scallops using ecomorphology as a tool may enable some predetermination. Similar ecomorphs are expected to utilise similar habitats and have either overlapping or coinciding ranges.

Shell design does not arise from biophysical demands alone, but includes modifications that have evolved along with the abilities of their principal natural predators. For example, architecture and shell strength may be modified according to sizes and shapes of crab chelae and crab behaviour. An introduced species may be vulnerable to these different predators and so suffer unpredicted mortality. Shell strength is an important criterion in determining levels of predation by crabs in on-bottom culture (Minchin, 2002). For this reason, an ecomorphological approach can only be considered to be at best a general guide.

Table 2
Scallops of economic importance and regions of introduction in bold. Regions of introduction are in bold. D, diver fished; exp., experimental; Ht, shell height; L, shell length. 1, Ansell et al. [a]; 2, Blake and Moyer [a]; 3, Bourne [a]; 4, Brand [a]; 5, Bull [a]; 6, P. Cook, personal communication; 7, Del Norte [a]; 8, J. Fang, personal communication; 9, Felix-Pico [a]; 10, Gwyther et al. [a]; 11, J. Himmelman, personal communication; 12, J. Illanes, personal communication; 13, Ito [a]; 14, Lodeiros et al., 1993; 15, Lodeiros et al., 1998; 16, Lou [a]; 17, Lykakis and Kalathakis [a]; 18, Margus [a]; 19, Mason, 1983; 20, Naidu [a]; 21, Orensanz et al. [a]; 22, P. Penchaszadeh, personal communication; 23, Parsons, et al. [a]; 24, Personal observation; 25, Piquimil et al. [a]; 26, Renzoni [a]; 27, Rhodes [a]; 28, Robins-Troeger and Dredge, 1993; 29, Rose and Dix, 1984; 30, de Villiers, 1976; 31, W. Stott, personal communication; 32, Wolossek [a]; 33, P. Zolotarev, personal communication

Ecomorph	Species	Range	Culture/fishery	Max age (years)	Commercial size (max) (cm)	Depth range normal (full range) (m)	Reference
A	*Crassadoma gigantea*	Pacific Canada and USA	"Fishery" (D), exp. culture	27	9–20 (25) Ht	(1–80)	3
B	*Aequipecten tehuelchus*	Southern Brazil to Argentina	Fishery (D), exp. culture, not larvae	11	6–9 (10) Ht	10–30 (10–90)	22, 25
B	*Chlamys farreri*	China seas, North Japan, West Korea	Fishery, culture	6	7–8 (10+) Ht	5–30 (5–147)	8, 16
B	*Chlamys hastata*	California to Alaska	Fishery (D) exp. culture	5+	6–7 (8) Ht	(5–150)	3
B	*Chlamys islandica*	North Atlantic, Canada to Norway, White Sea	Fishery, exp. culture	>23	8–14 (16) Ht	40–100 (10–250)	23, 33
B	*Chlamys rubida*	North California to Alaska	Fishery (D), exp. culture	6+	6–7 (7) Ht	(5–200)	3
B	*Chlamys vitrea*	Chile, Patagonia	Fishery (D)	~10	6–8 (10) Ht	15–30 (~50)	31
B	*Flexopecten glaber*	Mediterranean	Fishery, exp. culture, not larvae	2+	5–6 (8) Ht	(<5–19)	17
B	*Flexopecten flexuosus*	Mediterranean	Fishery	2+	(9) Ht	10+	18
B	*Mimachlamys asperrima*	Australia, Tasmania, West Pacific	Fishery, exp. culture		6–10 (12) Ht	(7–69)	29
B	*Mimachlamys nobilis*	South China, Japan, Indonesia	Fishery (D), culture	4+	8–10 (12) Ht	2–7 (~360)	16
B	*Mimachlamys senatoria*	Japan to Indonesia	Fishery, ranching, culture	<3	6–8 (12) Ht	2–7 (0–360)	13
B	*Mimachlamys varia*	Denmark to Senegal and Mediterranean	Fishery, ranching, exp. culture	6	4–6 (10) Ht	0–30 (~82)	1
B	*Nodipecten nodosus*	Caribbean Sea to Brazil	Fishery (D), exp. culture	2+	5–6 (15) Ht	8–34	14
B	*Nodipecten subnodosus*	California to Peru	Fishery (D), exp. culture	7	10–15 (20) Ht	3–35	9
B	*Swiftopecten swifti*	Sea of Othotsk to North Japan, Korea	Fishery	13	(12+) Ht	2–50	8
B	*Zygochlamys delicatula*	New Zealand	Fishery	5+	6–7 Ht	80–200	5
B	*Zygochlamys patagonica*	Chile to Argentina	Fishery (D), exp. culture	13+	5.5–7 (12) Ht	20–175 (2~960)	32
C/E	*Euvola laurenti*	Gulf of Mexico	Fishery (by catch)	1+	6–8 (9) Ht	20–30	22
C	*Euvola vogdesi*	South California to Peru	Fishery (D), exp. culture	3	6–8 (10) Ht	12–40 (~40)	9
C	*Euvola ziczac*	Gulf of Mexico, Atlantic North South America	Fishery (D), exp. culture	3+	6–11 (13) Ht	8–20 (~50)	15
C	*Pecten albicans*	Korea to Taiwan, Japan	Fishery, culture	4	6/8–12 L	20–120	13
C	*Pecten fumatus*	Australia, Tasmania	Fishery (D), ranching, exp. culture	14	8–10 (11) L	7–60	10
C	*Pecten jacobeus*	Mediterranean	Fishery	10	7–14 (17) L	5–50 (5–70)	18, 26
C	*Pecten maximus*	Northern Norway to West Africa, Faroes, **Chile, China**	Fishery (D), ranching, culture	~22	10–16 (21) L	10–45 (0–183)	19
C	*Pecten modestus*	West Australia	Fishery	10	6–8 (10) L	14–22 (5–35)	10
C	*Pecten novaezelandiae*	New Zealand	Fishery, ranching, exp. culture, no larvae	10	10–14 (16+) L	10–25 (~90)	5
C	*Pecten sulcicostatus*	South Africa	Exp. fishery, exp. culture	>9	6–9 (10) L	36–42	6, 30

(continued on next page)

Table 2 *(continued)*.

Ecomorph	Species	Range	Culture/fishery	Max age (years)	Commercial size (max) (cm)	Depth range normal (full range) (m)	Reference
D	*Aequipecten opercularis*	Norway to West Africa, Mediterranean	Fishery, exp. culture, larvae difficult	10	5–8 (9) Ht	15–50 (5–128)	4
D	*Annachlamys leopardus*	West North and East Australia	Fishery, exp. spat collections	2+	4–6 (7) Ht	10–30	24, 28
D	*Argopecten gibbus*	Bermuda to Gulf of Mexico	**Fishery**, exp. **culture**	2	3–4+ Ht	20–50 (5–370)	2
D	***Argopecten irradians***	Nova Scotia to New Jersey, **China, Canada**	Fishery, culture	2	4–7 (8) Ht	1–9 (0–20)	27
D	*Argopecten nucleus*	Florida and Caribbean	Exp. culture	<2	(5) Ht	15–20	11, 14
D	***Argopecten purpuratus***	Peru to Chile, **Chile**	Fishery (D), culture	8+	9–12 (16) Ht	2–40 (0–400)	12, 25
D	*Argopecten ventricosus*	Baja California to Peru	Fishery (D), culture	2	5–7 (10) Ht	0–20 (0–150)	9
D	*Equichlamys bifrons*	Southern Australia	Fishery, exp. culture		(10) Ht	2–40	10
D	*Patinopecten caurinus*	Alaska, West Canada to North California	Fishery	28	12–16 (25) Ht	70–110 (10–200)	3
D	***Patinopecten yessoensis***	Japan, China, West Russia, **Europe, Canada**	Fishery (D), culture	>20	4–18 (22) Ht	14–30 (0.5–82)	13
D	*Placopecten magellanicus*	St. Lawrence to North Carolina	Fishery, culture	29	10.5–18 (21) Ht	10–100 (0–384)	20
E	*Amusium japonicum*	China to northern and western Australia	Fishery, exp. culture	3+	9 (12) Ht	30–60 (10–75)	10
E	*Amusium pleuronectes*	China, Indonesia to North Australia	Fishery, exp. culture	2	5–8 (~10) Ht	18–40 (<14–80)	7
E	*Euvola marensis*	Caribbean	Fishery (bycatch)	1+	6–8 (8) Ht	32–65 (11–128)	22

[a] In Shumway (1991).

Scallops have a larval pelagic stage lasting about two to four, or more weeks, and so become widely dispersed. Once settled, they develop varying morphologies allowing the occupation of different habitats. A summary of ecomorphological features, together with other criteria, appears in Table 3. The five ecomorphs are.

2.3.1. Ecomorph "A"

Cementing scallops with a short benthic free-living/byssally attached juvenile stage before attachment at <4 cm and a confinement to hard substrata (Yonge, 1951). The juveniles cement themselves in dark spaces, such as barnacle "cups", shell spaces (personal observation) and clefts in rocks. Adults have massive and irregular shells. The ribs are not normally prominent because the shell strength comes from the shell thickness. Prominent scales may project from the surface of the shell. Sponges often extensively bore within the shells. The only known commercial species is found in the cold to temperate seas of the North Pacific.

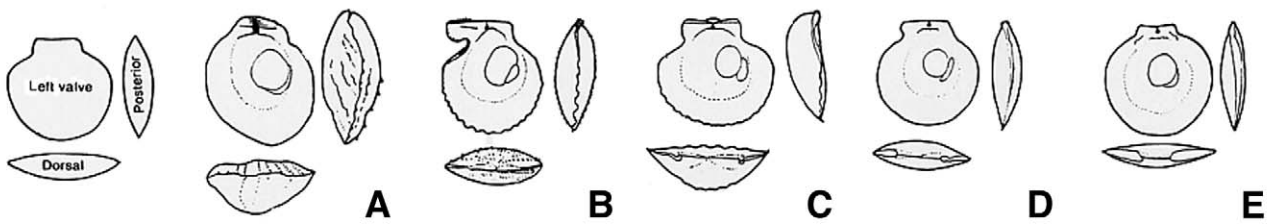
2.3.2. Ecomorph "B"

Use a byssus persistently throughout life and have a high dependency on hard substrata (rock, stones, shells or living reefs). Many remain cryptic throughout their life. A small toothed region, the ctenolium, present in the byssal notch on the right valve, holds the byssal tussock in a band and may reduce the ability of predators, such as crabs, to "twist-off" the shells from the substrate (Waller, 1984). The projecting anterior auricles stabilise anchorage and the smaller posterior auricles reduce leverage effects when handled by predators. The small slit-like ports on the dorsal margin of the discs reflect poor swimming ability but enable righting. Vahl and Clausen (1980) found byssal production consumed little energy in *Chlamys islandica* and although they occasionally swam they normally remained in one position over long periods. Principle movements in ecomorph "B" are from byssal reattachments and pedal creeping. This behaviour enables them to seek cryptic regions beneath rocks or within shell spaces. Scallops with a prominent byssus have a long extendable foot. The byssus and its associated glands are well developed in this ecomorph (Gruffydd, 1978). Projecting scales on the exterior surface of the ribs may promote fouling and encourage associations with commensal sponges that have been considered by Forester (1979) to result in reduced predation from sea stars. This form ranges from cold to tropical seas.

2.3.3. Ecomorph "C"

Byssal attachment occurs only in juveniles. Once detached they can form shallow depressions in silt to coarse sands and larger individuals may do so in gravels. Scallops

Table 3
Generalised ecomorphological features of commercial scallops from least active (A) to most active (E). Ht, shell height; L, shell length. Terminology used is that of Waller (1972)



Genera	*Crassadoma*	*Chlamys, Mimachlamys, Nodopecten, Zygochlamys, Swiftopecten*	*Pecten, Euvola* (in part)	*Annachlamys, Aequipecten, Argopecten, Patinopecten, Placopecten*	*Amusium, Euvola* (in part)
Habit	Cementing, normally cryptic	Byssally attached, cryptic to exposed	Fully recessing, concealed in sediment	Part recessing, partly exposed	Part recessing, exposed, active
Size of adult	8–28 cm Ht	3–20+ cm Ht	4–20 cm L	4–18 cm Ht	5–16 cm Ht
Shape	Once cemented, massive irregular shell. Shell height normally exceeds length	Regular, asymmetric, bi-convex, valves similarly arched or more arched left valve. Shell height normally exceeds length	Almost symmetrical, flattened left and curved right valve. Shell length normally exceeds height	Almost symmetrical, bi-convex, may be inflated. Left valve normally more arched, similar height to length of shell	Shell very light, symmetrical, bi-convex, more arched left valve, similar height to length of shell
Plicae (ribs) and carinae	Fine irregular, many, carinae absent	Regular, often with scales, carinae absent	Prominent to fine, smooth, carinae present	Fine to distinct, often with fine ornament, carinae absent	Outer shell smooth, carinae present
Auricles	Irregular, heavy with creeping hinge	Asymmetrical to strongly asymmetrical, with pronounced byssal notch	Enlarged, slightly asymmetrical, shallow byssal notch	Slightly asymmetrical, shallow to moderate byssal notch	Symmetrical reduced
Ctenolium	Absent in adults	Normally present, distinct	Absent in adults	Normally absent in adults	Absent
Shell overlap ventrally	Not usual	No	Overlapping right valve	Normally no, but may have overlapping left or right valve	Only very slight overlap if present
Disc gape ports	Very small	Small	Moderate	Moderate–large, small in *A. gibbus* and *A. irradians*	Large

are normally seated in sediment (recessed) with the left (flat) valve flush with or below the surface sediments. The depth of the depressions created depends on the sediment. In most sediments, the left valve is normally entirely covered with sediment thereby reducing shell fouling so enabling an improved swimming ability once disturbed. The ventral margin of the right valve overlaps that of the left and is more pronounced in finer sediments. This overlap may reduce sediment entry to the mantle cavity. Normally each valve has prominent corrugations of either plicae (shell corrugations) and carinae (internal ribs) as in *Pecten*, or less amplified corrugations and smoother outer surface and carinae as in *Euvola*. These architectural features add strength to a moderately thin shell and reduce weight burden when swimming. Two moderately large ports allow for forceful thrusts of water enabling a moderate swimming ability. This form is found in temperate to tropical seas.

2.3.4. Ecomorph "D"

Adults are freely distributed on fine to coarse sediments and lack a byssus although some (i.e. *P. magellanicus*) can extrude small numbers of byssal threads that are unlikely to secure a position (Caddy, 1972). Most valves normally meet equally at their ventral margin (*Argopecten, Aequipecten, Equichlamys, Annachlamys*) although some have overlap of the left (i.e. *Placopecten*) or right (i.e. *Patinopecten*) valves which may aid the mantle in creating depressions in which to partly recess. Caddy (1968) found rapid adductions in large *P. magellanicus*, displaced sediment near the shell margin creating shallow open depressions, facilitated by the overlapping upper (left) shell. Waller (1969); Gould (1971) considered it disadvantageous for the plane of commissure of scallops of this shape to lie below the surface of the substratum and Gruffydd (1976) experimentally demonstrated the plane of commissure needs to be inclined to create lift. This could explain why species of this ecomorph does not create deep depressions. The inflated upper (left) valve, in dorso-ventral section, provides a hydrodynamic shape and together with the large auricular ports enables good swimming ability (Dauter and Karpenko, 1983; Thorburn and Gruffydd, 1979). This form is found in cold to tropical seas.

2.3.5. Ecomorph "E"

Juveniles have a byssus and are active swimmers (Morton, 1980) and have thin smooth glossy shells throughout life. Radiating carinae (ridges) on the inner shell surfaces provide strength so do not interrupt laminar flow (Thayer, 1972). Because shell has a density of ~2.7, the reduced shell weight enables increased lift when swimming and allows for a slower descent (Gould, 1971). Species with this form have a hydrodynamic cross-sectional shape with "uplifted" anterior and posterior edges to the shell providing stability on descent following swimming, thereby maintaining an "upright" position. *Amusium* grows rapidly and seldom has fouled shells. Gould (1971) found the quick muscle surface area in relation to shell weight in *A. japonicum* was greater than in species representing ecomorphs "A", "B" and "D" (the only species of other ecomorphs examined by him). "*Amusium papyraceus*" is a convergent ecomorph derived from *Euvola* now considered to be *E. marensis* (Waller, in Shumway, 1991). The ecomorph "E" is found in semi-tropical to tropical seas.

2.3.6. Shell colour and ecomorph type

Although not clearly understood shell colour may be important in relation to predation, those with cryptic colours may be less vulnerable. Some notable differences are noted between ecomorphs. Thayer (1971) suggested shell colour differences between left and right valves contrasted more with increased swimming ability, the left valve being more pigmented. While true for many ecomorphs this hypothesis cannot be ascribed to all specimens. Frequently in *P. fumatus* and *P. ziczag* (ecomorph "C") the right valve can be darker and in the more errant (ecomorph "D") *A. irradians* and *A. opercularis* similarly coloured left and right valves may be found. The most active ecomorph *A. japonicum* (ecomorph "E") often has grey/brown left valves with white right valves, although contrasting, it is less so than in many species with a poorer swimming ability. Some scallops have extensive patterns with pigmentation of both valves during their period of byssal attachment and following detachment the range of pigmentation can become reduced, with a greater loss of colour to the right valve (Minchin, 1992a). However, in ecomorph "B", bright colours can remain throughout life. So generally the greater the colour contrast between the two valves the more adept it is at swimming.

2.4. Physiological requirement of a candidate species

Within the range of a species considered for introduction there may be populations adapted to specific local conditions. The population selected from the donor should come from an area that closely matches those of the recipient region. Selection should also take account of the occasional mortality events due to extremes of weather, or changes in coastal hydrodynamics, that can affect water quality within the range of a species (Crisp, 1964; Dickie and Medcoff, 1963; Tellebach et al., 1985).

A hatchery will be required for the production of spat and in rare cases scallops may need to be held in hatcheries when local weather conditions would be otherwise too extreme for them to survive.

Molluscan populations with similar latitude ranges to the east of continents generally have a wider tolerance of temperature when compared with those that have western ranges, where daily and annual temperatures are less. This may generally mean that east to west movements on a continent may result in a more successful introduction unless a wider range of temperature is required to trigger a developmental process. West to east movements may be less likely to succeed (Andrews, 1980). The majority of scallop introductions have been from either east to west, or to the same side of, the same or another continent (Fig. 1). Three introductions of *P. maximus* from Europe to China in 1997 and 1998 were unsuccessful (west to east movement) (J. Fang, personal communication), as would be expected according to this hypothesis. Whereas the movement of *A. irradians* moved from the East Coast of the United States to the East Coast of China was successful.

3. Potential impacts of scallop introduction

This ICES Code specifically refers to potential impacts to the ecosystem of the region a species is introduced. These include:

3.1. Hybridisation potential between introduced and native species

An introduced scallop might reproduce with native species. The duration and season of spawning in relation to physical and biological conditions in its native habitat, and in regions where it has become introduced, will provide some basis for a potential overlap and possible production of hybrids. Chromosome numbers will provide some indication as to whether hybridisation is possible, those with different chromosome numbers being less likely to produce embryos. Karyotype studies show different chromosome numbers, with haploid ranges of 13–19 for some selected species (Beaumont, 2000). Allele similarity between two species may lead to hybridisation. Where hybridisation may be possible, controlled studies while in quarantine may be desired.

3.2. Disease agents, pests and parasites and associated organisms carried with parent population

Organisms associated with an imported consignment, occurring either within or attached to scallop shell, contained in

Fig. 1. Introductions of scallops: **1**, Argopecten irradians from east coast of United States to China (1982, 1991, 1995), to Canada (1979); **2**, Argopecten purpuratus from northern Chile to southern Chile (1987,1988); **3**, *Patinopecten yessoensis* from Japan to northern China (1970's), to Denmark (1985), to France (1987), to Ireland (1990 as larvae and adults, 1991 adults), to Canada (1982, 1992) (from Canada as eyed larvae to Japan (1990's) and to Morocco (1998)). **4**, *Pecten maximus* from Norway to China (1997 to 1998), to Chile (1996, 1997) from France to Japan (1978), European source to Yellow Sea in China (1970's and 1980's).

scallop tissues or held within the mantle cavity and/or its fluids, should be considered (Table 4).

The comparatively short larval life of *A. irradians* and ease of rearing made it attractive for culture. It was introduced to the Gulf of St-Lawrence, Canada, where it remained in quarantine for several generations because of concerns over the vertical transmission thought to be due to a protozoan identified at that time within a quarantine facility as *Perkinsus karlssoni*. The scallops were not released to the wild for some years in case this protozoan would compromise other molluscan species (McGladdery et al., 1993a).

Molluscan diseases continue to be described and some have almost certainly yet to be become known. Although introduction through quarantine should eliminate parasites, competitors and other associated biota it may not remove vertically transmitted disease agents. Unless these are targeted these can be overlooked.

3.3. Specialised behavioural responses and associations

Cementing or byssally attaching scallops of ecomorphs "A" and "B" may select similar habitats and so will be closely associated, whilst others will be more widely dispersed. For reproduction to be effective these will need to both synchronise their spawning and be in close proximity to each other. It seems likely that some swimming species undergo directional movements resulting in congregations prior to spawning. The scallop *P. maximus* has the ability to move up slopes (Minchin, 1989) and seasonal movements are known in *P. yessoensis* (Golikov and Scarlato, 1970) and *A. pleuronectes* (Morton, 1980). Active swimmers subjected to strong currents (ecomorphs "D" and "E") may become concentrated regions where eddies occur. Such clustering is known to occur in *A. opercularis*, a "dribble" spawner (Beaumont, 2000), and capable of reproduction throughout most of the year (Mason, 1983).

Scallops have well-developed escape responses (Feder, 1968). In the case of *P. maximus* the most active responses were in response to the presence of the most predatory species within its range (Thomas and Gruffydd, 1971). Predators may not illicit these responses in a scallop that is introduced and this could result in a greater than expected mortality.

Some scallops, most usually the "B" ecomorph, have associations with sponges that result in reduced predation. Such associations according to Forester (1979) may improve scallop growth rates. Consequently, the introduction of the appropriate commensal sponge may also need to be considered.

4. Review by scientific forum

Examination of the prospectus by experts, it is likely to lead to specific requests including a study visit to the donor area to seek specific information from scientists, managers and fishermen. These concerns may arise over potential ecological competition, accounts of poor performance and mass mortality in culture and the release of elusive pathogens.

Should the results of the prospectus, and any follow-up study visit, satisfy the scientific forum that the risks of the introduction are acceptable, then approval to proceed to quarantine can be expected. The design and management of the quarantine facilities will need to be considered well in advance of the introduction; and when in operation all access of people, products and wastes should be strictly controlled.

5. Future introductions

In the past, consignments to quarantine have normally consisted of juveniles or adults, but more recently eyed-stage larvae (the stage before settlement) have been transferred for remote settling (N. Bourne, personal communication). This may become a more common practice in the future. The majority of scallops in cultivation (even experimentally) are mainly composed of the ecomorph "D" (Fig. 2). This includes three of the four species already introduced for which larval rearing and growout techniques are well established (Bourne and Hodgson, 1991; Broom, 1976; González et al., 1999; Mason, 1983). It is expected that future introductions will include species of the most frequent ecomorphs "B", "C" and "D" as these are the most abundant forms already in some form of culture. "A" is a sedentary form with a heavy shell that may be suited only for culture in cool seas. The fast swimming form "E" is unlikely to be used in bottom culture in the open sea as their activity is likely to lead to a high rate of dispersal and so poor recovery rate. In high density culture

Table 4
Some examples of pests, parasites and diseases of scallops

Organism	Host	Range	Author
Bacterial diseases of larvae	*P. maximus, P. magellanicus, A. irradians*	France, North America	Nicolas et al. (1996); Getchell in Shumway (1991)
Bacterial abscess lesions	*P. magellanicus, P. magellanicus, A. irradians*	Atlantic North America	McGladdery (1990)
Hinge ligament disease (bacterium)	A. irradians	Atlantic North America	Elston (1990)
Intracellular bacterial disease	P. yessoensis	British Columbia	Bower et al. (1994)
Rickettsiales (bacterium)	*P. magellanicus, P. yessoensis, P. maximus, A.irradians*	Widespread	Bower et al. (1994)
Alexandrium tamarense	P. magellanicus	World-wide	Scarratt et al. (1993)
Microsporidian (protozoa)	A. opercularis	North Europe	Torkildsen and Bergh (1999)
Chlamydiosis (protozoan) infecting larvae	A. irradians	Atlantic North America	Leibovitz (1989)
Haplosporidian (protozoa)	A. irradians	China	Fu Lin et al. (1996)
Kidney coccidia (protozoan)	P. maximus, A. irradians	North Atlantic	Whyte et al. (1994)
Marteilia sp. (protozoan)	A. gibbus	Eastern Florida	Blake and Moyer (1992)
Nematopsis spp. (protozoan)	*P. yessoensis, C. varia, A. irradians*	North America, North Europe	Bower et al. (1994)
Perkinsus sp. (protozoan)	A. irradians	Atlantic North America	Goggin et al. (1996)
Perkinsus qugwadi (protozoan)	P. yessoensis	British Columbia	Bower et al. (1999)
Protozoan G (SPG)	P. yessoensis	British Columbia, Japan	Bower et al. (1992)
Trichodinia sp. (protozoan)	*P. magellanicus, P. yessoensis*	Atlantic Canada, Japan	McGladdery et al. (1993b)
Cliona spp. (sponge)	Most scallops	World-wide	Bower et al. (1994); Minchin, personal observation
Bucephalus sp. (trematode)	*P. fumatus, C. asperrimus*	Australia	Heasman et al. (1996)
Ceratonereis tridentata (polychaete)	*A. gibbus, A. irradians*	SE North America	Wells and Wells (1962)
Polydora sp. (polychaete)	*P. maximus, P. fumatus, P. caurinus*	North Europe, Bass Strait, Bering Sea	Paice (1974)
Polydora spp., *Dodecaceria concharum* (polychaete)	*P. yessoensis, C. giganteum, P. magellanicus*	World-wide	Mori et al. (1985)
Turbellarian worm	P. magellanicus	Eastern Canada	McGladdery et al. (1993b)
Sulcascaris sulcata (nematode)	A. gibbus	Florida	Barber et al. (1987)
Porrocaecum pectinis (nematode)	A. gibbus	SE North America	Cummins (1971)
Pectenophilus ornatus (crustacean)	*P. yessoensis, C. farreri nipponensis, C.f. farreri, C. akazara*	Japan	Nagasawa and Nagata (1992); Elston (1990); Nagasawa et al. (1988)
Herrmannella longichaeta (copepod)	P. yessoensis	Korea	Ho and Kim, 1991
Herrmannella bullata (copepod)	C. hastate	Pacific USA	Humes and Stock (1973)
Herrmannella pecteni (copepod)	*A. opercularis, C. glaber, M. varia, P. maximus*	Black and Irish seas	Holmes and Minchin (1991)
Modiolicola inermis (copepod)	*A. opercularis, P. maximus*	Northern Europe	Humes and Stock (1973)
Doridicola chlamydis (copepod)	*M. varia*	France	Humes and Stock (1973)
Modiolicola maximus (copepod)	*P. maximus, A. opercularis*	Ireland	Holmes and Minchin (1991)
Pinnotheres spp. (decapod)	*P. magellanicus, A. irradians, A. gibbus, C. nipponensis, P. maximus, A. pleuronectes*	Japan, North Atlantic	Bower, et al. (1994); Minchin, personal observation; Llana (1979)
Pantonia margarita (decapod)	*A. gibbus*	SE North America	Wells and Wells (1962)
Crepidula fornicata (gastropod)	*P. maximus*	North Europe	Minchin et al. (1995)
Odostomia sp. (gastropod)	*P. maximus*	North Europe	Minchin (1984)
Muricanthus spp. *Hexaplex* (gastropod)	*A. circularis*	West coast Mexico	Felix-Pico in Shumway (1991)

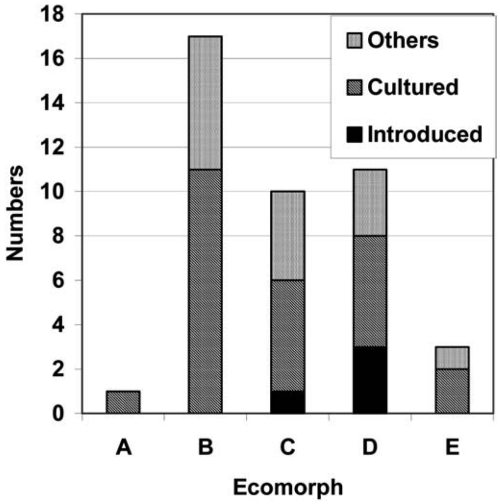


Fig. 2. Generalised distribution of ecomorphological forms of known economic importance or with potential for development. Based on examination of museum collections and Shumway (1991).

soft tissues of this active scallop are likely to become damaged on account of the sharp leading edge to the shells as well as damage to their thin shells from handling.

Some areas, such as the western Indo-Pacific, appear to be devoid of scallop fisheries or culture (Fig. 3). This may reflect a poor representation of culture or fishery activities in the general literature. Managers in such areas may consider developing a local species, such as, *Mimachlamys townsendi*, from the Arabian Sea, Persian Gulf and Red Sea, ~20 cm in shell height (Waller, in Shumway, 1991) as an introduction. Presently, most scallops in cultivation occur in temperate to Mediterranean-type regions.

Some species have strong year classes and have an ability to recover following population declines, for example *Argopecten purpuratus* following El Niño events (Pimiquil, in Shumway, 1991). The short-lived *Argopecten gibbus* and *A. irradians* also have the ability to develop frequent strong year classes (Allen and Costello, 1972). This may be an important feature to consider, because with more frequent extreme weather events, associated with changes in climate there, could be periodic declines of stock and a rapid recovery would provide a distinct economic advantage.

The unusually large and rare fast growing *P. maximus*, that can attain almost 1 kg wet weight (Minchin, 1992b), could provide useful in culture and fisheries. It is presently not known how such gigantism is controlled but production of such giants would have advantages. These should outgrow the capabilities of their predators sooner and so result in a shorter cultivation cycle leading to greater production with distinct economic benefits. Gigantism in two extinct genera *Chesapecten* and *Carolinapecten* suggested that with the genetic manipulation of existing scallop species such gigantism may be induced (Waller, in Shumway, 1991).

No matter what marine species are considered for introduction, the ICES code of practice provides a procedure where up-to-date information is employed in a decision making process reviewed by experts from several disciplines. It is likely that in the new millennium a wide range of species will be examined for their potential including food production. New technologies are likely to evolve disease resistance strains and allow for greater physiological tolerance. Scallops are likely to continue to be an important component of marine commerce and should be managed wisely if sustained production is to continue.

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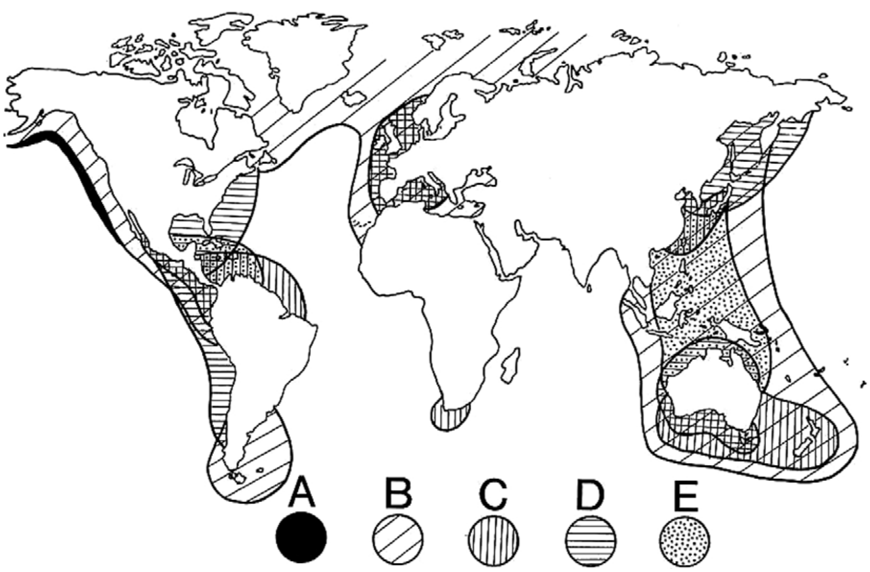

Fig. 3. Scallop ecomorphological forms that have been cultured or introduced.

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