Whelk

(*Buccinum undatum*)

Summary

Size	Max. 120 mm total shell length, 60mm wide (Ager, 2008)
Lifespan	>10 years (FAO,2020)
Size of maturity in the SIFCA district (L_{50})	45 – 66 mm (total shell length)
Fecundity	50 - 4100 eggs per capsule 80 - 150 capsules laid per female 2 - 10 juveniles hatch per capsule (Smith, 2012; Martel et al., 1986)
Reproductive frequency	Annual
Capture methods	Whelk pots
Minimum Conservation Reference Size	45 mm
Fishing Season	All year (peak March-May)

Description

Buccinum undatum known as the common whelk or waved whelk is a large marine gastropod (referred to as whelks throughout this document). It is widely distributed across the North Atlantic Ocean ranging from Norway to the Bay of Biscay in the east and along the coast of eastern Canada to Jersey in North America on the west (Hollyman, 2017). Whelks are commonly found around the entire UK coastline from the intertidal to depths of ~1200m (Ager, 2008; Hollyman, 2017) where they inhabit varied benthic substrates including sand, mud, and gravel (Haig et al., 2015). Using a highly developed chemosensory system whelks actively predate bivalve molluscs, crabs and polychaete worms and scavenge carrion (Scolding et al., 2007). Limited movement as adults is thought to contribute to localized populations (de Vooys and van der Meer, 2010) with a total daily movement of up to 155 m recorded (Robinson, 2015).

Reproductive Life history

The timing of the reproductive cycle for the common whelk varies across its distribution as copulation and egg laying are temperature dependent. In UK waters mating is triggered when temperatures fall below at least 12°C, in some cases 9°C as has been evidenced for populations found in the Solent (Kideys et al., 1993; Smith et al., 2013; Hollyman, 2017). Females attract males by releasing pheromones and egg fertilisation is internal (Hollyman, 2017). Egg laying takes place between the months of October and May, depending on location. In the Solent whelks were found to lay eggs between December and February (Smith et al., 2013) whereas egg laying in Plymouth has been recorded between October and May (Lebour, 1937 cited in Hollyman, 2017). Along the coast of Normandy spawning mainly occurs between October and December

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(Heude-Berthelin et al., 2011) whilst outside of the English Channel, in North Wales, spawning has been recorded between November and December (Hollyman, 2017).

Females deposit eggs in small spherical capsules onto hard substrates with each capsule containing up to 2,700 eggs (Martel et al., 1986). The act of a female laying eggs is thought to induce other females to spawn and collectively each female contributes between 80-150 egg capsules to a single egg mass (Smith and Thatje, 2013). Development takes place inside the egg for a duration of 2-5 months (Kideys et al., 1993, Hollyman, 2017; Smith et al., 2013) until fully developed juveniles emerge measuring 3 mm in shell length (Martel et al., 1986). Despite the large number of eggs contained in an egg mass successful recruitment is low. Studies on a Solent whelk population found approximately 1% of eggs developed to juveniles and the remaining eggs are used as nurse eggs for the developed embryos (Smith, 2013).

The sedentary lifestyle of the whelk and lack of planktonic larval stage limits the dispersal of individuals and consequently reduces the genetic variation in a population leading to distinct, localized populations (Ashfaq et al., 2019; Weetman et al., 2006; Martel et al., 1986).

Size of maturity (SOM)

Size of maturity (SOM) is often used to help establish an appropriate Minimum Conservation Reference Size (MCRS) to ensure individuals can reproduce at least once before capture. For whelks the SOM is commonly accepted as the total shell length at which 50% of a population are mature and is referred to as the L_{50}.

Several methods can be used to estimate sexual maturity in whelks: histological examination of the gonads; visual assessment of gonad development; gonadosomatic index using the weight of the gonad as an index; microscopic examination for presence of oocytes and sperm; or measurement of penis length to indicate male maturity (Haig et al., 2015; Couillard and Brulotte, 2020). Many studies choose to visually assess gonad development as it is a low-cost method with rapid results (Couillard and Brulotte, 2020).

The reviewed literature confirms SOM for the common whelk can vary greatly between populations on a small geographical scale (table 1). Across the Southern IFC District SOM ranges between 45-66 mm, a difference of up to 21 mm. In Portsmouth L_{50} was found to be 45 mm for females and 46 mm for males (McIntyre et al., 2015). However, Bell and Walker (1998) found SOM for males in Portsmouth to be larger at 57 mm. The largest SOM sampled in the district was 66 mm and 64 mm for males and females in Poole respectively (McIntyre et al., 2015). A male population sampled in the Solent at Nab Tower reached sexual maturity at 55 mm and whelks examined in Weymouth ranged from 55 mm for females and 59 mm for males (Bell and Walker, 1998; McIntyre et al., 2015).

SOM for populations outside the Southern IFC District but within the English Channel ranged between 45 mm at Selsey to 71 mm at Exmouth (table 1). In coastal waters around the rest of the UK SOM continues to vary significantly with the smallest L_{50} recorded at 45 mm along the Kent and Essex coastline and largest at 85 mm in the Shetland Islands, Scotland (Hollyman and Richardson, 2018; Hollyman, 2017). Overall males tend to mature at a larger size than females although this is not always significantly different. However, in some populations sampled in Eastbourne,

Normandy and Exmouth size at sexual maturity was found to be larger in females (table 1). Age at maturity also varies between 2 – 11 years depending on location but not sex (Ashfaq et al., 2019; Hollyman and Richardson, 2018; Heude-Berthlin et al., 2011; Hemer et al., 2006; Fahy et al., 2000 and Morel, 1997).

SOM for 91% of the 33 populations of whelks analysed and listed in Table 1 are above the EU/national MCRS of 45 mm. All studies undertaken within the Southern IFC District found SOM to be higher than 45 mm excluding female whelks sampled in Portsmouth, which were found to mature at 44.8 mm. This indicates the current minimum size of 45 mm is not appropriate for the sustainable management of the whelk fisheries within the District.

Table 1. Size of maturity estimates (L_{50}) for the common whelk (*Buccinum undatum*) in studies undertaken around the British Isles. Male and female total shell length given in mm. Methods include: Visual (an assessment of the differentiation of the digestive whorl); PL (penis length); and Histology (microscopic analysis). Refer to the Appendix for more information about each study.

Studies undertaken in the Southern IFC District				
Location	**Male**	**Female**	**Method**	**Reference**
Portsmouth 1	56.5	-	PL	Bell and Walker, 1998
Portsmouth 2	46.4	44.8	Visual	McIntyre et al., 2015
Solent (Nab Tower)	55.1	-	PL	Bell and Walker, 1998
Poole	66	63.5	Visual	McIntyre et al., 2015
Weymouth	59.1	54.7	Visual	McIntyre et al., 2015
Studies undertaken in the English Channel (excl. Southern IFC district)				
Location	**Male**	**Female**	**Method**	**Reference**
Selsey	64.6	59.6	Visual	McIntyre et al., 2015
Eastbourne	51.2	56.7	Visual	McIntyre et al., 2015
Exmouth	70.9	69.3	Visual	DSIFCA, 2015
Exmouth	69.2	72.4	Visual	McIntyre et al., 2015
Jersey	60.5	56.8	Visual	Hollyman, 2017
Jersey	56-63	-	PL	Morel, 1997
Start Bay	64.4	57.8	Visual	DSIFCA, 2016
Eastbourne	57.4	-	PL	Bell and Walker, 1998
Worthing	55.7-61.6	-	PL	Bell and Walker, 1998
Selsey	45.2	-	PL	Bell and Walker, 1998
Normandy - France	49	52	Histology	Heude-Berthelin et al., 2011
Studies undertaken outside the English Channel				
Location	**Male**	**Female**	**Method**	**Reference**
Ilfracombe	76.4	76.5	Visual	DSIFCA, 2015
Lundy	75.5	75.5	Visual	McIntyre et al., 2015
Irish Sea	69.6	67.6	Visual	Emmerson et al., 2018
Whitehaven	74	69.5	Visual	McIntyre et al., 2015
Wells	62.5	60.6	Visual	McIntyre et al., 2015
Inner Cromer Knoll	76.2	77.8	Visual	McIntyre et al., 2015
Ramsgate	49.5	52.8	Visual	McIntyre et al., 2015
Whitstable	61.9	60.7	Visual	McIntyre et al., 2015
Kent & Essex IFCA District	45.3- 56.1		Visual	Hollyman and Richardson 2018
South west Irish Sea	63-68	-	PL	Fahy et al., 2000
Location	**Male**	**Female**	**Method**	**Reference**
North west Ireland	83	82.6	Males – PL	Hemer et al., 2006

			Female - Histology	
Wales	51-76		Visual	Haig et al., 2015
Wales - Menai Strait	61.8	58.1	Visual	Hollyman, 2017
Wales - Amlwch	81.2	74.6	Visual	Hollyman, 2017
Wales - Holyhead	70.2	68.6	Visual	Hollyman, 2017
Wales - Nefyn	77.9	69.7	Visual	Hollyman, 2017
Scotland - Shetland	85.1	83.2	Visual	Hollyman, 2017

A range of anthropogenic and environmental pressures have been attributed to variations in SOM for whelks including water temperature, depth, fishing pressure, food availability and predation (McIntyre et al., 2015; Heude-Berthelin et al., 2011). Haig et al, (2015) found the SOM for whelk populations in Wales was positively influenced by depth with individuals in shallow water (0-10m) found to mature at a smaller size than individuals in deeper water. Temperature is also significantly related to SOM as lower temperatures correlate with increased SOM (McIntyre et al., 2015). Other factors that can affect SOM on a local scale are those that impact growth such as high predator densities. Whelks have been found to grow thicker shells in areas where they co-exist with large populations of brown crabs (Fahy et al., 2006). Fishing has also been demonstrated to reduce the size at which a population becomes sexually mature over time when compared to unfished populations (Fahy et al., 1995).

The variability in SOM over a small spatial scale deems large scale management measures such as the national minimum landing size inappropriate. The introduction of local management measures has been described as the most beneficial option to consider for a sustainable fishery (Shelmerdine et al., 2007; Blue Marine Foundation, 2018).

Southern IFCA Fishery

Fishing activity

Whelk are amongst the most economically valuable shellfisheries in the UK after nephrops, scallops, crab and lobster (MMO, 2018). In 2018 UK landings totalled 17,900 tonnes at a value of £21.9 million (MMO, 2018). Of this, 10,800 tonnes were landed in England, worth £13 million. Whelks are caught along the entire coastline of England but total annual landings indicate the largest fisheries exist along the south coast in the Southern and Sussex IFCA district followed by Devon and Severn IFCA district (Blue Marine Foundation, 2018). Whelk fishing takes place across the entire Southern IFC District but is most prominent in the Solent and west Dorset. There are 250 permitted pot fishers registered as undertaking potting activity in the Southern IFC District, of which 227 fish fulltime. Some of these fishers solely target whelks whilst others fish for whelks intermittently around crab and lobster potting.

Whelks within the Southern IFC District are exclusively caught using baited traps but a very limited number of landings are caught as bycatch from other fisheries. Pots are specifically designed to target whelks and comprise of a weighted cylindrical structure with a mesh covered opening. Some are purposefully built whilst others are made from re-purposed plastic containers weighted down with concrete (Southern IFCA, 2018). Escape gaps allow for undersized individuals to escape. Pots are baited with crab and

fish to exploit the whelks' strong sense of smell and attract them to the trap before being set between 15 m and 20 m apart for approximately 24 hours. The number of pots worked in the district ranges from 150 to 1,200 depending on the size of the vessel (C.Smith 2020, pers. comm., 16 September). Once collected, a riddle of parallel bars is often used to sort the catch and return undersized individuals.

Whelk potting can take place throughout the year but landings in the district indicate a seasonal peak between March and May whilst the lowest landings tend to occur from October to December (Southern IFCA, 2018).

Landings & Value of Fishery

Southern IFCA do not currently hold effort or catch data for the whelk fishery and little is known about the stock status of the common whelk throughout its range (Blue Marine Foundation, 2018). However, landings data from the MMO can help indicate the scale of the fishery over time. In 2019 approximately 2,192* tonnes of whelk worth £2,917,268* was landed into ports across the Southern IFC District (Fig.1). Weymouth, West Bay, Poole and Portsmouth are the key ports for whelk landings within the district (Southern IFCA, 2018).

*these figures represent vessels that land into ports in the Southern IFC District, some of which would have fished outside the district and be >12 metres in length.

Whelk landings have increased over the last 14 years from 1,279 to 2,192 tonnes between 2005 and 2019 with a high of 3,352 tonnes landed in 2011. Between 2005 and 2011 (excluding 2007) whelk landings in the Southern IFC District increased by an average of 400 tonnes year-on-year (Fig.2). However, in 2007 landings increased substantially from the previous year by 42% increasing from 1,951 to 3,339 tonnes followed by a decline to 2,414 tonnes in 2008 in line with the previous annual increases. Following 2011 annual landings in the district remained relatively stable for five years ~3,000 tonnes per year. In 2017 landings declined by 900 tonnes and have remained ~2,000 tonnes per year for the last three years.

The value of the fishery has increased by 63% over the last 14 years from £498 per tonne in 2005 to £1,330 per tonne in 2019 (Fig.2). In 2019 the total value of whelk landings into the Southern IFC District was just over £2.9 million, an increase of 27% on the value of the fishery in 2016 despite a reduction in landings of 740 tonnes.

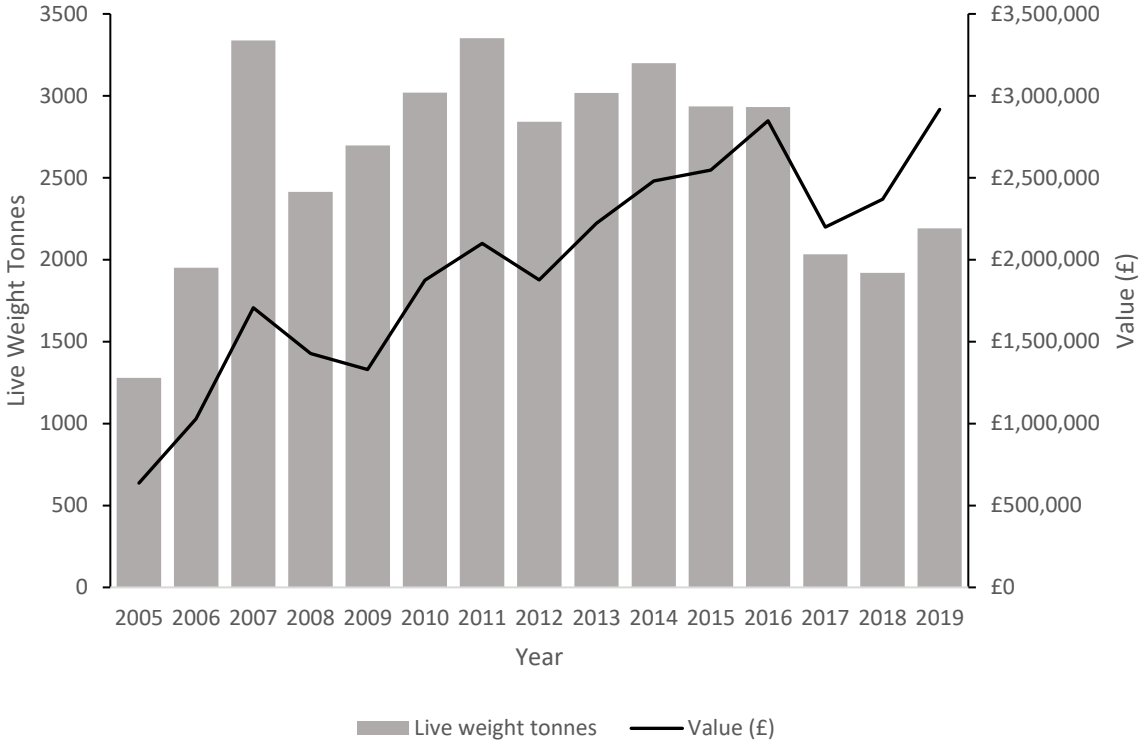

Figure 1. Landings of whelk (*Buccinum undatum*) into the Southern IFC District from 2005 to 2019. Data received from the Marine Management Organisation (MMO).

Associated management

Whelk fisheries within Southern IFCA waters are managed solely by a Minimum Conservation Reference Size (MCRS) of 45 mm (total shell length) under European legislation (Regulation (EU) 2019.1241). However, fishing effort is also indirectly managed through the 'Vessels used in fishing 2012' byelaw that prohibits commercial vessels over 12 metres from fishing in the Southern IFC District. The reduction in vessel size naturally restricts fishing effort as it limits the quantity of static gear that can be worked by each vessel. A voluntary code of conduct also operates in the Lyme Bay Special Area of Conservation (SAC) which includes pot limitation of 500 per vessel, with no more than 30 pots in a string. Registered vessels also voluntarily fit Vessel Monitoring Systems (VMS) in this area.

The EU/national MCRS of 45 mm has been increased regionally up to 75 mm in some areas around the British Isles (table 2). Following studies on SOM of whelks within the Devon and Severn IFC District the Authority increased the MCRS of whelks to 65 mm in November 2020. North Western IFCA are also in the process of increasing their MCRS based on SOM data. The MCRS for whelks within the Eastern IFC District currently sits above the EU/national minimum size at 55 mm but further increases are under consideration. Additional management measures such as pot limitations, riddle sizes and permit schemes have also been introduced around the UK (Southern IFCA, 2018; Blue Marine Foundation, 2018).

Table 2. Minimum Conservation Reference Sizes (MCRS) for the common whelk (*Buccinum undatum*) in Inshore Fisheries and Conservation Authority (IFCA) Districts in England and other regions around the British Isles. All measurements in mm for total shell length.

IFCA	**Minimum Conservation Reference Size (MCRS) (mm)**
Northumberland	45
North Eastern	45
Eastern	**55**
Kent & Essex	45
Sussex	45
Southern	45
Devon & Severn	**65**
Cornwall	45
Isles of Scilly	45
North Western	45 (Measures under development to increase MCRS to **75** in a staged process)
Other British Isles	**Minimum Conservation Reference Size (MCRS) (mm)**
Isle of Man	**70**
Wales	**55**
Shetland Islands	**75**
States of Jersey	**75**

Bold: MCRS above the EU/national size of 45mm

References

Ager, O.E.D., 2008. Buccinum undatum common whelk. In Tyler-Walters, H., and Hiscock, K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews [online]. Plymouth: Marine Biological Association of the United Kingdom. [cited 14.09.2020]. Available from: https://www.marlin.ac.uk/species/details/1560

Ashfaq, U., Mugridge, A., Hatcher, B.G., 2019. Size at sexual maturity of waved whelk (Buccinum undatum) on the Eastern Scotian Shelf. Fisheries Research, 212: 12-20

Bell, M.C., and Walker, P., 1998. Size at maturity in common whelks Buccinum undatum L. in England and Wales. ICES Report CM 1998/CC:9

Blue Marine Foundation, 2018. Management recommendations for English non-quota fisheries: Common whelk. Report produced by MRAG Ltd

Couillard, C.M., and Brulotte, S., 2020. Comparison of a visual method, mass-based and surface-based gonadal indices and gonad histology to assess sexual maturity in the waved whelk, Buccinum undatum. Fisheries Research, 224: 105468

DSIFCA, 2016. Determination of the size of maturity of the whelk Buccinum undatum within the Devon and Severn IFCA District. Supplementary report: Start Bay. Research report KS012016 by Stephenson, K

DSIFCA, 2015. Determination of the size of maturity of the whelk Buccinum undatum within the Devon and Severn IFCA District. Research report KS012015 by Stephenson, K

Emmerson, J.A., Haig, J.A., Bloor, I.S.M., and Kaiser, M.J., 2018. The complexities and challenges of conserving common whelk (Buccinum undatum L.) fishery resources: spatio-temporal study of variable population demographics within an environmental context. Fisheries Research, 204: 125-136

Fahy, E., Groga, S., Byrne, J., and Carroll, J., 2006. Some thick shelled whelk Buccinum undatum characteristics and fisheries in Ireland. Irish Fisheries Bulletin No. 25.

Fahy, E., Masterson, E., Swords, D., and Forrest, N., 2000. A second assessment of the whelk fishery Buccinum undatum in the southwest Irish Sea with particular reference to its history of management by size limit. Marine Fisheries Services Division, Marine Institute, Dublin.

Fahy, E., Yalloway, G., Gleeson, P., 1995. Appraisal of the whelk Buccinum undatum fishery of the Southern Irish Sea with proposals for a management strategy. Ir. Fish. Investig. Ser. B 42.

FAO, 2020. FAO Fisheries & Aquaculture – Species Fact Sheets – Buccinum undatum (Linnaeus, 1758). http://www.fao.org/fishery/species/2659/en (Accessed 14. September 2020).

Gendron, L., 1992. Determination of the size at sexual maturity of the waved whelk Buccinum undatum Linnaeus, 1758, in the Gulf of St. Lawrence, as a basis for the establishment of a minimum catchable size. J. Shellfish Res. 11, 1–7.

Haig, J.A., Pantin, J.R., Salomonsen, H., Murray, L.G., Kaiser, M.J., 2015. Temporal and spatial variation in size at maturity of the common whelk (Buccinum undatum). ICES J. Mar. Sci. J. Cons. 72, 2707–2719.

Hemer, J.A., 2006. An assessment of biological and population parameters of the common whelk, Buccinum undatum (L.) in the region of the North West Irish whelk fishery. Masters Thesis, Galway-Mayo Institute of Technology, Ireland

Heude-Berthelin, C., Hégron-Macé, L., Legrand, V., Jouaux, A., Adeline, B., Mathieu, M., Kellner, K., 2011. Growth and reproduction of the common whelk Buccinum undatum in west Cotentin (Channel), France. Aquat. Living Resour. 24, 317–327

Hollyman, P., 2017. Age, growth and reproductive assessment of the whelk, Buccinum undatum, in coastal shelf seas. PhD Thesis, Bangor University, Anglesey

Hollyman, P., Richardson, C., 2018. Age and growth rate of whelks, Buccinum undatum, in Kent and Essex waters. Bangor University report funded by Kent and Essex IFCA

Kideys, A.E., Nash, R.D.M., Hartnoll, R.G., 1993. Reproductive cycle and energetic cost of reproduction of the negastropod Buccinum undatum in the Irish Sea. Journal of the Marine Biological Association of the United Kingdom, 73: 391-403

Martel, A., Larrivée, D.H., and Himmelman, J.H., 1986. Behaviour and timing of copulation and egg-laying in the neogastropod Buccinum undatum L. J. Exp. Biol. Ecol. 96, 27–42

Marine Mangement Organisation (MMO)., 2018. UK Sea Fisheries Statistics 2018

McIntyre, R., Lawler, A., Masefield, R., 2015. Size of maturity of the common whelk, Buccinum undatum: is the minimum landing size in England too low? Fish. Res. 162: 53–57

Morel, G., 1997. Determination of the size at sexual maturity of the common whelk, Buccinum undatum, off the Isle of Jersey (Channel Islands) as a basis for the assessment of the minimum landing size. Masters Thesis, University of Southampton, Southampton

Robinson, M., 2015. The abundance, movement and site fidelity of the adult whelk, Buccinum undatum, in the territorial waters of the Isle of Man. Masters thesis, Bangor University, Anglesey.

Scolding, J.W.S., Richardson, C.A., and Luckenbach, M.J., 2007. Predation of cockles (Cerastoderma edule) by the whelk (Buccinum undatum) under laboratory conditions. J Mollus Stud 73(4):333-337

Shelmerdine, R.L., Adamson, J., Laurenson, C.H., and Leslie, B., 2007. Size variation of the common whelk, Buccinum undatum, over large and small spatial scales: Potential implications for micro-management within the fishery. Fisheries Research 86: 201-206

Smith, K.E., 2013 Physiological thresholds through early ontogeny: the effects of temperature and hydrostatic pressure on the common whelk Buccinum undatum (Linnaeus 1758) PhD Thesis, University of Southampton, Southampton

Smith, K.E., and Thatje, S., 2013. Nurse egg consumption and intracapsular development in the common whelk Buccinum undatum (Linnaeus, 1758). Helgo Mar Res 67:109-120

Smith, K.E., Thatje, S., and Hauton, C., 2013. Thermal tolerance during early ontogeny in the common whelk Buccinum undatum (Linnaeus 1785): Bioenergetics, nurse egg partitioning and developmental success. J Sea Res 79:32-39

Southern IFCA, 2018. Review of research and management approaches for whelk (Buccinum undatum) fisheries in the UK. Report compiled as part of a Southern IFCA internship by Laura Baker.

Vooys, C.G.N., and de Meer J van der., (2010) The whelk (Buccinum undatum L.) in the western Dutch Wadden Sea in the period 1946-1970: Assessment of population characteristics and fishery impact. J Sea Res 63:11–16

Weetman, D., Hauser, L., Bayes, M., Ellis, J., Shaw, P., 2006. Genetic population structure across a range of geographical scales in the commercially exploited marine gastropod Buccinum undatum. Mar. Ecol. Prog. Ser. 317, 157–169.

Appendix

Table A. Estimates of size at maturity for the common whelk (*Buccinum undatum*) in studies undertaken around the British Isles. Table shows study location, total number of individuals sampled overall, size range sampled, total number of individuals used to assess size at maturity, size of smallest mature individual, size at 50% maturity (L_{50}), size range of mature individuals and method used to assess maturity. All sizes based on total shell length in mm.

Study location	Total No. of individuals surveyed	No. of individuals (n)		Length Data		Size at Maturity Data										Reference
				Size range (mm)		Total No. of individuals	No. of individuals (n)		Size of smallest mature individual (mm)		Size at 50% maturity (L_{50}) (mm)		Size range of mature individuals (mm)		Maturity Method	
		M	F	M	F		M	F	M	F	M	F	M	F		
Studies undertaken inside the Southern IFCA District																
Portsmouth 1	98	58	40	-	-	-	-	-	-	-	56.5	-	-	-	PL	Bell and Walker, 1998
Portsmouth 2	294	-	-	-	-	-	-	-	-	-	46.4	44.8	-	-	Visual	McIntyre et al., 2015
Solent (Nab Tower)	320	146	174	-	-	-	-	-	-	-	55.1	-	-	-	PL	Bell and Walker, 1998
Poole	310	-	-	-	-	-	-	-	-	-	66	63.5	-	-	Visual	McIntyre et al., 2015
Weymouth	339	-	-	-	-	-	-	-	-	-	59.1	54.7	-	-	Visual	McIntyre et al., 2015
Studies undertaken inside the English Channel (excl. SIFCA district)																
Selsey	254	-	-	-	-	-	-	-	-	-	64.6	59.6	-	-	Visual	McIntyre et al., 2015
Eastbourne	243	-	-	-	-	-	-	-	-	-	51.2	56.7	-	-	Visual	McIntyre et al., 2015
Exmouth	1600*	-	-	-	-	-	-	-	59	59	70.9	69.3	-	-	Visual	DSIFCA, 2015
Exmouth	245	-	-	-	-	-	-	-	-	-	69.2	72.4	-	-	Visual	McIntyre et al., 2015
Jersey	277	-	-	-	-	-	-	-	-	-	60.5	56.8	-	-	Visual	Hollyman, 2017
Jersey	953	-	-	-	-	-	-	-	-	-	56-63	-	-	-	PL	Morel, 1997
Start Bay	175	86	89	-	-	-	-	-	52	55	64.4	57.8	-	-	Visual	DSIFCA, 2016
Eastbourne	497	245	252	-	-	-	-	-	-	-	57.4	-	-	-	PL	Bell and Walker, 1998
Worthing	799	343	456	-	-	-	-	-	-	-	55.7 – 61.6	-	-	-	PL	Bell and Walker, 1998
Selsey	387	183	204	-	-	-	-	-	-	-	45.2	-	-	-	PL	Bell and Walker, 1998

France - Normandy	9087	-	-	-	-	-	-	-	49	52	49	52	-	-	Histology	Heude-Berthelin et al., 2011
Studies undertaken outside the English Channel																
Ilfracombe	1600*	-	-	-	-	-	-	-	66	62	76.4	76.5	-	-	Visual	DSIFCA, 2015
Lundy	348	-	-	-	-	-	-	-	-	-	75.5	75.5	-	-	Visual	McIntyre et al., 2015
Irish Sea	9234	-	-	-	-	2451	-	-	-	-	69.6	67.6	-	-	Visual	Emmerson et al., 2018
Whitehaven	397	-	-	-	-	-	-	-	-	-	74	69.5	-	-	Visual	McIntyre et al., 2015
Wells	833	-	-	-	-	-	-	-	-	-	62.5	60.6	-	-	Visual	McIntyre et al., 2015
Inner Cromer Knoll	278	-	-	-	-	-	-	-	-	-	76.2	77.8	-	-	Visual	McIntyre et al., 2015
Ramsgate	613	-	-	-	-	-	-	-	-	-	49.5	52.8	-	-	Visual	McIntyre et al., 2015
Whitstable	264	-	-	-	-	-	-	-	-	-	61.9	60.7	-	-	Visual	McIntyre et al., 2015
Kent & Essex IFCA District	1000	-	-	-	-	-	-	-	-	-	45.3- 56.1		-	-	Visual	Hollyman and Richardson 2018
South west Irish Sea	-	-	-	-	-	-	-	-	-	-	63-68	-	-	-	Visual	Fahy et al., 2000
North west Ireland	-	-	-	-	-	322	146	176	-	-	83	82.6	-	-	M -PL F - Histology	Hemer et al., 2006
Scotland - Shetland	218	-	-	-	-	-	-	-	-	-	85.1	83.2	-	-	Visual	Hollyman, 2017
Wales	5080	-	-	-	-	1659	-	-	-	-	51-76		-	-	PL	Haig et al., 2015
Wales -Menai Strait	900	-	-	-	-	-	-	-	-	-	61.8	58.1	-	-	Visual	Hollyman, 2017
Wales - Amlwch	151	-	-	-	-	-	-	-	-	-	81.2	74.6	-	-	Visual	Hollyman, 2017
Wales - Holyhead	107	-	-	-	-	-	-	-	-	-	70.2	68.6	-	-	Visual	Hollyman, 2017
Wales - Newfyn	107	-	-	-	-	-	-	-	-	-	77.9	69.7	-	-	Visual	Hollyman, 2017

*total sample size of 1,600 across Ilfracombe and Exmouth sites sampled by DSIFCA, 2015