RESEARCH ARTICLE

Enhanced survival of 0-group gadoid fish under jellyfish umbrellas

Christopher P. Lynam · Andrew S. Brierley

Received: 10 January 2006/Accepted: 4 July 2006/Published online: 10 August 2006 © Springer-Verlag 2006

Abstract Young (0-group) gadoid fish, which have been observed sheltering beneath jellyfish (Scyphozoa and Hydrozoa) umbrellas, may find refugia from predation by retreating among medusan tentacles. The survival of juvenile gadoids may therefore be improved by high abundances of medusae. Jellyfish (including Cyanea lamarckii and C. capillata) were caught in the North Sea during routine sampling for 0-group gadoids (cod Gadus morhua, haddock Melanogrammus aeglefinus, Norway pout Trisopterus esmarkii and whiting Merlangius merlangus) between 1971 and 1986, and considerable overlaps have been shown between the spatial distributions of these fish and medusae. Here correlations are made between the abundance of medusae in the North Sea and the residual survival of 0-group fish, as quantified by the deviation in 1-group recruitment from the expected Ricker modelled estimate. Significant positive correlations between the residual survival of whiting and medusa abundance are evident for each individual Cyanea sp. and for the combined Cyanea spp. ln(maximum) abundance (all $R \ge 0.60, P < 0.01, N = 15$). The abundance of jellyfish may thus be an important factor influencing the

Communicated by J. P. Thorpe, Port Erin

C. P. Lynam (⊠) · A. S. Brierley Gatty Marine Laboratory, University of St. Andrews, Fife KY16 9LB, Scotland e-mail: chrisl@mcs.st-andrews.ac.uk

Present Address:

C. P. Lynam

Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, The Observatory, Buchanan Gardens, St. Andrews, Fife KY16 9LZ, Scotland mortality of whiting in the North Sea, and as such should be considered in the development of 'ecosystem-based' management of whiting stocks.

Introduction

Although jellyfish prey on fish eggs and larvae (Purcell and Arai 2001; Lynam et al. 2005a; Titelman and Hansson 2006), juveniles of some fish species may actively seek shelter among jellyfish tentacles. Commensal relationships such as these have been described between medusae (including many species of the Scyphozoa, such as Cyanea spp., Rhizostoma spp., Chrysaora spp., Stygiomedusa gigantean and Catostylus mosaicus, and three species of the Hydrozoa: Physalia pelagica, Vellela sp. and Porpita sp.) and fish from nine families: four essentially pelagic fish families (Carangidae, Stromateidae, Centrolophidae and Nomeidae), three relatively demersal families (Gadidae, Girellidae and Centriscidae) and two abyssal families (Tetragonuridae and Zaproridae) (Mansueti 1963; Russell 1970; Brodeur 1998; Drazen and Robison 2004; Browne and Kingsford 2005). These rarely studied commensal relationships occur principally in coastal areas, where medusae are abundant, of the Pacific (e.g. Marshall Islands and the Okhotsk Sea), Indian (e.g. Palk Bay) and Atlantic Oceans (e.g. Bay of Fundy and Georges Bank) and in seas (e.g. North, Barents and Mediterranean) worldwide (Mansueti 1963). It has been proposed that 0-group (i.e. fish in their 1st year of life, distinguished by a lack of winter rings in their otoliths) gadoids (cod Gadus morhua, haddock Melanogrammus aeglefinus, Norway pout Trisopterus esmarki and whiting *Merlangius merlangus*) in the North Sea, and whiting in particular, may attain a greater chance of survival to the 1-group as a direct result of the shelter relationship (Mansueti 1963 and references therein; Hay et al. 1990).

Sheltering gadoids, protected from jellyfish stinging cells (nematocysts) by a mucous coating, may steal prey from the medusa and feed on the crustaceans (Hyperiidea) that parasitise jellyfish (Mansueti 1963; Russell 1970; Purcell and Arai 2001). Evidence of this behaviour by young whiting in association with *Rhizostoma octopus* in the Irish Sea has been reported; up to 46 live fish (25–46 mm total length), many with *Hyperia* sp. in their stomachs, were found among the tentacles of a single parasitised medusae (Nagabhushanam 1959, cited in Russell 1970). The number of fish that shelter under a medusa is variable and may range from 1 to ~50, most likely dependent upon their respective densities in the water column, species composition and both fish and medusa size.

Although gadoids are generally demersal fish, 0-group cod, whiting and haddock live in the upper water layers (≤ 40 m) for a period of a few months prior to migrating to the seabed (Daan et al. 1990; Bjorke and Saetre 1994) and it is in these months that an association with jellyfish may prove beneficial. Even though the gadoid spawning areas and timings are particular to each species, 0-group fish of each species have been found in association with Cyanea spp. during June-August in the North Sea (Hay et al. 1990). Cod spawning takes place in the North Sea between January and April, occurring in most offshore areas, but predominantly in the northern and central North Sea (Rogers and Stocks 2001). Newly hatched cod (2-3 weeks post-spawning) are distributed over a large proportion of this area but many are advected towards Jutland, leading to high concentrations of larvae in the shallow Wadden Sea. Haddock release their eggs in a number of batches from March until May between the Scottish coast and Norwegian inshore waters. Although most haddock larvae do not travel far from their spawning grounds, larvae from spawning grounds off the Scottish western coast can be transported into the northern North Sea (Rogers and Stocks 2001). The spawning season of whiting extends from late January until June, and an individual female will release many batches of eggs over a period of at least 10 weeks (Rogers and Stocks 2001). High numbers of 0-group whiting are found both off the Scottish coast and in the Wadden Sea, where medusae are particularly abundant (Coull et al. 1998; Lynam et al. 2004).

In this study, the possible effect of the shelter relationship on gadoid 1-group recruitment is explored by correlating the abundance of *Cyanea* spp. in the North Sea with the survival of 0-group cod, whiting and haddock. Norway pout were excluded from the analysis since the 0-group are thought to spend a much greater period of time close to the seabed (Bailey 1975). For each gadoid species considered, a Ricker model was used to separate out the component of variability in 1-group recruitment due to changes in Spawning Stock Biomass (SSB) (Lynam et al. 2005a). The remaining variability in the 1-group recruitment data, the residual survival, was correlated with the maximum abundance of each Cvanea sp. in the North Sea from 1971 to 1986. Correlative analyses were also conducted to determine whether sea temperature, salinity or the North Atlantic Oscillation Index were significant covariates with each residual survival index.

Materials and methods

Data collection

Over 15 years (1971–1986, excluding 1984), >430,000 medusae (1-47 cm diameter) were caught in 2,030 trawls during the routine summer (June-August) by International Council for the Exploration of the Sea (ICES) International 0-group Gadoid Surveys of the North Sea (Hay et al. 1990). Standardised surveys were conducted using the International Young Gadoid Pelagic Trawl (IYGPT) and jellyfish (including Cyanea lamarckii and C. capillata) were a by-catch of these surveys. The trawl had mesh sizes of 100 mm in wings, bosom and belly, tapering through intermediate mesh size to 10 mm knotless meshing in the extension piece and codend. When the net (mouth opening $\approx 14 \text{ m}^2$) was fished at a maximum speed of 2.5 knot for 1 h, about 65,000 m³ of water was filtered assuming 100% filtration efficiency (Hay et al. 1990). During the gadoid surveys, the trawl was fished for 1 h in a standard depth profile. For the first third (0–20 min) of the trawl duration the net was fished close to the seabed. The net was then hauled to mid-water, or to thermocline depth where known, and fished for a further 20 min. During the third period of the trawl the net was fished close to the surface (5-10 m). In depths >150 m, 125 m was taken as the bottom depth; in depths <30 m only the bottom and surface were fished (for 30 min each, Hay et al. 1990). Full survey methods are given in Hay et al. (1990).

Fish Spawning Stock Biomass (SSB, tonnes) and 1-group recruitment (thousands of individuals) data are published by ICES: cod (*Gadus morhua*) data are produced for the North Sea combined with the eastern English Channel (ICES 2002), whiting (*M. merlangus*) data are given for the North Sea and Skagerrak (ICES 1996b) and haddock (*M. aeglefinus*) data for the North Sea are combined with the Skagerrak and Kattegat regions (ICES 2003).

During the survey period, major hydroclimatic changes occurred in the North Sea, which may have affected both the abundance of jellyfish and the survival of young fish (Edwards et al. 2002; Beaugrand 2004). From 1968 to 1981 a large volume of cold, low salinity water, described as 'The Great Salinity Anomaly', travelled around the North Atlantic gyre (Dickson et al. 1988; Belkin et al. 1998). This water entered the northern North Sea from 1977 to 1979, coinciding with a phase shift of the North Atlantic Oscillation Index (NAOI) from high to low, and a period of high jellyfish abundance (Dickson et al. 1988; Reid et al. 2003; Lynam et al. 2004, 2005b). To determine whether changes in the environment were important covariates with the survival of those gadoid fish studied, correlations were also made between residual survival and surface salinity, temperature and the North Atlantic Oscillation (NAO) index. Mean monthly salinity and temperature data for the surface (top 5 m) layer in one degree of longitude by halfdegree of latitude grid squares throughout the North Sea were supplied by ICES. Data for the NAO winter (December-March) index, based on the difference of normalised sea level pressure between Lisbon, Portugal and Stykkisholmur, Iceland were obtained from http://www.cgd.ucar.edu/cas/jhurrell/indices.html.

Residual survival index for fish larvae

Hay et al. (1990) were unable to determine any influence of *Cyanea* abundance on the survival of 0-group fish to the 1-group. However, they only tried correlations between *Cyanea* biomass and the abundance of 1-group fish in the following years. To identify if there are any external impacts on the recruitment of a fish species either by another species or by the environment, we should first factor out from the recruitment data any 'internal' effect due to changes in spawning stock biomass (Lynam et al. 2005a). The Ricker model (Eq. 1) is used to account for this variation in recruitment due to long-term population change:

$$R_{\text{Ricker}} = (a\text{SSB})\exp(-b\text{SSB}) \tag{1}$$

where R_{Ricker} = recruits (millions) to 1-group for haddock, cod and whiting for year class y. The constants a and b were fitted, for each gadoid species, by non-linear least-squares estimation using the *Gauss-Newton* algorithm in *R Version* 1.8.1 (R Development Core Team 2003): for whiting $a = 6.60 \times 10^{-4}$ and $b = 1.68 \times 10^{-3}$, cod a = 3.57 and $b = 2.9 \times 10^{-6}$ and for haddock a = 480 and $b = 4.65 \times 10^{-6}$. The external impacts on larval survival (i.e. variability in recruitment not due to changes in SSB) were then measured by the dimensionless residual survival (Eq. 2)

$$S_{\rm residual} = \ln(R_{\rm observed}/R_{\rm Ricker}) \tag{2}$$

where R_{observed} is the recruitment value reported by ICES.

All time series data (residual survival, jellyfish abundance, temperature, salinity and NAOI) were assessed for first- and second-order autocorrelation using the Breusch–Godfrey LM test (Johnston 1984). For each test, the 0.05 significance level was chosen to minimise corresponding Type II error (Krzanowski 1998), and no evidence of significant autocorrelation was found.

Results

The residual survival from 1971 to 1986 of whiting, but not haddock or cod, correlated positively with the ln(maximum) abundance of both *Cyanea* species combined (R = 0.64, Fig. 1) and individually: *C. lamarckii* (R = 0.65) and *C. capillata* (once a long-term



Fig. 1 a *Merlangius merlangus* (whiting) and *Cyanea* spp. **b** *Gadus morhua* (cod) and *Melanogrammus aeglefinus* (haddock). Correlation coefficient between whiting residual survival and *Cyanea* spp. abundance: 1971–1986, R = 0.64, P < 0.01

rise in C. capillata abundance was detrended) (R = 0.60) (all P < 0.01, N = 16); note that C. lamarckii abundance did not correlate significantly with C. capillata abundance. As fluctuations in temperature and salinity during the early life stages of fish can impact greatly on the development and survival of hatchlings, the mean surface salinity and temperature were calculated for the whiting spawning period (from January to August) in the western North Sea, from 5°W to 3°E and between 55°N and 66°N, where these larvae spawned. No significant correlations were found between the residual survival of whiting and either temperature or salinity. As climatic oscillations can also alter hydrographic conditions (i.e. wind-induced mixing, surface currents and river input) in the North Sea, whiting residual survival was correlated against the North Atlantic Oscillation Index, but no significant correlations were found.

Discussion and conclusions

A considerable spatial and temporal overlap exists between jellyfish aggregations and 0-group whiting (Hay et al. 1990), and the survival of whiting appears higher than expected, on the basis of whiting SSB, in years of high Cyanea spp. abundance. Whiting are known to exploit jellyfish for shelter and produce a mucous coating that grants them immunity to stinging by the tentacles of Cyanea spp. (Russell 1970 and references therein). Although 0-group haddock and cod have both been observed sheltering under medusae (Russell 1970; Hay et al. 1990 and references therein), no effect of sheltering on the survival of these species was found. As cod spawns earlier (peak spawning during February-March), and over a greater area, than the majority of whiting (April-May) they may pass the critical early mortality period (first few months of postlarval stage) before finding shelter under medusae. The majority of haddock are spawned in an highly advective region of the North Sea to the east of the Shetland Isles, and although Cyanea spp. are often abundant there during the summer, the majority of young haddock may be swept away before dense aggregations of medusae have had the opportunity to form.

Cyanea spp. are characterised by particularly numerous, long tentacles that may trail for many metres behind even a comparatively small jellyfish (~10 cm diameter). By associating with medusae, gadoid fish may take refuge among the tentacles and even retreat into the umbrella in order to flee predation by other fish that are vulnerable to the medusa's sting (Mansueti 1963). Young whiting follow the vertical

migration of *Cyanea* closely (Russell 1928) and it is possible that whiting spawned inshore travel offshore under the protection of jellyfish (Hay et al. 1990). However, an alternative explanation for the fish-medusa association could be that the fish are present in order to steal prey from the medusa. If the fishes profit in this way, then they would effectively forage over the range of the jellyfish's tentacles with relatively little effort; however, no observations have been made to verify this hypothesis.

Within shoals, 0-group whiting are highly cannibalistic and individually they are particularly likely to succumb to predation by other fishes. So, the hypothesis that whiting 1-group recruitment is enhanced through the association of 0-group fish with Cyanea spp. would appear to be the most likely explanation of the positive correlation found here between whiting 0-group residual survival and Cyanea spp. abundance. Whiting is one of the most numerous and widespread fish species in the North Sea and, in addition to preying upon crustacean zooplankton, they also prey on other commercially important fish (gadoids and clupeids) (Knijn et al. 1993; ICES 1996a; Bromley et al. 1997; Rogers and Stocks 2001; Wennhage and Pihl 2002; Rindorf 2003; Titelman and Hansson 2006). In order to develop ecosystem-based fisheries management strategies, it will be vital that the interactions between fish and the plankton community be understood (Verity et al. 2002; Pikitch et al. 2004).

Further research is required to determine the importance of fish-medusae commensal relationships explored here in fisheries and to fully understand the nature of these relationships. Specifically, the typical number of fish per medusa and the duration of any association should be identified, as should the total number of medusae available for association and the proportion that provide shelter. The relationship between the improvement in survival for a particular fish species and the densities or abundances of both the fish and medusae should be clarified. For those species that are found to associate regularly, the spatial overlap of the fish and medusa distributions and the relative improvement to survival of the fish species should be determined. Given the numerous associations reported, and the wide-ranging distribution of these reports, the potential for commensal relationships that are important to fisheries to exist is high and deserves further study. Rather than the solely detrimental effects on fisheries that are often reported (Lynam et al. 2005a, 2006), jellyfish may have a more complex ecosystem role, whereby medusae prey upon eggs and larvae, yet benefit juvenile gadoid fish through the provision of refugia from predation.

Acknowledgements We are grateful to S. Hay and colleagues at FRS Marine Laboratory, Aberdeen, who collected the jellyfish data. We also thank S. Reimert of ICES for the hydrographic data and J. Hurrell for making the NAOI data freely available. C.P.L. was funded by the Natural Environment Research Council, UK.

References

- Bailey RS (1975) Observations on diel behaviour patterns of North Sea gadoids in the pelagic phase. J Mar Biol Assoc UK 55:133–142
- Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245–262
- Belkin IM, Levitus S, Antonov J, Malmberg SA (1998) "Great Salinity Anomalies" in the North Atlantic. Prog Oceanogr 41:1–68
- Bjorke H, Saetre R (1994) Transport of larvae and juvenile fish into central and northern Norwegian waters. Fish Oceanogr 3:106–119
- Brodeur RD (1998) In situ observations of the association between juvenile fishes and scyphomedusae in the Bering Sea. Mar Ecol Prog Ser 163:11–20
- Bromley PJ, Watson T, Hislop JRG (1997) Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. ICES J Mar Sci 54:846–853
- Browne JG, Kingsford MJ (2005) A commensal relationship between the scyphozoan medusae *Catostylus mosaicus* and the copepod *Paramacrochiron maximum*. Mar Biol 146(6):1157–1168
- Coull KA, Johnstone R, Rogers SI (1998) Fisheries sensitivity maps in British Waters. Published and distributed by UKOOA Ltd
- Daan N, Bromley PJ, Hislop JRG, Nielsen NA (1990) Ecology of North Sea Fish. Neth J Sea Res 26:343–386
- Dickson RR, Meincke J, Malmberg SA, Lee AJ (1988) The "great salinity anomaly" in the Northern North Atlantic 1968–1982. Prog Oceanogr 20:103–151
- Drazen JC, Robison BH (2004). Direct observations of the association between a deep-sea fish and a giant scyphomedusa. Mar Freshw Behav Physiol 37(3):209–214
- Edwards M, Beaugrand G, Reid PC, Rowden AA, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. Mar Ecol Prog Ser 239:1–10
- Hay SJ, Hislop JRG, Shanks AM (1990) North-Sea scyphomedusae—summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25:113–130
- ICES (1996a) Report of the multispecies assessment working group. ICES CM 1996/Assess:3. Copenhagen, Denmark
- ICES (1996b) Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 1996/Assess:6, Copenhagen, Denmark
- ICES (2002) Report of the ICES advisory committee on fish management 3.5.2: cod in sub-area IV (North Sea), Division VIId (Eastern English Channel) and Division IIIa (Skagerrak). ICES, Copenhagen
- ICES (2003) Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 2004/ACFM:07, Boulogne-sur-Mer, France

- Johnston J (1984) Econometric methods, 3rd ed. McGraw Hill, New York
- Knijn RJ, Boon TW, Heessen HJL, Hislop JRG (1993) Atlas of North Sea fishes. ICES Cooperative Research Reports. Copenhagen, ICES 194. 268
- Krzanowski WJ (1998) An introduction to statistical modelling. Arnold
- Lynam CP, Hay SJ, Brierley AS (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol Oceanogr 49:637–643
- Lynam CP, Heath MR, Hay SJ, Brierley AS (2005a) Evidence for impacts by jellyfish on North Sea herring recruitment. Mar Ecol Prog Ser 298:157–167
- Lynam CP, Hay SJ, Brierley AS (2005b) Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J Mar Biol Assoc UK 85:435–450 DOI 410.1017/s0025315405011380
- Lynam CP, Gibbons MJ, Axelsen BE, Sparks CAJ, Coetzee J, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in an heavily fished ecosystem. Curr Biol 16(13):R492–R493
- Mansueti R (1963) Symbiotic behavior between small fishes and jellyfishes, with new data on that between the Stromateid, *Peprilus alepidotus*, and the Scyphomedusa, *Chrysaora quinquecirrha*. Copeia 1:40–90
- Nagabhushanam (1959) Studies on the biology of the commoner gadoids in the Manx area, with special reference to their food and feeding habits. PhD Thesis, University of Liverpool
- Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305:346–347
- Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:27–44
- R Development Core Team (2003) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish Oceanogr 12:260–269
- Rindorf A (2003) Diel feeding pattern of whiting in the north sea. Mar Ecol Prog Ser 249:265–276
- Rogers S, Stocks R (2001) North Sea fish and fisheries. Department of Trade and Industry. Strategic Environmental Assessment—SEA2 Technical Report 003—Fish and Fisheries CEFAS
- Russell FS (1928) The vertical distribution of marine macro-plankton. VIII. Further observations on the diurnal behaviour of the pelagic young of teleostean fishes in the Plymouth area. J Mar Biol Assoc UK 14:557–608
- Russell FS (1970) The medusae of the British Isles. II. Pelagic Scyphozoa with a supplement to the first volume on hydromedusae. Cambridge University Press, London
- Titelman J, Hansson LJ (2006) Feeding rates of the jellyfish *Aurelia aurita* on fish larvae. Mar Biol 149:297–306 DOI 10.1007/s0022700502005
- Verity PG, Smetacek V, Smayda TJ (2002) Status, trends and the future of the marine pelagic ecosystem. Environ Conserv 29:207–237
- Wennhage H, Pihl L (2002) Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. J Fish Biol 61:207–228