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Differences in growth and survival between cod *Gadus morhua* and herring *Clupea harengus* early stages co-reared at variable prey concentrations

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It was hypothesized that the survival and growth strategies of herring *Clupea harengus*, displaying a flexible reproductive activity, are adapted to coping with longer periods of prey deprivation (*i.e.* more variable prey availability), in contrast to cod *Gadus morhua*, which are adapted to match growth and survival at high prey concentrations. Experimental larval growth and survival data for the two naturally co-occurring species reared either in separate tanks or in combination are presented to test this hypothesis. Natural zooplankton was supplied either *ad libitum* or in a periodically restricted manner to mimic natural suboptimal conditions. Periodically restricted feeding significantly reduced initial growth of *G. morhua* larvae co-reared with *C. harengus*, while no such initial effect was seen for co-reared *C. harengus*. Overall survival of *G. morhua* was higher when reared together with *C. harengus* (32 v. 24%), while *C. harengus* had higher survival without the presence of *G. morhua* (59 v. 44%), indicating that both species were affected by higher densities of *G. morhua* larvae. Furthermore, the final survival in *G. morhua* was inversely related to average final size, while in *C. harengus* an opposite trend was observed. How potential behavioural interactions may drive the present results are discussed and contended that a better insight into field vital rates may be gained from further exploration of co-rearing experiments.

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Key words: competition; feeding; juveniles; larvae; zooplankton.

INTRODUCTION

In a series of ground breaking papers in the 1970s and 80s, ample evidence was provided for species-specific differences in larval fish foraging efficiencies, growth and mortality rates (Houde, 1978; Houde & Schekter, 1981). Larvae of three different species were shown to have different minimum threshold levels of prey concentration sustaining positive growth and survival (Houde, 1978), *e.g.* the sparid sea bream *Archosargus rhomboidalis* (L.1758) larvae, had higher growth and survival than the clupeid bay anchovy *Anchoa mitchilli* (Valenciennes 1848) larvae and the lined sole

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Achirus lineatus (L. 1758) at prey concentrations below 50 individuals l^{-1} . At the same time, growth of survivors was higher for *A. rhomboidalis* larvae than for *A. mitchilli* and *A. lineatus* larvae at prey concentrations >600 individuals l^{-1} , indicating a higher capacity for growth. In a review paper, Houde (1989) showed that, between taxa, the estimated required food concentrations at first feeding in order to meet the reported species-specific mean growth rates varied two-fold. Few experimental studies, however, have focused on how fish larvae would react to temporal and spatial variability in prey concentration, a situation expected to be more prevalent in the field (Gallego *et al.*, 1996; Munk, 2007; Huwer *et al.*, 2011). In a study simulating pulses of available prey, Houde & Schekter (1981) found that red sea bream *Pagrus major* (Temminck & Schlegel 1843) were more likely to increase survival when offered short-term (3 h) pulses of elevated prey concentrations compared with constant concentrations, and as such were considered more adapted to survive under fluctuating food conditions. Larvae of several species have been shown to alter prey search behaviours at reduced prey concentrations (Hunter & Thomas, 1974; Munk, 1992, 1995), but to what extent it affects long-term growth and survival remains unresolved.

Along the Norwegian coast, there are several commercially important fish species spawning during the early spring season, with offspring being transported further north-east into the Barents Sea (Vikebø *et al.*, 2011). A marked positive co-variability in growth and initial survival has been documented among three co-occurring species, *Gadus morhua* L. 1758, haddock *Melanogrammus aeglefinus* (L. 1758) and *Clupea harengus* L. 1758, with ambient temperature and juvenile density being main contributors to the observed patterns (Ottersen & Loeng, 2000; Dingsør *et al.*, 2007). Elevated temperatures may also result in increased prey productivity and availability in addition to directly supporting higher growth rates. The response of these species to different prey concentrations was not further investigated, however, despite being a potential driving factor of growth and survival patterns. Based on a series of laboratory experiments with constant prey concentrations, Folkvord *et al.* (2009a) concluded that *G. morhua* larvae not only have a higher growth capacity but also have a higher minimum prey level requirement than *C. harengus* larvae. Thus, it was suggested that the *C. harengus* larvae were more likely to survive at lower prey concentrations than co-occurring *G. morhua* larvae. Although autumn-spawning *C. harengus* clearly face less favourable food fields, it has been suggested that spring-spawning *C. harengus* larvae may be extremely plastic too, having to cope with variable environments (Fossum & Moksness, 1993; Folkvord *et al.*, 2009b).

A major limitation of laboratory experiments is that they can artificially elevate levels of interaction between individuals, *e.g.* through prey competition or aggressive behaviour (Laurence *et al.*, 1981; Puvanendran *et al.*, 2008; Vollset *et al.*, 2009). The estimated threshold levels for survival and growth may thus be biased, and subject to uncontrolled factors. The experienced feeding conditions can also diverge between experiments with different cohorts or species, complicating inter-cohort or -species comparisons. By applying common-garden rearing, it is possible to isolate the group or species-specific effect on feeding treatments and compare how the two groups or species respond within the same holding conditions (Laurence *et al.*, 1981; Lankford *et al.*, 2001; Paulsen *et al.*, 2009). By comparing these results to parallel single group and species treatments, it is possible to tease out how much survival and growth are affected by group and species-specific interactions.

Thus, to further evaluate potential growth and survival differences between larval *G. morhua* and *C. harengus*, an experiment with co-rearing in addition to single species rearing was set up. The single species rearing involved high pre-determined prey levels (to enable *ad libitum* feeding). The co-rearing was carried out using two different prey regimes, one mimicking the conditions in the single species rearing, and in addition a periodically restricted regime where prey concentration was allowed to drop down to c. 25% of the high level before replenishment of prey to pre-determined levels, simulating a temporally food limited setting. Growth, survival and condition of the two species were closely monitored over a 6 week period, and analysed with respect to (1) species interaction, *i.e.* co-rearing versus single species rearing, (2) feeding regime, *i.e.* full feeding *v.* periodically restricted feeding.

MATERIALS AND METHODS

LARVAL REARING

Clupea harengus eggs were obtained from six stripped females caught in Lindåspollane (60.72° N; 5.12° E), western Norway, and incubated at 5.7° C in the laboratory at the High Technology Centre in Bergen. About 50% of the *C. harengus* eggs had hatched on 21 March 2008, defined as 0 days post-hatch (dph). *Gadus morhua* eggs were obtained from a naturally spawning, wild-caught brood stock originating from Møre, western Norway, and incubated at 6° C, and 50% had hatched by 24 March (0 dph). The experiment was terminated on 5 May, 44 and 41 dph for *C. harengus* and *G. morhua*, respectively. Further details on larval groups and parental fishes are provided in the studies of Catalán *et al.* (2011) and Vollset *et al.* (2013). On 22 March, newly hatched *C. harengus* larvae were counted and stocked into 500 l rectangular tanks and on 25 March, 0 day-old *G. morhua* larvae were also added to the tanks. The rearing system has already been described elsewhere (Otterlei *et al.*, 1999; Folkvord *et al.*, 2009b), and was chosen for this study since it has provided high growth and survival rates for these species. Only the main features of the system are repeated here. A semi-stagnant green water system was used and temperature was kept between 8 and 9° C throughout the experimental period. The larvae were fed live cultured algae, *Rhodomonas* sp. and *Isochrysis* sp., and live wild zooplankton from 28 March to the rearing tanks (representing 6 and 3 dph for *C. harengus* and *G. morhua*, respectively). The zooplankton was obtained with a Hydrotech filter system (<http://technomaps.veoliawatertechnologies.com/hydrotech/en/>) and size graded to accommodate larval prey size requirements during the experiment following Seljeset *et al.* (2010). All groups were provided with the same size fraction of wild zooplankton retained in the filter, increasing from 80 to 250 µm until 21 dph to 80–400 µm at the end of the experiment. The wild zooplankton was collected weekly and kept in the laboratory zooplankton holding tanks, from where it was size-graded at the required phases and fed to the fishes daily around noon. The concentrations of the main prey types, copepod nauplii, copepodites, rotifers and a combined group of other miscellaneous edible prey types (*e.g.* veliger, trochophora and cirriped nauplii), were monitored daily in all larval rearing tanks and plankton holding tanks. The total prey concentrations in the rearing tanks were adjusted daily if necessary according to the feeding regimes. The experiment conducted in this study was approved according to Norwegian animal welfare regulations (approval number FDU 08/33853-1).

Species interaction

The null hypothesis of no species interaction under co-rearing on growth, condition or survival under constant (*ad libitum*) food regime was tested. *Gadus morhua* and *C. harengus* larvae were co-reared in three replicate tanks with interaction full-feeding regime (IFF; Table I). The growth and survival of larval *G. morhua* and *C. harengus* from these tanks were contrasted against those from three tanks with only *G. morhua* larvae (SFF-C, single full-feeding regime), and three tanks

TABLE I. Design of species interaction and feeding regime experiment. Periodically restricted feeding permitted reduction of prey concentration to *c.* 25% of pre-determined concentrations of interaction full-feeding treatments (IFF) before replenishment of prey. Growth was analysed from weekly regular samplings of 10 larvae per species per tank and the IFF group is common for both experiments and is made of the same tanks

Species interaction	SFF-H	IFF	SFF-C
Species interaction	Single	Inter	Single
Feeding level	Full	Full	Full
Initial number of <i>G. morhua</i> larvae	0	1500	3000
Initial number of <i>C. harengus</i> larvae	3000	1500	0
Age of larvae (dph)	9–44	6–44	6–41
Number of replicate tanks	3	3	3
Feeding regime	IRF		IFF
Species interaction	Inter		Inter
Feeding level	Restrict		Full
Initial number of <i>G. morhua</i> larvae	1500		1500
Initial number of <i>C. harengus</i> larvae	1500		1500
Age of larvae (dph)	6–44		6–44
Number of replicate tanks	3		3

Inter, tanks where both *Gadus morhua* and *Clupea harengus* larvae were present and could potentially interact; Single, tanks holding single species; SFF-H, single full-feeding *C. harengus*; IRF, interaction periodically restricted feeding; SFF-C, single full-feeding *G. morhua*; dph, days post-hatch.

with only *C. harengus* larvae (SFF-H). The total initial number of larvae in each tank was 3000, with equal amounts of each species in the co-rearing tanks (Table I).

Feeding regime

The null hypothesis of no effect of feeding regime (full feeding *v.* periodically restricted feeding) on growth, condition and survival of co-reared *C. harengus* and *G. morhua* was tested (Table I). Three replicate tanks with both *G. morhua* and *C. harengus* larvae (IFF) had zooplankton concentrations adjusted on a daily level to pre-determined nominal concentrations (initially 2000 zooplankters l^{-1} , lowered to 1500 zooplankters l^{-1} from 30 dph). In the remaining three tanks, zooplankton was only replenished once the concentration had dropped below one fourth of the pre-determined concentration in the other tanks (interaction periodically restricted feeding regime, IRF; Fig. 1). This resulted in a mean \pm s.d. prey concentrations in the morning prey counting of 1024 ± 521 individuals l^{-1} in full-feeding regimes *v.* 733 ± 404 individuals l^{-1} in the periodically restricted feeding regime. Prey concentration was estimated every morning between 0800 and 1000 hours in all tanks, and additional zooplankton was supplemented to respective tanks shortly thereafter if necessary to maintain the assigned feeding regime.

SAMPLING

Every week, 10 larvae of each species from each tank were sampled and photographed for subsequent length and mass measurements. In the single species tanks, twice that number was used to ensure equal effect of sampling mortality on the tanks. Standard lengths (L_S) were obtained from calibrated images using ImageJ software (<http://imagej.nih.gov/ij/>) and dry mass (D_M) was measured to the nearest μg with a Sartorius (www.sartorius.com) microbalance after 24 h prior drying at 60°C. A total of 1080 larvae were sampled, but mass data from two tanks at first sampling and one tank at final sampling, and the L_S data from the first and last sampling are missing

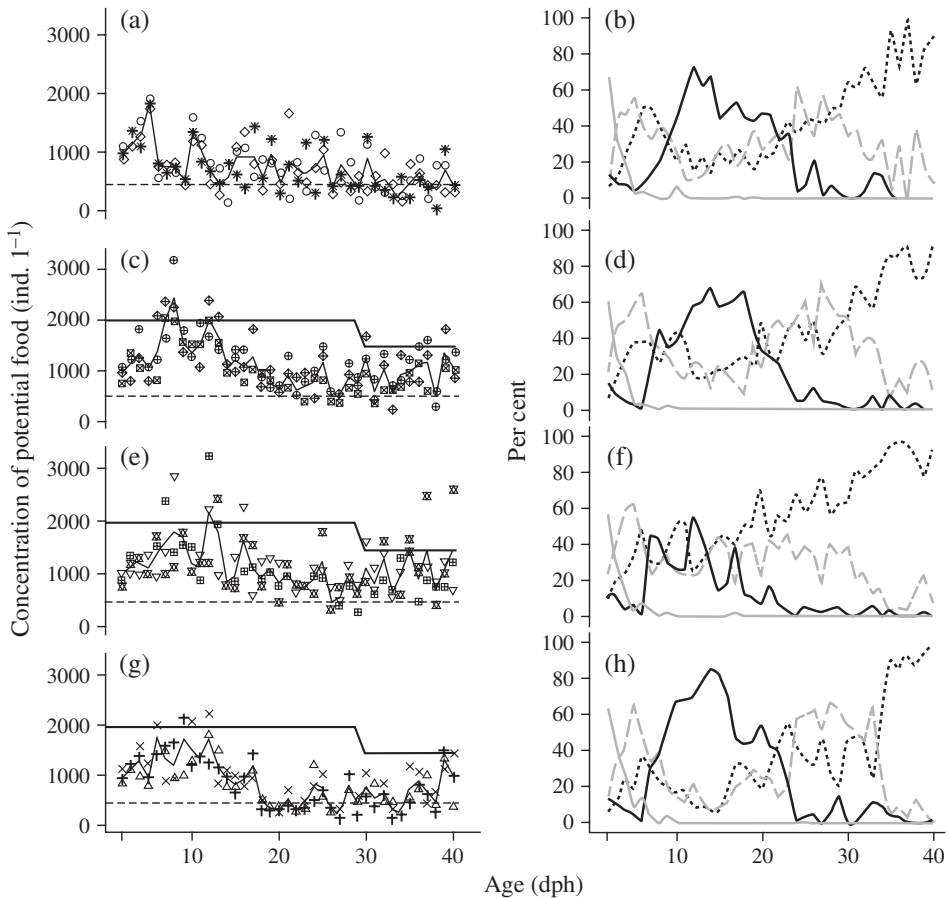


FIG. 1. Schematic presentation of total prey concentrations observed in the tanks of the different treatments (see Table I) every morning prior to replenishment of new plankton. (a) IRF, interaction periodically restricted feeding *Clupea harengus* and *Gadus morhua*; (c) IFF, interaction full feeding *C. harengus* and *G. morhua*; (e) SFF-C, single full-feeding *G. morhua* and (g) SFF-H, single full-feeding *C. harengus*. —, pre-determined targeted prey concentrations in full-feeding groups; ----, prey concentration levels in restricted feeding groups which elicited replenishment of prey to full-feeding levels. Daily mean estimates of main prey categories (in %) prior to replenishment are also indicated, (e) IRF, (f) IFF, (g) SFF-C and (h) SFF-H, with copepods (.....), copepod nauplii (---), rotifers (—) and other prey types (—). Each replicate in each treatment is indicated with separate symbols. Both x-axes are relative to age (days post-hatch, dph) of *Gadus morhua* larvae.

due to freezer and data storage problems, yielding in total 990 and 705 larval masses and L_S , respectively, available for further analysis. The number and timing of additional sampling of larvae for other purposes (Catalán *et al.*, 2011; Vollset *et al.*, 2013) are accounted for in the estimation of overall survival and average daily mortality in each tank (Folkvord *et al.*, 2009b), but otherwise these larvae are not used in this paper.

STATISTICAL ANALYSIS

Differences in survival between species were tested by a *t*-test for the SFF-H and SFF-C treatments, while a paired *t*-test was used for the IRF and IFF treatments. The effects of species

interaction and feeding regime on survival were also tested with *t*-tests for each species separately by contrasting survival in IFF and SFF treatments (species interaction) or IRF and IFF treatments (feeding regime).

Species interaction effects and feeding regime effects on larval mass at age were analysed by general linear model (GLM, nested ANOVA) on a per species and date basis for both experiments, while morphometric condition, estimated as residuals from the overall L_S and mass relationship, was analysed by separate GLM (ANCOVA) analyses. When needed, variables were ln transformed to obtain homogenous variances, and an $\alpha = 0.05$ was set as the level of significance for all tests.

RESULTS

Survival of *C. harengus* larvae tended to be higher when reared without the presence of *G. morhua* (average of 59 v. 44% in the SFF and IFF groups, respectively, *t*-test, $t = 2.67$, d.f. = 4, $P > 0.05$; Fig. 2), while the survival of *G. morhua* was not similarly affected by the presence of *C. harengus* (24 v. 32% in the SFF and IFF groups, respectively, *t*-test, $t = 0.98$, d.f. = 4, $P > 0.05$; Fig. 2). Species-specific analyses demonstrated that the final survival did not significantly differ between IRF and IFF groups (species interaction, *t*-tests, $t < 0.57$, d.f. = 4, $P > 0.05$; Fig. 2). Survival was higher in the *C. harengus* SFF group compared with SFF-C group (59 v. 24%, *t*-test, $t = 10.1$, d.f. = 4, $P < 0.001$; Fig. 2). Survival also tended to be higher among *C. harengus* larvae than *G. morhua* larvae when reared together in the IRF and IFF tanks (42 v. 31%), but this difference was not significant (paired *t*-test, $t = 2.1$, d.f. = 5, $P > 0.05$).

There were no significant differences in size at age between IFF and SFF groups within either species at any sampling date (species interaction, GLMs, $P > 0.05$; Fig. 3). When comparing the feeding regime, *G. morhua* in the IRF group showed significantly smaller size at age than those of the IFF group already by 13 dph (GLMs, $P < 0.001$). *Clupea harengus* larvae from the IRF treatment were also smaller than IFF larvae but only from 30 dph onwards (feeding regime, GLMs, $P < 0.01$). In addition, the variability in size was higher in the IRF groups of both species for the last 3 weeks, with mass-at-age c.v. averaging 52% for the IRF groups compared with 38% for the other groups. The feeding regime also resulted in a more marked growth divergence between the IRF and IFF groups in *G. morhua* than in *C. harengus* (Fig. 3). Among *G. morhua*, the IFF group was on average more than twice the average IRF mass at age while in *C. harengus* the mass difference was <50%. The size variability at age among larvae for the last 3 weeks was also higher in the *G. morhua* groups than *C. harengus* groups, with average group mass-at-age c.v. of 48 and 38%, respectively. Growth was higher in *G. morhua*, and by 34 dph, the initially smaller *G. morhua* had on average attained a larger size at age than *C. harengus* in the IFF and SFF groups (Fig. 3).

There were no differences in morphometric condition (residuals of mass at L_S) between *G. morhua* larvae from different treatments, while a significant difference was detected for *C. harengus* (species interaction, GLM, co-rearing \times ln L_S , $F_{1,229} = 14.76$, $P < 0.001$; Fig. 4). For *C. harengus* larvae <16.4 mm, the larvae from the SFF group were on average 12% heavier at a given L_S than the larvae from the IFF group (GLM co-rearing effect, $F_{1,131} = 46.5$, $P < 0.001$), while for larvae >16.4 mm no significant differences were apparent (GLM, $P > 0.05$).

When comparing average final size and survival from all treatments combined, a different pattern was apparent between species. In *G. morhua*, there was a significant

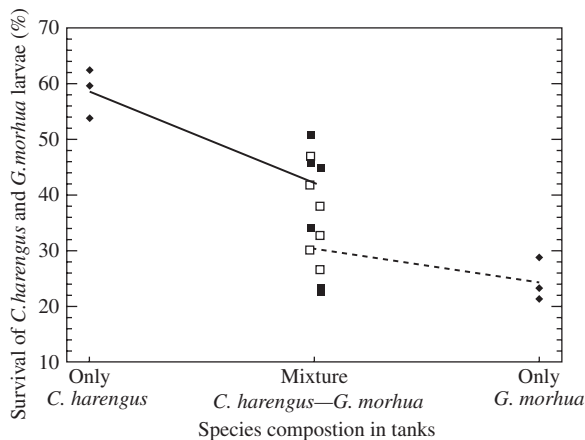


FIG. 2. Overall final survival of all *Gadus morhua* and *Clupea harengus* groups in single species tanks or species interaction tanks (initially 50:50 mix of *G. morhua*:*C. harengus*). Individual treatments are shown: IRF (□), interaction periodically restricted feeding; IFF (■), interaction full feeding; SFF (◆), single full feeding treatments (see Table I), but — and - - - are drawn from species-specific averages. Note that values of *G. morhua* and *C. harengus* are obtained from same tanks in IFF and IRF treatments. Species-specific values in mixed groups are offset for visual clarity.

negative relationship between average final mass and overall survival in the tanks at the end of the period [Fig. 5(b)]. In *C. harengus*, an opposite trend was apparent, but this was not significant [Fig. 5(a)].

No systematic observations of individual larval behaviour were recorded, but the results of different feeding behaviours in the treatments were indirectly assessed as differences in amounts and types of prey remaining in the tanks during daily plankton sampling in the tanks. The median prey concentration prior to addition of prey in the IRF treatment was 6901 l^{-1} , compared with 800, 1000 and 1020 prey l^{-1} in the SFF-C, IFF and SFF-H groups, respectively [Fig. 1(a)–(d)], and the overall pattern of prey composition in the tanks was relatively similar [Fig. 1(e)–(h)]. The major difference of any treatment to the overall proportion of any prey type varied on a weekly basis between 0.5 and 1.8 fold. Also, the average c.v. of total food within tanks for any given week ranged from <9% (8–14 dph) to 21% (36–42 dph). The most notable difference was observed between the SFF-H and SFF-C treatments in terms of copepod abundance where there were on average 60% more copepods remaining in the SFF-C tanks prior to feeding than the overall average, while the SFF-H tanks contained 40% fewer copepods from 8 to 35 dph (Fig. 6).

DISCUSSION

The periodically restricted feeding treatment in the co-rearing tanks reduced the growth rate of both *G. morhua* and *C. harengus* larvae compared with larvae from the full-feeding treatment. The reduction in growth was more marked initially in *G. morhua* than in *C. harengus* and eventually the feeding restriction did not promote further size divergence compared with the full-feeding treatment in either species. This pattern may partly be explained by differences in species-specific prey search patterns

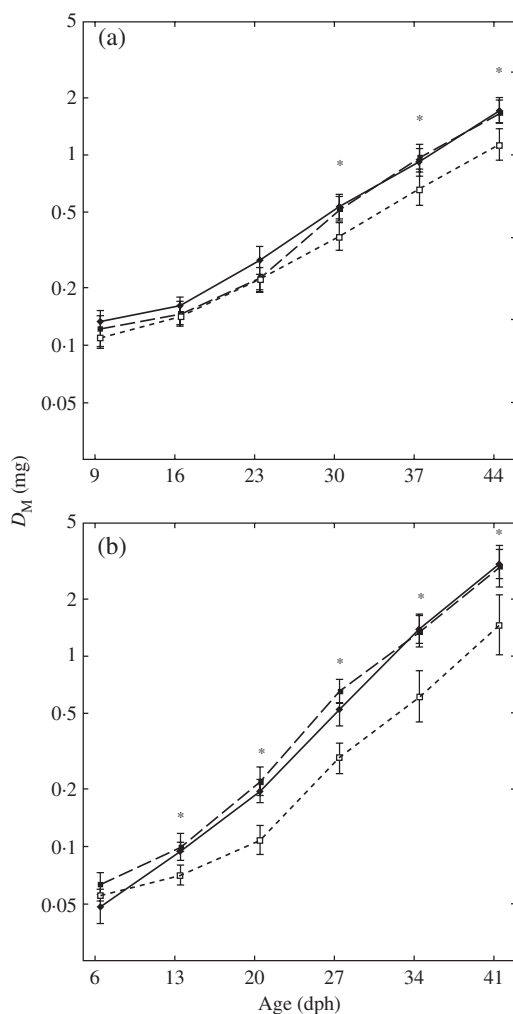


FIG. 3. Mass (D_M) at age (days post-hatch, dph) of (a) *Clupea harengus* and (b) *Gadus morhua* larvae during the species interaction and feeding regime experiment in IRF (\square), interaction periodically restricted feeding; IFF (\blacksquare), interaction full feeding; and SFF (\blacklozenge), single full feeding (see Table I). No significant differences were found between IFF and SFF groups (species interaction). *, cases where there are significant differences ($P < 0.05$) between IRF and SFF groups (feeding regime).

and improvements in swimming speed and foraging capabilities as the larvae develop and increase in size (Munk & Kiørboe, 1985; Munk, 1992; Hunt von Herbing & Gallager, 2000; Vollset *et al.*, 2011). The survival was also similar in the IRF and IFF treatments, suggesting that the extent of the food restriction was modest, especially for the larger-sized larvae. Food restriction implied on average between 65 and 85% of the total food concentration in the other treatments [raw data in Fig. 1(a)–(h)], which is not a severe food restriction according to literature values. The variability in the prey composition, by type of prey and treatment, was modest (between 0.5 and less than two-fold for any given week). Prey composition was apparently similar in the co-rearing tanks at both feeding regimes, despite the slightly lower total food

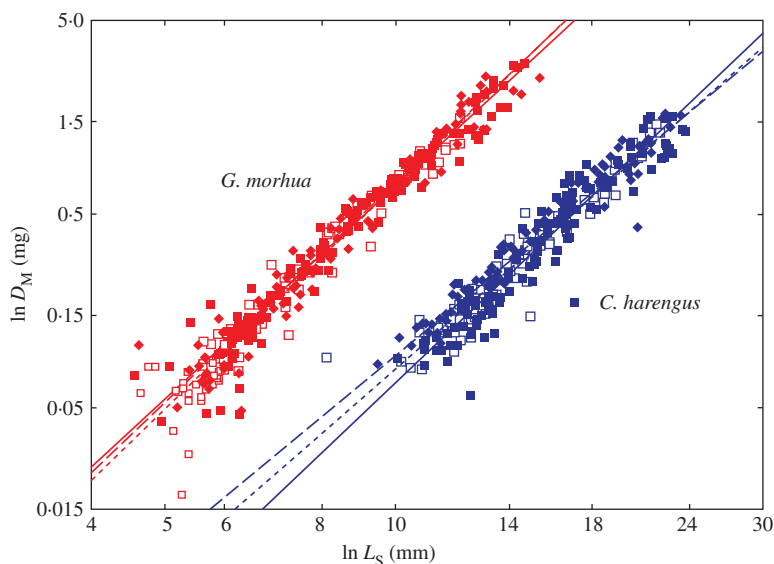


FIG. 4. Mass (D_W) and standard length (L_S) of *Gadus morhua* (red symbols and lines) and *Clupea harengus* (blue symbols and lines) larvae from 13 to 37 days post-hatch (dph) in the species interaction and feeding regime experiment in IRF (□ and ◻), interaction periodically restricted feeding; IFF (■ and ◼), interaction full feeding; and SFF (◆ and ◈), single full feeding (see Table I). Individual group-specific regression equation curves were fitted by: *G. morhua*, IRF (---), $y = -9.2 + 3.85x$ (95% c.i. = 0.18) ($r^2 = 0.942$); SFF (— · —), $y = -8.9 + 3.72x$ (95% c.i. = 0.14) ($r^2 = 0.961$); IFF (—), $y = -8.8 + 3.68x$ (95% c.i. = 0.15) ($r^2 = 0.954$); *C. harengus*, IRF (- - - -), $y = -10.5 + 3.47x$ (95% c.i. = 0.19) ($r^2 = 0.924$); SFF (— · —), $y = -9.9 + 3.29x$ (95% c.i. = 0.13) ($r^2 = 0.958$); IFF (—), $y = -11.4 + 3.78x$ (95% c.i. = 0.23) ($r^2 = 0.905$).

concentration in the IRF tanks compared with the other tanks. The higher reduction of prey concentrations in full-feeding tanks with *G. morhua* larvae compared with those with *C. harengus* larvae mirrored the higher growth of *G. morhua* larvae compared with *C. harengus* larvae, indicating that *G. morhua* larvae had higher foraging and growth capacity than *C. harengus* larvae at high prey concentrations. Previous experiments with *G. morhua* and *C. harengus* larvae at relatively low constant nominal prey concentrations (40–250 individuals l^{-1}) have yielded similar results as for the IRF groups in this study with an initial growth reduction among young larvae followed by growth rates approaching those fed *ad libitum* (Folkvord *et al.*, 2009a, b).

In this study, *C. harengus* larvae were initially less affected by temporarily lower prey concentrations than *G. morhua* larvae. Houde & Schekter (1978) found that a 10 to 20 fold increase of local prey concentrations to 500 individuals l^{-1} over 6 h periods during the first 5 days after the start of exogenous feeding resulted in significantly increased survival in *A. rhomboidalis* larvae, while *A. mitchilli* continued to increase survival after longer exposures to elevated prey concentrations (up to 13 h, *i.e.* the entire daily light period). The increased survival at elevated prey concentrations in *A. mitchilli* was not accompanied by a corresponding increase in final larval size. This is in contrast with the obtained results for *C. harengus* larvae from this study, which suggest that the observed species-specific life-history patterns may vary substantially among closely related species. In another study on yellowtail flounder *Limanda ferruginea*

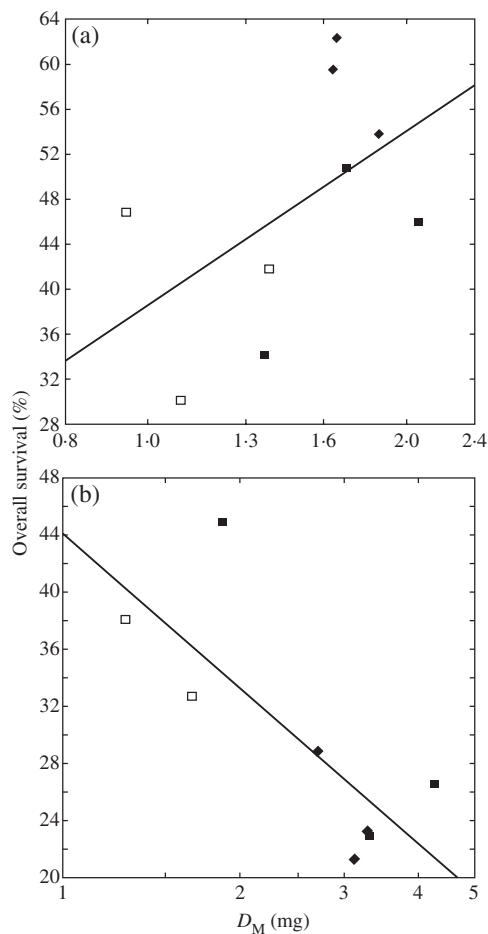


FIG. 5. Survival of (a) *Clupea harengus* and (b) *Gadus morhua* larvae and final average mass (D_M) in IRF (□), interaction periodically restricted feeding; IFF (■), interaction full feeding and SFF (◆), single full feeding treatments (see Table I). The x-axes are on a ln scale. (b) The curve was fitted by $y = 44.1 - 15.6x$ (95% c.i. = 12.5) ($r^2 = 0.54$, $P < 0.05$).

(Storer 1839) larvae, Rabe & Brown (2000) found that two pulse feeding incidences per day were sufficient to promote comparable survival and growth rates obtained under a constant high prey concentration setting. Periodic restriction of prey abundance led to a lowered growth in both species in this experiment. How many hours of optimal feeding conditions *G. morhua* and *C. harengus* larvae would require to attain maximum growth rates are still to be determined, but are likely to be dependent on ambient temperature and metabolic costs (Finn *et al.*, 2002).

In the *C. harengus* groups, in this experiment, growth rates were generally correlated with survival in respective tanks. High growth rates in culture conditions are often accompanied by low mortality rates in the absence of predators (Houde, 1978; Buckley *et al.*, 1993). This was not the case in the *G. morhua* groups, where those with the highest average mass and growth also had the lowest survival. This has been observed for *G. morhua* in previous laboratory studies (Vollset *et al.*, 2009), and may

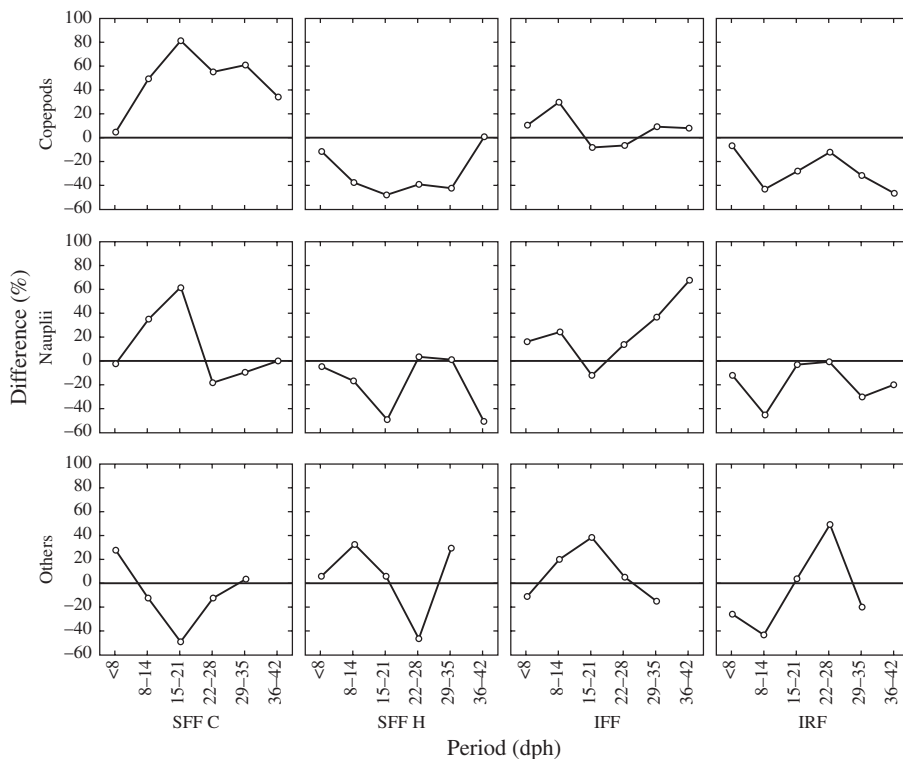


FIG. 6. Average deviation in prey type proportion of three main prey-type categories. Values are estimated on a weekly basis for the four larval groups (IFF, interaction full feeding; IRF, interaction periodically restricted feeding; SFF, single full feeding; see Table I). Rotifers were excluded from the analysis as this prey group only contributed to the first two time periods. dph, days post-hatch.

be due to intra-cohort interactions at the late larval stage and early juvenile stage (Puvanendran & Brown, 1999; Puvanendran *et al.*, 2008), either through cannibalism or density-dependent effects on important prey items. The experiment was terminated relatively early (41 dph for *G. morhua*) to prevent cannibalism in the tanks, but the occurrence of density-dependent agonistic and aggressive interactions is still the most likely explanation for the inverse relation between growth and survival among *G. morhua* groups. According to Puvanendran *et al.* (2008), notable aggressive behaviour of *G. morhua* larvae was observed in the laboratory from a size of *c.* 9 mm, which would indicate that the effect of aggressive behaviour should mainly occur in the last 2 weeks of this experiment. Furthermore, the reduction in growth after 30 dph in the *C. harengus* IRF group compared with the IFF group may also have been a result of elevated competition and agonistic interactions with relatively large *G. morhua* larvae.

In all treatments, the *G. morhua* larvae grew faster than the *C. harengus* larvae and this confirms previous findings that *G. morhua* larvae have higher growth rates under medium to high food concentration conditions (Folkvord *et al.*, 2009a). The difference in survival was higher when the larvae were reared in a single species rather than multi-species setting. In a study on the western Atlantic populations, *G. morhua* larvae were shown to out-perform *M. aeglefinus* larvae in terms of growth and survival when

reared in combination at all prey concentrations used, while *M. aeglefinus* increasingly had higher survival than *G. morhua* at higher prey concentrations when reared in a single species setting (Laurence *et al.*, 1981). As in the case of *G. morhua* and *M. aeglefinus* co-rearing, *C. harengus* also performed poorly in the presence of *G. morhua* compared with being reared in the absence of *G. morhua*. In addition, the *C. harengus* reared together with *G. morhua* in this study had a lower morphometric condition compared with those reared without the presence of *G. morhua* which may indicate an added stress caused by *G. morhua* behaviour. Any potential spatial segregation of *C. harengus* in the presence of *G. morhua* (and thus interactions with prey distribution), however, was not explored. Still, a relatively aggressive behaviour may benefit the growth capacity of *G. morhua* larvae under good feeding conditions, but may also imply an uncovered energetic cost when food concentrations are low. This may explain the finding that vertical distribution of *G. morhua* is tightly related to that of the main copepod species and that *G. morhua* recruitment is particularly sensitive to larval starvation and feeding conditions (Huwert *et al.*, 2011).

Unlike *A. rhomboidalis* larvae that had both higher growth potential at high prey concentrations and lower prey concentration requirements for survival than *A. mitchilli* larvae, the higher growth capacity of *G. morhua* larvae was not mirrored by a higher tolerance to poorer feeding conditions. In the field, the apparent advantage in foraging efficiency of *A. rhomboidalis* larvae compared with *A. mitchilli* larvae at all prey levels must be balanced by other factors, such as superior adaptations to ambient temperature conditions or reduced predation risk (McNamara & Houston, 1987; Fiksen & Jørgensen, 2011). The growth strategy of *C. harengus* larvae could be an adaptation to relatively poorer feeding conditions than those experienced by *G. morhua*; alternatively, it could also represent an adaptation to different predation pressures. Predation rates on planktonic fish larvae appear to be more affected by larval size than type of species (Miller *et al.*, 1988; Bailey & Houde, 1989), and *C. harengus* larvae hatch out at about twice the L_S of *G. morhua* larvae, but also lack pigmentation (Blaxter & Hunter, 1982). Consequently, *C. harengus* larvae will face a completely different trade-off between starvation risk and hunger initially, compared with *G. morhua* (Skajaa *et al.*, 2003; Kristiansen *et al.*, 2009) which will be reflected in their respective initial survival and growth patterns.

The relative abundance of prey categories were similar in the interaction tanks, but differed in the full-feeding treatments. *Gadus morhua* appeared to select for prey other than copepods, which in the SFF-C tanks remained at *c.* 60% higher relative abundance compared with the average for all treatments. On the contrary, in the SFF-H tanks, the relative abundance of copepods was *c.* 40% below the average for all treatments, suggesting that this prey type was selectively removed. It was unexpected that *C. harengus* appeared to remove a wider size range of prey than *G. morhua* during most of this study; however, any firm conclusions regarding comparative prey consumption in this study is difficult without a detailed analysis of stomach contents. This was not performed owing to practical limitations and high gut evacuation rates of *C. harengus*. In a comparative diet study on silver hake *Merluccius bilinearis* (Mitchill 1814) and *G. morhua* in the north-western Atlantic, *G. morhua* larvae exhibited a broader niche width than *M. bilinearis* larvae (Reiss *et al.*, 2005). In this case, larger *G. morhua* larvae also continued to feed on younger stages of copepods, while *M. bilinearis* larvae increasingly restricted their diet to larger prey items. Typically, *G. morhua* larvae have preference for prey sizes of a given relative size, most likely to optimize energy

gain and growth (Munk, 1997). In a laboratory study on *G. morhua* larvae fed different diets, larvae offered a wider and increasing size range of natural zooplankton eventually outperformed, in terms of growth, those offered smaller and more evenly sized rotifer prey (Koedijk *et al.*, 2010). As the nutritional composition of the prey in this case was noticeably different, it could not be concluded, however, whether the growth difference was due to the prey size variability *per se*. Still, the generally high prey concentrations and supply relative to overall prey consumption in this experiment probably precluded a more diverse prey composition from developing in the tanks.

The interaction between individuals in a constrained space such as an experimental tank may be artificial, but it also reveals important ecological strategies at early larval stages that are otherwise difficult to detect. An aspect of the observed differences in interactions between species is that direct comparisons between experiments can be difficult. For example, the survival of *C. harengus* appears to be similar to *G. morhua* in the interaction tanks, but higher when reared in isolation. This could indicate that the density-dependent interactions are stronger in the presence of *G. morhua*. A solution to avoid such interactions is to dilute the number of individuals to the concentrations observed at sea (Øiestad, 1990). Practical limitations in terms of space and number of larvae needed to obtain adequate samples and replicates remain a major obstacle. Consequently, direct intra-species comparisons of growth of survival estimates from replicated common-garden laboratory and mesocosm experiments will continue to be an important approach, keeping in mind that the results may be sensitive to inter-species and cohort interactions.

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